# Imagery and Spatial Cognition

Edited by
Tomaso Vecchi
Gabriella Bottini



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Imagery and Spatial Cognition

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**Volume 66**

Imagery and Spatial Cognition: Methods, models and cognitive assessment
Edited by Tomaso Vecchi and Gabriella Bottini

# Imagery and Spatial Cognition

## Methods, models and cognitive assessment

*Edited by*

Tomaso Vecchi

Gabriella Bottini

Università di Pavia

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# Table of contents

List of contributors ix
Introduction xiii

**Section I. Methodology of imagery and visuo-spatial functions**

CHAPTER 1.1
Early methods for assessing imagery and nonverbal abilities 3
*John T. E. Richardson*

CHAPTER 1.2
The assessment of imagery and visuo-spatial working memory functions in children and adults 15
*Irene C. Mammarella, Francesca Pazzaglia, and Cesare Cornoldi*

CHAPTER 1.3
Do we only remember where we left our things when we expect to need them again? Expectancy manipulations and object-location memory 39
*Albert Postma and Roy P. C. Kessels*

CHAPTER 1.4
Variations on the image scanning paradigm: What do they contribute to our knowledge of mental imagery? 49
*Michel Denis and Grégoire Borst*

CHAPTER 1.5
The use of transcranial magnetic stimulation in spatial cognition 69
*Massimiliano Oliveri, Giacomo Koch, Sara Torriero, and Carlo Caltagirone*

**Section II. Models and components of imagery and visuo-spatial processes**

CHAPTER 2.1
Neural bases and cognitive mechanisms of human spatial memory 85
*Panagiota Panagiotaki, and Alain Berthoz*

CHAPTER 2.2
Working memory, imagery and visuo-spatial mechanisms 101
*Zaira Cattaneo, Maria Chiara Fastame, Tomaso Vecchi, and Cesare Cornoldi*

CHAPTER 2.3
The episodic buffer: Implications and connections with visuo-spatial research 139
*David G. Pearson*

CHAPTER 2.4
Visuo-spatial components of numerical representation 155
*Maria-Dolores de Hevia, Giuseppe Vallar, and Luisa Girelli*

CHAPTER 2.5
Motor components and complexity effects in visuo-spatial processes 173
*Robert H. Logie and Tomaso Vecchi*

**Section III. Aging and visuo-spatial abilities**

CHAPTER 3.1
Aging and visuo-spatial working memory 187
*Elena Cavallini and Tomaso Vecchi*

CHAPTER 3.2
Imagery and aging 203
*Paola Palladino and Rossana De Beni*

CHAPTER 3.3
Object-location memory in ageing and dementia 221
*Roy P. C. Kessels and Albert Postma*

CHAPTER 3.4
Visuospatial and constructional impairments in mental deterioration 239
*Dario Grossi, Massimiliano Conson, and Luigi Trojano*

CHAPTER 3.5
Using visual imagery as a mnemonic for verbal associative learning:
Developmental and individual differences 259
*Christopher Hertzog and John Dunlosky*

**Section IV. Neuropsychological aspects of space representation**

CHAPTER 4.1
Spatial navigation: Cognitive and neuropsychological aspects 283
*Cecilia Guariglia and Luigi Pizzamiglio*

CHAPTER 4.2
Visuomotor control of spatially directed action 297
*A. David Milner and Monika Harvey*

CHAPTER 4.3
Visual peripersonal space 323
*Andrea Serino, Alessandro Farnè, and Elisabetta Làdavas*

CHAPTER 4.4
Visual perceptual processing in unilateral spatial neglect: The case of visual illusions 337
*Giuseppe Vallar and Roberta Daini*

CHAPTER 4.5
The impairment of the body image in the unilateral neglect syndrome 363
*Gabriella Bottini, Martina Gandola, Lorenzo Pia, and Anna Berti*

CHAPTER 4.6
Simulating object-centred neglect with head-centred coding of space based on non-linear gaze-dependent units 381
*Massimo Silvetti, Fabrizio Doricchi, and Eliano Pessa*

CHAPTER 4.7
Omission vs. shift of details in spatial representations 395
*Alessio Toraldo and Gabriella Bottini*

Index 417

# List of contributors

Alain Berthoz
LPPA-College de France-CNRS,
11 Marcelin Berthelot,
75005, Paris, France
E-mail: alain.berthoz@college-de-france.fr

Annamaria Berti
Dipartimento di Psicologia,
Università di Torino, via Po 14,
10123 Torino, Italy
E-mail: berti@psych.unito.it

Grégoire Borst
Groupe Cognition Humaine,
LIMSI-CNRS, BP 133, 91403
Orsay Cedex, France

Gabriella Bottini
Dipartimento di Psicologia,
Università di Pavia, P.za Botta 6,
27100 Pavia, Italy;
and Laboratorio di Neuropsicologia
Cognitiva, Ospedale Niguarda,
Milano, Italy
E-mail: gabriella.bottini@unipv.it

Carlo Caltagirone
Fondazione "Santa Lucia" IRCCS,
00179 Roma, Italy;
and Clinica Neurologica,
Università di Roma "Tor Vergata",
Italy

Zaira Cattaneo
Dipartimento di Psicologia,
Università di Pavia, P.za Botta 6,
27100 Pavia, Italy
E-mail: zaira.cattaneo@unipv.it

Elena Cavallini
Dipartimento di Psicologia,
Università di Pavia, P.za Botta 6,
27100 Pavia, Italy
E-mail: ecava@unipv.it

Massimiliano Conson
Department of Psychology,
Second University of Naples,
via Vivaldi 43, 81100 Caserta, Italy

Cesare Cornoldi
Dipartimento di Psicologia Generale,
Università di Padova, via Venezia 8,
35131 Padova, Italy
E-mail: cesare.cornoldi@unipd.it

Roberta Daini
Dipartimento di Psicologia,
Università di Milano-Bicocca,
20126 Milano and IRCCS Instituto
Auxologico Italiano, Milano, Italy
E-mail: roberta.daini@unimib.it

Rossana De Beni
Dipartimento di Psicologia Generale,
Università di Padova, via Venezia 8,
35131 Padova, Italy
E-mail: rossana.debeni@unipd.it

Maria-Dolores de Hevia
Dipartimento di Psicologia,
Università di Milano-Bicocca,
20126 Milano, Italy;
and Department of Psychology,
Harvard University, USA
Email: lola.dehevia@unimib.it

Michel Denis
Groupe Cognition Humaine,
LIMSI-CNRS, BP 133, 91403
Orsay Cedex, France
E-mail: denis@limsi.fr

Fabrizio Doricchi
Department of Psychology,
Università di Roma "La Sapienza",
via dei Marsi 78, Roma, Italy;
and Neuropsychology Laboratory,
Fondazione Santa Lucia,
IRCCS Roma, Italy
E-mail: fabrizio.doricchi@uniroma1.it

John Dunlosky
P.O. Box 5190,
Psychology Department,
Kent State University, Kent,
OH 44242, Kent State University, USA
E-mail: jdunlosk@kent.edu

Alessandro Farnè
Inserm U 534, Espace et action,
16 Av. Du Doyenne Lepine,
69500 Bron, France
and CsrNC, Centro studi e ricerche
Neuroscienze Cognitive,
Cesena, Italy
E-mail: farne@lyon.inserm.fr

Maria Chiara Fastame
Dipartimento di Psicologia,
Università di Pavia, P.za Botta 6,
27100 Pavia, Italy
E-mail: fastame@unipv.it

Martina Gandola
Dipartimento di Psicologia,
Università di Pavia, P.za Botta 6,
27100 Pavia, Italy;
and Laboratorio di Neuropsicologia
Cognitiva, Ospedale Niguarda,
Milano, Italy
E-mail: martina.gandola@unipv.it

Luisa Girelli
Dipartimento di Psicologia,
Università di Milano-Bicocca,
20126 Milano, Italy
E-mail: luisa.girelli@unimib.it

Dario Grossi
Department of Psychology,
Second University of Naples,
via Vivaldi 43, 81100 Caserta, Italy

Cecilia Guariglia
Department of Psychology,
Università di Roma "La Sapienza",
via dei Marsi 78, Roma, Italy;
and Neuropsychology Laboratory,
Fondazione Santa Lucia,
IRCCS Roma, Italy
E-mail: cecilia.guariglia@uniroma1.it

Monika Harvey
Department of Psychology,
University of Glasgow, G12 8QB, UK
E-mail: m.harvey@psy.gla.ac.uk

Christopher Hertzog
School of Psychology,
654 Cherry Street, Room 235,
Georgia Institute of Technology,
Atlanta, GA 30332-0170, USA
E-mail: christopher.hertzog@psych.gatech.edu

Roy P. C. Kessels
Psychological Laboratory,
Helmholtz Instituut, Utrecht University,
Heidelberglaan 2, 3584 CS Utrecht,
The Netherlands;
and Department of Neurology,
University Medical Centre Utrecht,
The Netherlands
E-mail: r.p.c.kessels@fss.uu.nl

Giacomo Koch
Fondazione "Santa Lucia" IRCCS,
00179 Roma, Italy
E-mail: giakoch@libero.it

Elisabetta Làdavas
Dipartimento di Psicologia,
Università degli Studi di Bologna,
V.le Berti Pichat 5,
40127 Bologna, Italy;
and CsrNC, Centro studi e ricerche
Neuroscienze Cognitive,
Cesena, Italy
E-mail: elisabetta.ladavas@unibo.it

Robert H. Logie
Human Cognitive Neuroscience,
PPLS, University of Edinburgh, UK
E-mail: rlogie@staffmail.ed.ac.uk

Irene C. Mammarella
Dipartimento di Psicologia Generale,
Università di Padova, via Venezia 8,
35131 Padova, Italy
E-mail: irene.mammarella@unipd.it

A. David Milner
Department of Psychology
and Wolfson Research Institute,
University of Durham, UK
E-mail: a.d.milner@durham.ac.uk

Massimiliano Oliveri
Dipartimento di Psicologia,
Università di Palermo, Italy;
and Laboratorio di Neurologia Clinica
e comportamentale, Fondazione
"Santa Lucia" IRCCS, via Ardeatina 306,
00179 Roma, Italy
E-mail: maxoliveri@tiscali.it

Paola Palladino
Dipartimento di Psicologia,
Università di Pavia, P.za Botta 6,
27100 Pavia, Italy
E-mail: paola.palladino@unipv.it

Panagiota Panagiotaki
LPPA-College de France-CNRS,
11 Marcelin Berthelot,
75005, Paris, France
E-mail: panagiota.panagiotaki@college-de-france.fr

Francesca Pazzaglia
Dipartimento di Psicologia Generale,
Università di Padova, via Venezia 8,
35131 Padova, Italy
E-mail: francesca.pazzaglia@unipd.it

David G. Pearson
School of Psychology,
William Guild Building,
University of Aberdeen, Aberdeen,
Scotland, UK
E-mail: d.g.pearson@abdn.ac.uk

Eliano Pessa
Dipartimento di Psicologia,
Università di Pavia, P.za Botta 6,
27100 Pavia, Italy
E-mail: eliano.pessa@unipv.it

Lorenzo Pia
Dipartimento di Psicologia,
Università di Torino,
via Po 14, 10123 Torino, Italy

Luigi Pizzamiglio
Department of Psychology,
Università di Roma "La Sapienza",
via dei Marsi 78, Roma, Italy;
and Neuropsychology Laboratory,
Fondazione Santa Lucia, IRCCS
Roma, Italy
E-mail: luigi.pizzamiglio@uniroma1.it

Albert Postma
Psychological Laboratory,
Helmholtz Instituut, Utrecht University,
Heidelberglaan 2, 3584 CS Utrecht,
The Netherlands
E-mail: a.postma@fss.uu.nl

John T. E. Richardson
Institute of Educational Technology,
The Open University, Walton Hall,
Milton Keynes MK7 6AA, UK
E-mail: J.T.E.Richardson@open.ac.uk

Andrea Serino
Dipartimento di Psicologia,
Università degli Studi di Bologna,
V.le Berti Pichat 5,
40127 Bologna, Italy;
and CsrNC, Centro studi e ricerche
Neuroscienze Cognitive, Cesena, Italy

Massimo Silvetti
Department of Psychology,
Università di Roma "La Sapienza",
via dei Marsi 78, Roma, Italy;
and Neuropsychology Laboratory,
Fondazione Santa Lucia, IRCCS
Roma, Italy

Alessio Toraldo
Dipartimento di Psicologia,
Università di Pavia, P.za Botta 6,
27100 Pavia, Italy;
and Laboratorio di Neuropsicologia
Cognitiva, Ospedale Niguarda,
Milano, Italy
E-mail: alessio.toraldo@unipv.it

Sara Torriero
Fondazione "Santa Lucia" IRCCS,
00179 Roma, Italy

Luigi Trojano
Department of Psychology,
Second University of Naples,
via Vivaldi 43,
81100 Caserta, Italy;
and Maugeri Foundation, IRCCS,
Telese Terme, Italy
E-mail: luigi.trojano@unina2.it

Giuseppe Vallar
Dipartimento di Psicologia,
Università di Milano-Bicocca,
20126 Milano, IRCCS Instituto
Auxologico Italiano, Milano, Italy
E-mail: giuseppe.vallar@unimib.it

Tomaso Vecchi
Dipartimento di Psicologia,
Università di Pavia, P.za Botta 6,
27100 Pavia, Italy
E-mail: vecchi@unipv.it

# Introduction

The interest of cognitive neuroscience and of neuropsychology on imagery and spatial cognition is remarkably increased in the last decades. Different areas of research contribute to the clarification of the multiple cognitive processes subserving spatial perception and exploration, and to the definition of the neurophysiological mechanisms underpinning these cognitive functions. Observation of normal subjects and patients' behaviour allows to better clarify these different aspects implicated in spatial processing also considering the important contribution of neuroimaging. Theoretical issues involved in space processing include different levels such as: perception, exploration and mental representation.

An adequate use of spatial competencies needs the balanced interaction of perception, working memory and action. Moving through the world, in fact, implies the ability to integrate different signals (visual, acoustic, somatosensory, vestibular). These elementary stimuli, continuously presented to the brain, have to be integrated in order to build up a complex space representation which takes into account the relationship between our body movements in the environment.

The aim of this book is to provide the reader (post-graduate students as well as experts) with a complete overview of this field of research. It illustrates the way how brain, behaviour and cognition interact in normal and pathological subjects in perceiving, representing and exploring space.

Each chapter provides and updated review of the relevant literature as well as illustrates empirical data some of them collected by the authors themselves, addressing practical and/or theoretical issues in this domain.

The first section is dedicated to the methodology of both imagery and visuo-spatial functions. Experimental methods and instruments to assess imagery and spatial abilities are illustrated for both adults and children. Particular aspects of object-location memory are also explored. The interaction between experimental and neurophysiological components have also been investigated with special attention to transcranial magnetic stimulation

The second part of the book is centred on the theoretical aspects of mental imagery from the cognitive and the neural point of view. Particular attention is devoted to different models of working memory subserving visuo-spatial mechanisms. The spatial representation of numbers is also extensively described.

Age-related differences in visuo-spatial abilities represent an important issue of debate in the literature, and the third section is completely devoted to this topic pro-

viding a review addressing differences both in normal subjects and in patients suffering from cognitive deterioration.

The last part of the book focuses on the cognitive/neuropsychological processing involved in the representation of personal, peripersonal and extrapersonal space. Further, theoretical issues concerning the body representation are treated from both semantic (body-parts-knowledge) and more spatial aspects (body-segments-relationship). Evidence of different cognitive processes and neurophysiological mechanisms is provided from experiments on normal and brain damaged humans. Part of this section illustrates the role of neuroimaging techniques in exploring the neurophysiological correlates of different spatial components, involving bodily, peripersonal (allocentric), and extrapersonal (retinotopic) coordinates. Data from functional and morphological studies in normal subjects and in brain damaged patients are largely discussed.

During the preparation of this book, we benefited from helpful discussion and suggestions by friends and colleagues in Pavia and Milan, and we would like to take this occasion to thank all the people working in our laboratories who make us possible enjoying doing research. During the years, we have been financially supported by Fondazione Cariplo, Bracco spa, University of Pavia and the Italian Ministry for University and Research.

SECTION I

# Methodology of imagery and visuo-spatial functions

CHAPTER 1.1

# Early methods for assessing imagery and nonverbal abilities

John T. E. Richardson

## Introduction

Imagery is a personal or phenomenal experience, and it is "private" or "subjective" in the sense that we cannot directly observe other people's images. Moreover, there is no nonverbal behaviour that is characteristic of having any particular image: for example, there is no natural behaviour that is characteristic of having an image of Salisbury Cathedral (Quinton 1973: 328). Hence, we cannot come to know about other people's images on the basis of their observable nonverbal behaviour. Instead, we have to depend upon their verbal behaviour: upon what they say, rather than what they do. Accordingly, in the first part of this chapter, I shall describe early attempts to collect systematic verbal accounts of people's experience of imagery.

Nevertheless, for contemporary cognitive psychologists, imagery is not simply an interesting kind of phenomenal experience. It also provides a form of mental representation in which information about the appearance of physical objects, events and scenes can be depicted and manipulated. As a result, it is able to make a distinctive contribution to performing everyday tasks, especially where the use of linguistic representations is impossible or unhelpful. In the second part of this chapter, I shall describe early attempts to construct nonverbal tests of ability. Initially, these tests were intended as alternative methods of measuring intelligence in individuals who lacked the linguistic or cultural knowledge needed for more conventional verbal tests. In the final part of the chapter, I shall explain how these tests came to be regarded as measures of a distinctive kind of nonverbal or spatial ability.

## Imagery questionnaires

Galton (1880; see also 1883: 83–114) developed a questionnaire in which respondents were asked to describe the quality of the mental imagery that was evoked when they tried to visualise familiar objects or scenes (for instance, the appearance of their break-

fast table that morning). Most of the questions were concerned with visual imagery, although one question asked the respondents to describe their imagery in other sensory modalities, and another referred to imagery for music. Galton began by collecting accounts from his friends in the scientific community as well as a wider cross-section of people whom he met "in general society". He found that there was great diversity in the experience of imagery among the general population.

He then obtained responses from a larger sample of 100 of his male acquaintances, of whom a majority were "distinguished in science or in other fields of intellectual work" (Galton 1883: 304). He found that he could order their accounts in terms of the vividness of their experienced imagery from "brilliant, distinct, never blotchy" to "almost no association of memory with objective visual impressions" (310–312). Galton obtained a similar distribution of responses from 172 boys taking science classes at the Charterhouse School in London. He also concluded that "the power of visualising is higher in the female sex than in the male" (99), although his published results were based solely upon the responses of men and boys.

Galton's questions were open-ended, and his respondents were left to describe their mental experiences in their own words. Betts (1909) used Galton's questions as the basis for a quantitative instrument that he called a "Questionnaire upon Mental Imagery" (QMI). This consisted of 150 items covering seven sensory modalities (for instance, the sight of the sun sinking below the horizon, or the smell of fresh paint). In each case, respondents were asked to judge the vividness of the image that was evoked when they thought about the item on a scale from 1 for "Perfectly clear and as vivid as the actual experience" to 7 for "No image present at all, you only knowing that you are thinking of the object" (20–21).

Betts found that a group of psychology students tended to report relatively vivid images (with median scores around 2 or 3 on his 7-point scale), whereas a group of professional psychologists reported less vivid images (with median scores around 4 or 5). Nevertheless, within both of these groups there was considerable individual variation in each of the seven sensory modalities covered by the QMI. Finally, Betts found that there was essentially no relationship between the reported vividness of the students' mental imagery and their academic performance (31, 48).

Sheehan (1967) found that with group administration Betts's QMI took about 55 min to administer, which he considered to be prohibitively long for any serious research applications. He therefore developed a short form of the QMI that contained just five items from each of the sensory modalities and took about 10 min to administer. In subsequent research this version of the QMI has been shown to have good internal consistency and satisfactory test-retest reliability; the application of factor analysis tends to yield a primary factor that reflects the vividness of experienced imagery in general, sometimes with secondary factors contrasting particular sensory modalities (for a review, see A. Richardson 1994: 17–19, 42).

Marks (1973) argued that it was more appropriate to focus upon the sensory modality that was most likely to be evoked in specific tasks, and he therefore devised the Vividness of Visual Imagery Questionnaire (VVIQ). This contained 16 items to be

judged in terms of evoked visual imagery on a 5-point scale similar to that used with the QMI. The items themselves are concerned with four familiar objects or scenes, each of which is to be rated on four different aspects. The internal consistency of the VVIQ is good, its test-retest reliability is satisfactory, and the application of factor analysis yields a single underlying dimension that reflects the vividness of visual imagery (for reviews, see McKelvie 1995; A. Richardson, 1994: 27, 158).

A key issue in research using imagery questionnaires is whether the scores obtained on these instruments predict the participants' performance on tasks that are believed to involve the use of mental imagery. Sheehan and Neisser (1969) failed to find any reliable relationship between scores on the short version of the QMI and performance in tests of visual memory. Marks (1973) argued that this was because their memory task had involved abstract geometrical patterns with little inherent interest or meaning, and also because they had averaged their participants' responses to the QMI across all seven sensory modalities instead of focusing on visual imagery.

In three different memory experiments using coloured photographs of objects or scenes, Marks found that people who had been classified as "good visualisers" according to their scores on the VVIQ produced better performance than people who had been classified as "poor visualisers". However, this study was vulnerable to experimenter effects: that is, people who are classified in advance as good or poor visualisers may produce the results that the researcher wants, either because they have become aware of the purpose of the experiment or because they are (perhaps unconsciously) treated differently by the experimenter (see Rosenthal 1966).

Since the 1970s, the VVIQ has been used in a very large number of investigations, and McKelvie (1995) provided an integrative review of their findings with regard to its predictive validity. He found a clear relationship (a mean correlation of +0.377) between rated vividness of visual imagery according to the VVIQ and other measures based on self-reports of mental states. There was a somewhat weaker but still appreciable relationship (a mean correlation of +0.273) between scores on the VVIQ and performance in cognitive or perceptual tasks. Finally, there was only a relatively weak relationship (a mean correlation of +0.137) between scores on the VVIQ and performance in tests of learning and memory.

One final questionnaire that might be mentioned is Gordon's (1949) Test of Visual Imagery Control (TVIC). This was devised with the intention of classifying the respondents in terms of whether their imagery tended to be "controlled" or "autonomous". (Gordon's own interest was in the extent to which this affected how strongly the respondents held stereotypes about particular cultural groups.) It contained 11 questions relating to views of a car, both stationary and in motion, that were answered on a yes/no basis. Start and A. Richardson (1964) changed one of the items into two separate items and included an "unsure" response category. Their revised version of the TVIC is the one that was generally used in subsequent research.

The internal consistency of the instrument is good and its test-retest reliability is satisfactory. However, applications of factor analysis tend to yield four separate (though correlated) factors relating to the different kinds of images prompted by the

different items. Scores on the TVIC tend to be correlated with scores on both the VVIQ and the shortened version of the QMI. They have been found to show a positive relationship with measures of creative thinking, but they are not consistently related to performance on tests of memory and cognition function (McKelvie 1995; A. Richardson 1994: 29–32, 60, 80, 82, 90–94, 159–160). This confirms the same general picture that has been obtained with the QMI and the VVIQ.

## Performance tests of intelligence

Galton (1885) was also responsible for devising some of the earliest (chiefly psychophysical) tests of ability, and his proposals were developed by researchers in the United States under the theme of "mental testing". However, doubts were raised about whether their simple laboratory-based tasks measured a unitary construct of "intelligence" and whether they were appropriate for diagnosing mental retardation (Popplestone & McPherson 1994: 65–67). The "intelligence scale" devised by Binet and Simon (1905, 1908) was specifically intended for this purpose, and English translations of their tests were published in the United States by H. H. Goddard.

Nevertheless, many of these tests were verbal in nature or required verbal instructions. They were therefore problematic when administered to people from homes where English was not spoken or people with a hearing loss. Healy and Fernald (1911) proposed that in these contexts tests should be used that did not rely on verbal skills but could be administered through pantomime alone. Among the tests that they described were "formboards", in which participants were required to fit geometrical shapes into matching recesses in the surface of a board. The first formboard had been constructed by E. Seguin in France in attempting to develop the intellectual abilities of a mentally retarded child, but it was Norsworthy (1906) who first suggested that these tasks could be used for the purposes of educational assessment.

Healy and Fernald (1911) extended these tasks to make "picture formboards" or "picture puzzles", in which participants were guided both by the shapes of the figures and by the fragments of a drawn scene that they contained. For instance, one of these was a jigsaw based on a picture of a mare and her foal taken from a child's picture book, and most of the pieces followed the natural lines of the two animals. Tests of this kind, intended to rely purely on nonverbal skills, came to be described as "performance tests" (Popplestone & McPherson 1994: 76–77). Indeed, both Binet and Goddard had incorporated such tests into their intelligence scales to try to reduce the impact of verbal skills on performance (see Zenderland 1998: 241–243).

Another situation where the use of Binet's scale proved problematic was the screening of potential immigrants to the United States. Physicians at the immigration stations were charged with identifying people who had contagious diseases or who had diseases or deformities which would render them unable to earn a living. In 1907, "imbeciles" and the "feeble-minded" were explicitly mentioned as people who should be excluded on this basis. Initially, the physicians claimed to be able to identify such

people based on routine clinical examination, but they came under increasing criticism from politicians, fellow professionals, and the general public for failing to spot mentally defective people and prevent them from entering the country.

Accordingly, the physicians at the Ellis Island immigration station in New York Harbour began to assess existing performance tests (Gwyn 1914; Sprague 1914) and also to develop new ones of their own. The one person who was chiefly responsible for the latter activity was H. A. Knox. Between September 1913 and April 1914, he published a series of articles describing 12 new performance tests (see J. T. E. Richardson 2003). Many were formboards or picture puzzles based on existing tests, but there was also a "Visual Comparison Test" that involved matching simple drawings presented in groups of varying size and complexity, and a "Cube Imitation Test" where participants had to copy a tapped sequence of cubes (Figure 1).

In devising these tests, Knox's aim was to construct a scale for the diagnosis of mental deficiency that was explicitly modelled on Binet's. He published a number of accounts of this scale, although only one of these accounts was cited widely in the subsequent literature (Knox 1914). He also produced an illustrated account for the popular magazine *Scientific American* (Knox 1915). During 1915, he arranged for many of his tests to be produced commercially by C. H. Stoelting Co. of Chicago, already an established supplier of laboratory equipment and test materials. As a result, Knox's tests became widely used during World War I and throughout the period between the two World Wars.

Pintner and Paterson (1917) included many of the Ellis Island tests as well as previous instruments in a performance scale for use both with normal children and with mentally retarded adults. Many of their tests were in turn included in the Army Performance Scale (Yoakum & Yerkes 1920), intended for the assessment of military personnel. Others who adopted the Ellis Island tests for use in performance scales were Johnson and Schriefer (1922), Worthington (1926), Gaw (1923, 1925), Arthur (1925), Drever and Collins (1928), Babcock (1930, 1932) and Cornell and Coxe (1934).

After World War II, the initial generation of performance tests was largely replaced by new instruments and especially by the Wechsler scales. Kent (1950) commented at the time: "The sub-tests of the Pintner–Paterson series are either obsolete or obsolescent, and those that remain in use will probably be superseded within a generation" (p. 44). However, this gives a somewhat misleading impression. Boake (2002) argued that most, if not all, of the subtests in Wechsler's scales have their origins in procedures devised between the 1880s and World War I. Indeed, Wechsler (1939:78) himself explained that his aim had not been to produce brand new tests but to select the best combination from those that were already available.

In particular, in constructing his scales, Wechsler felt it important to maintain the distinction between verbal and performance tests. In his own experience as a psychological examiner in World War I, the use of verbally dominated tests led to an overdiagnosis of mental deficiency even in native English speakers (Wechsler 1935:256). Nowadays, it is generally taken for granted that any adequate measure of intelligence

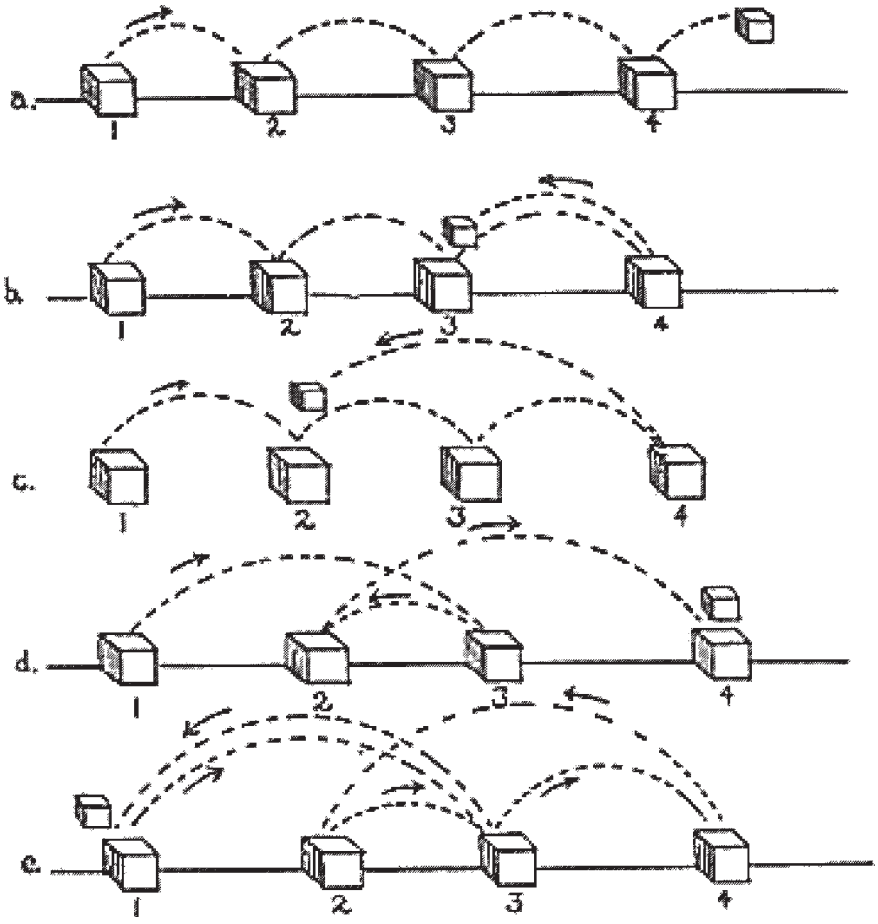



**Figure 1.** The Cube Imitation Test: "This consists of four large [cubes] and one small black cube. Beginning on the left, the examiner moves the small cube, as shown by the dotted lines, and the subject is asked to do what the examiner did" (Knox 1913: 564).

must include both verbal and performance subtests, but the origins of this idea lie in the work carried out by Knox and his colleagues at Ellis Island more than 90 years ago.

## Tests of spatial ability

Wechsler (1939: 138) assumed that performance tests provided an alternative means of assessing general intelligence, whereas others have argued that they measure distinctive kinds of nonverbal ability. However, the expression "performance test" is ambiguous between (1) "a test that is *administered* without the use of linguistic communication" (which implies that it must be scored through observation of the participants' *perfor-*

*mance*) and (2) "a test that is *executed* without the use of linguistic processing" (which implies that their performance will not be affected by variations in their linguistic abilities). It is nevertheless possible to dissociate the two.

An example of this is the cube imitation test, which was mentioned earlier (see Figure 1). Knox (1914:742) himself described it as "one of the most valuable single performance tests". Pintner (1915) asked participants who had performed especially well on this test how they had achieved this. Some said that they had mentally assigned verbal labels such as numbers or letters to the four individual cubes and had then remembered sequences of labels. Reymert and Hartman (1933) found this strategy both in children and in adults. From interviews with large numbers of participants, Stone (2002:8) concluded that the most common codes were: *1*, *2*, *3*, *4*; *a*, *b*, *c*, *d*; and *f*, *a*, *c*, *e* (the names of the spaces in the treble clef).

In Knox's version of the cube imitation test, the four cubes were actually painted in different colours. This was not made explicit in Knox's original descriptions, but it is evident from one of the photographs in his *Scientific American* article (Knox 1918). This provided yet another basis for assigning verbal labels; indeed, Rachofsky (1915) reported that most participants tested using this apparatus had remembered the colour names. Even when the cubes are all the same colour, verbal recoding seems to be a common strategy in the cube imitation test. This is supported by the finding that performance is impaired if the participants engage in the simultaneous articulation of irrelevant speech sounds (Vecchi & Richardson 2001).

For this reason, Corsi (1972) devised a cube imitation test that was less likely to be vulnerable to verbal recoding. His apparatus contained nine black cubes that were arranged in an irregular manner in two dimensions on a black rectangular board. The cubes were identical to the participants but were numbered on the side facing the examiner. Corsi used this apparatus to measure "spatial span" using a procedure similar to the digit-span task. Similar tests have been widely used in subsequent research (see Berch et al. 1998). Unlike Knox's cube imitation test, performance on the "Corsi blocks task" is not impaired if the participants engage in the concurrent articulation of irrelevant speech sounds (Vecchi & Richardson 2001).

Knox's cube imitation test is an example of a performance test that can be carried out using verbal processing. Conversely, some tests that are presented verbally can be carried out using nonverbal or spatial processing. An early example is contained in the study by Betts (1909) cited earlier. He asked a class of 28 psychology students to solve the following problems:

1. A squirrel is clinging to one side of a tree, and a man is standing opposite on the other side of the tree. The man walks around the tree, but the squirrel also moves around the tree, so as to keep just out of the man's sight. They continue this movement until each has gone entirely around the tree. Has the man gone round the squirrel,

   a. in the sense of having been in front, behind, and on both sides of him?
   b. In the sense of having been east, west, north and south of him?

2. A three-inch cube, painted red, is sawn into inch cubes.
   a. How many of the inch cubes have paint on three faces?
   b. How many on two faces?
   c. How many on one face?
   d. How many have no paint on them? (70–71)

The majority of participants managed to solve these problems, and nearly all reported using imagery to do so.

In general, then, the operational distinction between verbal tests and performance tests does not map very neatly onto the functional distinction between verbal and nonverbal processing. Although factor analyses of the scores obtained by large samples of participants on the Wechsler scales do typically identify separate "verbal" and "performance" factors, some have found a third factor (variously described as "attention/concentration" and "freedom from distractibility"), while in some clinical populations there is evidence for yet a fourth factor that has been termed "processing speed" (Spreen & Strauss 1998: 98–99). Attempts have been made to incorporate this multifactorial structure into recent versions of the Wechsler scales.

Instead of relying upon an a priori classification of existing tests, some researchers have followed Betts (1909) in trying to devise tasks that can plausibly only be carried out by manipulating some visual or spatial representation rather than more abstract linguistic information. These are usually described as tests of "spatial ability", though this is a rather vague, catch-all expression that covers a diverse collection of tasks. To refine the concept, Linn and Petersen (1985) proposed the following classification:

1. In "spatial perception" tests, the participants are required to determine spatial relationships with respect to the orientation of their own bodies in the face of distracting information. Examples of this include the Rod and Frame Test and the Water Level Test.
2. In "mental rotation" tests, the participants are required mentally to rotate two- or three-dimensional figures quickly and accurately. Examples of this include the Cards Rotation Test and the Spatial Relations subtest of the Primary Mental Abilities Test. Other writers have called these tests of "spatial orientation".
3. In "spatial visualisation" tests, the participants are required to solve problems by manipulating complex spatial information through several discrete stages. Examples include the Embedded Figures Test and the Minnesota Paper Form Board.

Linn and Petersen found this classification helpful in making sense of the literature on gender differences in spatial ability. They found that, in general, men tended to outperform women on spatial tests. However, the effects tended to be large and consistent on tests of mental rotation, large but less consistent on tests of spatial perception, and highly variable and often not statistically significant on tests of spatial visualisation. Voyer et al. (1995) obtained similar results, but they found that gender differences varied even between different tests of the same type. They concluded that Linn and

Petersen's classification of spatial tests was somewhat arbitrary and in need of further refinement.

Nevertheless, the scores obtained on different tests of spatial ability tend to correlate moderately well with one another, and they load on the same factor or factors when factor analysis is applied to the scores obtained on a battery of such tests. On the other hand, objective performance on tests of spatial ability does not show any consistent relationships with subjective ratings of the vividness of experienced imagery obtained by means of questionnaires of the sort reviewed in the first part of this chapter, and the two sorts of instrument typically load on different factors in the results of factor analyses (see McKelvie 1995; J. T. E. Richardson 1980: 130–131).

These results suggest that the functional value or effectiveness of imagery in tests of spatial ability is probably unrelated to the vividness of experienced imagery. This would explain the relatively poor predictive value of the self-reported vividness of mental imagery that was noted earlier. Nevertheless, the results obtained by Betts (1909) suggest that tests of spatial ability do indeed implicate the use of imagery. This needs to be tested not by measuring the quality of experienced imagery in general among the participants, but by measuring the quality of the imagery that they experience whilst they are carrying out a particular spatial task.

Barratt (1953) administered a battery of psychological tests to 180 schoolboys. After each test, they were asked to look back through the test materials and to rate the vividness, importance, and manipulability of the visual images that they had experienced in tackling the various problems. Barratt compared the performance of the boys whose combined imagery ratings fell in the highest 25% (whom he called "high imagers") with the performance of the boys whose combined imagery ratings fell in the lowest 25% (whom he called "low imagers").

From the results of a pilot study, Barratt had found that the 12 tests fell into two groups. One group was concerned with "spatial manipulation"; in Linn and Petersen's (1985) terms, it combined tests of mental rotation with tests of spatial visualisation. The other group of tests was concerned with (nonverbal) reasoning. Barratt found that the high imagers produced significantly higher scores than the low imagers on every test of spatial manipulation, but there was no sign of any difference between the two groups on any of the tests of reasoning. Similar results were found by other researchers (Hiscock 1978; Lorenz & Neisser 1985; A. Richardson 1977).

These results are of course correlational in nature, and it cannot therefore be inferred that differences in experienced imagery gave rise to differences in performance. For instance, it is possible that the subjects simply gave higher or lower ratings on the basis of how successful they had been on each test (in which case differences in performance would have given rise to differences in their reports of experienced imagery). However, as Barratt himself pointed out, in this case it is extremely odd that a similar correlation was not obtained in the case of his tests of reasoning. It is much simpler to explain these findings by supposing that experienced imagery is employed in tests of spatial manipulation but not in tests of reasoning.

## Conclusions

Questionnaires concerned with the characteristics of experienced imagery were widely used for over a century. However, their application has declined in recent years, mainly because subjective reports concerning the features of imagery in general are largely unrelated to performance in particular cognitive tasks. Instead, researchers have become more interested in obtaining "on-line" accounts of imagery in particular situations.

"Performance" tests, too, have been used for nearly a century, and for most of that time they have had an established role within intelligence testing. However, some performance tests can be carried out using verbal processing, and some verbal tests can be carried using nonverbal or spatial processing. Consequently, researchers are less interested in performance tests in general than in particular tests of spatial ability.

The latter category contains a very diverse collection of tasks, but as a starting point these can be classified as tests of spatial perception, tests of mental rotation, and tests of spatial visualisation. Imagery seems to play an important role in at least some of these. Performance is largely unrelated to the vividness of imagery in general but is related to the quality of imagery experienced while carrying out the task.

## References

Arthur, G. (1925). A new point performance scale. *Journal of Applied Psychology*, *9*, 390–416.

Babcock, H. (1930). An experiment in the measurement of mental deterioration. *Archives of Psychology*, *117*, 1–105.

Babcock, H. (1932). The short Army Performance Scale in clinical practice. *Journal of Applied Psychology*, *16*, 532–548.

Barratt, P. E. (1953). Imagery and thinking. *Australian Journal of Psychology*, *5*, 154–164.

Berch, D. B., R. Krikorian, & E. M. Huha (1998). The Corsi block-tapping task: Methodological and theoretical considerations. *Brain and Cognition*, *38*, 317–338.

Betts, G. H. (1909). *The distribution and functions of mental imagery* (Contributions to Education, No. 26). New York: Columbia University, Teachers College.

Boake, C. (2002). From the Binet–Simon to the Wechsler–Bellevue: Tracing the history of intelligence testing. *Journal of Clinical and Experimental Neuropsychology*, *24*, 383–405.

Cornell, E. L. & W. W. Coxe (1934). *A performance ability scale: Examination manual*. Yonkers, NY: World Book.

Corsi, P. M. (1972). *Human memory and the medial temporal region of the brain*. Unpublished doctoral dissertation, McGill University, Montreal.

Drever, J., & M. Cauns (1928). *Performance Tests of Inteligence*. Oxford, U.K.: Oliver and Boyd.

Galton, F. (1880). Statistics of mental imagery. *Mind*, *5*, 301–318.

Galton, F. (1883). *Inquiries into human faculty and its development*. London: Macmillan.

Galton, F. (1885). On the Anthropometric Laboratory at the late International Health Exhibition. *Journal of the Anthropological Institute of Great Britain and Ireland*, *14*, 205–221.

Gaw, F. (1923). The use of performance tests and mechanical tests in vocational guidance. *Journal of the National Institute of Industrial Psychology*, *1*, 333–337.

Gaw, F. (1925). A study of performance tests. *British Journal of Psychology*, *15*, 374–392.

Gordon, R. (1949). An investigation into some of the factors that favour the formation of stereotyped images. *British Journal of Psychology*, *39*, 156–167.

Gwyn, M. K. (1914). The Healy puzzle picture and defective aliens. *Medical Record*, *85*, 197–199.

Healy, W. & G. M. Fernald (1911), Tests for use in practical mental classification. *Psychological Monographs*, *13* (2, Whole No. 54), 1–53.

Hiscock, M. (1978). Imagery assessment through self-report: What do imagery questionnaires measure? *Journal of Consulting and Clinical Psychology*, *46*, 223–230.

Johnson, B. & L. Schriefer (1922). A comparison of mental age scores obtained by performance tests and the Stanford Revision of the Binet–Simon Scale. *Journal of Educational Psychology*, *13*, 408–418.

Kent, G. H. (1950). *Mental tests in clinics for children*. New York: Van Nostrand.

Knox, H. A. (1913). The differentiation between moronism and ignorance. *New York Medical Journal*, *98*, 564–566.

Knox, H. A. (1914). A scale, based on the work at Ellis Island, for estimating mental defect. *Journal of the American Medical Association*, *62*, 741–747.

Knox, H. A. (1915, January 9). Measuring human intelligence: A progressive series of standardized tests used by the Public Health Service to protect our racial stock. *Scientific American*, *112*, 52–53, 57–58.

Linn, M. C. & A. C. Petersen (1985). Emergence and characterization of sex differences in spatial ability: A meta-analysis. *Child Development*, *56*, 1479–1498.

Lorenz, C. & U. Neisser (1985). Factors of imagery and event recall. *Memory and Cognition*, *13*, 494–500.

Marks, D. F. (1973). Visual imagery differences in the recall of pictures. *British Journal of Psychology*, *64*, 17–24.

McKelvie, S. J. (1995). The VVIQ as a psychometric test of individual differences in visual imagery vividness: A critical quantitative review and plea for direction. *Journal of Mental Imagery*, *19* (3 & 4), 1–106.

Norsworthy, N. (1906). The psychology of mentally deficient children. *Archives of Psychology*, *1*(Whole No. 1), 1–111.

Pintner, R. (1915). The standardization of Knox's cube test. *Psychological Review*, *22*, 377–401.

Pintner, R. & D. G. Paterson (1917). *A scale of performance tests*. New York: Appleton.

Popplestone, J. A. & M. W. McPherson (1994). *An illustrated history of American psychology*. Madison, WI: Brown & Benchmark.

Quinton, A. M. (1973). *The nature of things*. London: Routledge & Kegan Paul.

Rachofsky, L. M. (1918). Speed of presentation and case of recall in the Knox Cube test. *Psychological Bulleten*, *15*, 61–64.

Reymert, M. L. & M. L. Hartman (1933). A qualitative and quantitative analysis of a mental test. *American Journal of Psychology*, *45*, 87–105.

Richardson, A. (1977). The meaning and measurement of memory imagery. *British Journal of Psychology*, *68*, 29–43.

Richardson, A. (1994). *Individual differences in imaging: Their measurement, origins, and consequences*. Amityville, NY: Baywood Publishing.

Richardson, J. T. E. (1980). *Mental imagery and human memory*. London: Macmillan.

Richardson, J. T. E. (2003). Howard Andrew Knox and the origins of performance testing on Ellis Island, 1912–1916. *History of Psychology*, *6*, 143–170.

Rosenthal, R. (1966). *Experimenter effects in behavioral research*. New York: Appleton-Century-Crofts.

Sheehan, P. W. (1967). A shortened form of the Betts' Questionnaire Upon Mental Imagery. *Journal of Clinical Psychology*, *23*, 247–252.

Sheehan, P. W. & U. Neisser (1969). Some variables affecting the vividness of imagery in recall. *British Journal of Psychology*, *60*, 71–80.

Sprague, E. K. (1914). Mental examination of immigrants. *The Survey*, *31*, 466–468.

Spreen, O. & E. Strauss (1998). *A compendium of neuropsychological tests: Administration, norms, and commentary* (2nd ed.). New York: Oxford University Press.

Start, K. B. & A. Richardson (1964). Imagery and mental practice. *British Journal of Educational Psychology*, *34*, 280–284.

Stone, M. H. (2002). *Knox's Cube Test – Revised: A manual for clinical and experimental* uses. Wood Dale, IL: Stoelting.

Vecchi, T. & J. T. E. Richardson (2001). Measures of visuospatial short-term memory: The Knox cube imitation test and the Corsi blocks test compared. *Brain and Cognition*, *46*, 291–294.

Voyer, D., S. Voyer, & M. P. Bryden (1995). Magnitude of sex differences in spatial abilities: A meta-analysis and consideration of critical variables. *Psychological Bulletin*, *17*, 250–270.

Wechsler, D. (1935). The concept of mental deficiency in theory and practice. *Psychiatric Quarterly*, *9*, 232–236.

Wechsler, D. (1939). *The measurement of adult intelligence*. Baltimore: Williams & Wilkins.

Worthington, M. R. (1926). A study of some commonly used performance tests. *Journal of Applied Psychology*, *10*, 216–227.

Yoakum, C. S. & R. M. Yerkes (1920). *Army mental tests*. New York: Holt.

Zenderland, L. (1998). *Measuring minds: Henry Herbert Goddard and the origins of American intelligence testing*. New York: Cambridge University Press.

CHAPTER 1.2

# The assessment of imagery and visuo-spatial working memory functions in children and adults

Irene C. Mammarella, Francesca Pazzaglia, and Cesare Cornoldi

## Introduction

Experimental evidence has shown the involvement of visuo-spatial working memory (VSWM) in a large number of every-day tasks, such as generation, maintenance and transformation of visual mental images (Kosslyn 1980), processing of visual and spatial coordinates (Hanley, Young & Pearson 1991), map learning and navigation (Denis, Daniel, Fontaine & Pazzaglia 2001; Garden, Cornoldi & Logie 2002), drawing and memory for the positioning of objects (Postma & De Haan 1996; Zimmer, Speiser, & Seidler 2003). In Baddeley's (1986) original model the system responsible for the storage and processing of non-verbal information was the visuo-spatial sketchpad, or, following the naming used in more recent models (Logie 1995; Cornoldi & Vecchi 2003), visuospatial working memory (VSWM). Although there is converging evidence supporting the multi-componential nature of the VSWM, so far there is no agreement on the number and identity of its components. For example, Logie (1995) distinguished between the *visual cache*, which temporarily stores visual information (i.e. memory for objects, shapes or colours) and the *inner scribe,* for the rehearsal of motor spatial sequences. Neuroanatomical data provide support for the distinction between a spatial and a visual component: Ungerleider and Mishkin (1982) proved that the primates' visual system can be differentiated in a "*where*" system, or dorsal stream, processing spatial information and a "*what*" system, or ventral stream, processing the features of perceived objects. Spatial-storage tasks activate cells in the dorso-lateral prefrontal cortex of monkeys, while object-storage tasks activate cells in a more ventral region of the prefrontal cortex (see Smith & Jonides 1999, for a review). Walsh, Ellison, Battelli and Cowey (1998), in a study using transcranial magnetic stimulation (TMS), reported that subjects' performance was disrupted by TMS applied over cortical area V5, when the task required attention to motion, but was improved when motion processing was irrelevant. Studies using the dual-task paradigm showed that reten-

tion of visual shapes or colours is disrupted by the presentation of irrelevant pictures (Logie & Marchetti 1991) or by dynamic visual noise (Quinn & McConnell 1996), whereas retention of location is interfered with by spatial tracking tasks (Baddeley & Lieberman 1980), spatial tapping tasks (Della Sala, Gray, Baddeley, Allamano & Wilson 1999) and eye movement (Postle, Idzikowski, Della Sala, Logie, & Baddeley 2006). This fractionation between the visual and spatial working memory components is also corroborated by neuropsychological evidence from patients showing a selective deficit in the performance of either visual or spatial working memory tasks (Carlesimo, Perri, Turriziani, Tomaiuolo, & Caltagirone 2001; Luzzatti, Vecchi, Agazzi, Cesa-Bianchi, & Vergani 1998; Farah, Hammond, Levine, & Calvanio 1988).

Moreover, regarding memory for object location, a further distinction was made; according to Postma and De Haan (1996), the object location memory can be subdivided into three separate processes: the first process requires encoding metric information and the coordinates of a particular object located in the environment, the second process, called *object-location binding,* requires linking the object's identity to the its position; finally, the last process integrates the first two mechanisms and combines metric information with object identity and location (Kessels, De Haan, Kappelle, & Postma 2002a; Kessels, Kappelle, De Haan & Postma 2002b). This distinction is in agreement with that made by Kosslyn (1987) between exact metric coordinates encoding and memory for the relative relation between objects (see also Landsdale 1998). Furthermore, studies regarding the specialized involvement of different brain structures shows that the right hemisphere is important in processing metric spatial information, whereas the left hemisphere participates in processing relative spatial relations (Kosslyn, Koenig, Barett, & Cave 1989).

Another fractionation in VSWM processing was suggested by Pickering, Gathercole, Hall and Lloyd (2001). The authors distinguish between a static format, as for example in a matrix in which locations are presented simultaneously, and a dynamic format, like in the Corsi test (Corsi 1972), where the reproduction of moving paths between blocks is required. In their studies, participants were presented with matrix and maze tasks in either a static or a dynamic format. The static version of both tasks involved the presentation of static images on matrices or mazes, whilst the dynamic version involved the presentation of squares presented one at a time in a matrix, or required remembering a route traced by the experimenter in a maze. A developmental fractionation in performance was found for static and dynamic conditions, suggesting that a critical distinction may concern not the visual and spatial properties of the tests, but the static and dynamic nature of the tasks, that tap different subcomponents of VSWM.

Recently, Lecerf and de Ribaupierre (2005) proposed the existence of a different way of processing visuospatial stimuli: *extrinsic encoding* important for anchoring objects with respect to an external frame and *intrinsic encoding* based on the relation among items within a complex pattern. The latter involves a *pattern encoding*, which leads to a global image of the stimulus and a *path encoding*, related to spatial-sequential links created between different positions. Both static vs. dynamic (Pickering

et al. 2001) and pattern encoding vs. path encoding (Lecerf & de Ribaupierre 2005) share similarities with the distinction made by Pazzaglia and Cornoldi (1999) between spatial-sequential and spatial-simultaneous processing: a spatial-sequential task requires recalling spatial positions presented in a sequential format, i.e. one at a time following the presentation order, whereas in a spatial-simultaneous task all the participants have to recall positions presented simultaneously. They distinguished these two spatial components from a visual one in which participants have to memorize objects with different shapes, colours and textures. These components are located in the horizontal continuum of Cornoldi and Vecchi's *continuity model* (2000, 2003) which depends on the different types of material used in a task and, therefore, involves the distinction between visual, spatial-sequential and spatial-simultaneous tasks.

The continuity model hypothesized another dimension, i.e. the vertical continuum, involved in all tasks but requiring different degrees of active control; in this framework a visual or a spatial-sequential task might be passive, if for example the task requires recalling the visual properties of a picture, or a pathway, but may be active, if the task requires subjects to actively manipulate the memory material in order to produce an output different from the original input. In other words, the *continuity model* proposes that each task could vary not only with respect to content-dependent processes, but also with respect to the position in the vertical continuum, i.e. the degree of control necessary to perform it.

The architecture of the VSWM is therefore still questionable and any of the proposed viewpoints may be considered as definitive; moreover, for each model different tests have been used leading to different results. For this reason, the specific choice of tasks for the assessment of VSWM may be critical and there is need for the identification and classification of VSWM tasks. In the next paragraphs we will review tests used to assess VSWM and imagery and we will then focus on our VSWM battery.

## Instruments and materials used to assess imagery and visuospatial memory

The specialized literature has generated a variety of measures to assess imagery and visuospatial memory. Tasks can be divided into at least two categories (Bunton & Fogarty 2003:1) subjective tasks, which are based on introspective reports, and include qualitative and quantitative evaluations for assessing individual differences in imagery and spatial abilities and 2) objective tasks, for collecting quantitative scores of the individual's performance in different imagery, memory or spatial tasks. An example of the first category is represented by the Vividness of Visual Images Questionnaire (VVIQ) (Marks 1973). Participants are required to judge, in two different modalities (imagining when eyes are open, and when eyes are closed), the vividness of scenes, situations or details. Objective or indirect tests are visuo-spatial tests; classic examples of this kind of tasks require the mental manipulation of visual shapes or the recall of spatial or visual patterns. For example in a simple paper-pencil adaptation of the *Mental Rotation Test* (Vanderberg & Kuse 1978) a series of three-dimensional configurations composed by

cubes are administered. The task consists of choosing which cube, presented rotated in depth, is the same as the given target item.

In a recent study, Burton and Fogarty (2003) examined the relationship between visual imagery and spatial abilities with a confirmatory factor analyses. They used 40 different measures: 5 tasks classified as self-report questionnaires of visual imagery, including the Comprehensive Ability Battery-Spatial (CAB-S; Hakstian & Cattel 1975), the Vanderberg and Kuse's (1978) Mental Rotation Test[1] and the Vividness of Imagery Questionnaire (VVIQ; Marks 1973); 26 markers of cognitive abilities comprising measures of fluid and crystallized intelligence, speeded rotation tests (Thurstone & Thurstone 1965), closure speed and flexibility of closure tasks (Lohman, Pellegrino, Alderton, & Regian 1987), and visual memory tests (Ekstron, French, Harman, & Dermen 1976). They also included 7 experimental imagery tasks, as for example the Dot Matrix task (adapted from Juhel 1991), in which participants were presented with four dots on a 5x5 matrix and had to recall their positions on an empty matrix. Two creative imagery tasks were developed on the basis of the stimuli used by Finke, Pinker and Farah, (1989) and involved the ability to mentally inspect or transform visual imagery; in particular, participants were instructed to begin with a starting pattern (for example a B), then to imagine transforming the pattern in specified ways (rotate the B 90 degrees to the left), adding another image (put a triangle below) and finally report what the resulting pattern looked like (a love heart). Burton and Fogarty's (2003) confirmatory factor analysis supported the notion that all the tasks can be classified along a continuum. The self-report imagery questionnaires are located on the left side of the continuum, while the experimental tasks studying spatial-imagery and visual memory can be located in the middle of the scale. In the right part of the continuum they located Finke et al.'s (1989) creative imagery tasks, close to objective tests of spatial abilities such as, for example, spatial intelligence tests, (the Primary Mental Abilities; Thurstone & Thurstone 1965 and the Raven's Advanced Progressive Matrices; Raven 1965), which are placed at the end of the scale. The effort of Benton and Fogarty (2003) is important because it offers a description of the relationships between visual imagery, visuospatial memory and spatial abilities, but does not offer a specific framework for VSWM.

As regards VSWM, we will describe in detail the tasks most used in the literature. Pickering (2001), reviewing the literature, stressed the importance of the Corsi blocks task (see Milner 1971; Corsi 1972; De Renzi & Nichelli, 1975) and the Visual Pattern Test (VPT) (Della Sala, Gray, Baddeley, & Wilson 1997) as pure measures of VSWM. The classical apparatus of the Corsi blocks task consists of nine cubes located irregularly on a wooden board (see Berch, Krikorian, & Huha 1998 for a review). The cubes are numbered on the examiner's side, and are tapped by the examiner in sequences of increasing length. Participants are usually required to recall the blocks either in forward or backward order. Differently from the digit span test, in the Corsi blocks task administered with the classical apparatus, there is no clear difference between performance on the forward and the backward version (e.g. Isaacs, & Vergha-Khadem 1989). The outcome of several studies (Vecchi & Richardson 2001; Vandierendonck, Kemps,

Fastame, & Szmalec 2004; Vandierendonck & Szmalec 2005) have suggested that, in disagreement with Pickering (2001), the backward version of the Corsi blocks task is not a pure measure of VSWM. Vecchi and Richardson (2001), Vandierendonck, and co-workers (2004) found a strong involvement of the central executive in the performance of the Corsi block test. However, Mammarella and Cornoldi (2005b) found that the performance on the backward version was based on the activation of spatial-simultaneous processes. In Table 1 a classification of the visuospatial tasks used in the literature and the hypothesized working memory components involved are reported.

The VPT (Della Sala et al. 1997) is composed of two-dimensional matrices in which half of the cells are filled. Participants have to reproduce the location of the filled cells in a completely empty matrix. According to Della Sala, and co-workers, (1999; see also Logie & Pearson 1997) the VPT involves visual working memory (the visual cache), whereas the Corsi blocks task examines spatial working memory (the inner scribe). However, these tasks, used (Logie & Pearson 1997; Della Sala et al. 1999; Pickering et al. 2001) to investigate the *visual cache* of Logie's model (1995), seem to involve spatial-simultaneous processes (Pazzaglia & Cornoldi 1999). In fact, the consideration of the VPT as a visual test may cause some perplexities given that this test is characterised by the presentation of a series of matrices in which some of the boxes are outlined in black and participants have to indicate on a blank matrix their location: thus there is a request to recall locations which may only partially assume visual form. These spatial-simultaneous processes can be distinguished from spatial-sequential processes: where the position of each block pointed at by the examiner in the Corsi blocks task needs to be sequentially encoded and retrieved in order to reproduce the correct sequence; in this test the positions are presented sequentially and the order is paramount. Also the dissociation observed by Della Sala and co-authors (1999), who described two brain-damaged adults impaired in the performance of a spatial task (the Corsi blocks task) but performing normally on the VPT, and a third patient who showed the opposite pattern, can be interpreted as examples of a dissociation between spatial-sequential and spatial-simultaneous tasks, rather than a double dissociation between visual and spatial tasks as suggested by Della Sala et al. (1999).

Another task examining visual and spatial memory (Logie 1995) derives from a classical neo-piagetian task (the Peanut task, see for example de Ribaupierre & Lecerf, in press) and was used by Hamilton, Coates and Heffernan (2003) with the name "Mr. Blobby" (see Figure 1). In the visual span format, participants have to remember the locations of spots presented simultaneously and in the recognition phase they must decide if the locations were the same or different to those presented initially. In the spatial span task the green spots appear in sequence. The participants task is to determine whether the sequence presented in the test phase is the same or different from that observed during the recognition phase. Hamilton et al. (2003) found that the visual span task reveals a relatively large developmental change in performance level, whereas the spatial span task shows a more modest developmental change in performance in participants aged between 5 and 25 years-old.

**Table 1.** Tests used to assess VSWM and the components they tap into according to the authors of the studies and according to the Continuity Model (Cornoldi & Vecchi 2003)

| Athors | Tests | VSWM components according to the authors | VSWM components according to the continuity model |
|---|---|---|---|
| Vecchi & Richardson (2001); Vandierendonck et al. (2004); Pickering et al. (2001) | Backward Corsi test | Central Executive<br>Dynamic | Spatial-simultaneous processes |
| Della Sala et al. (1997, 1999); Logie & Pearson (1997) Pickering et al. (2001) | VPT | Visual<br>Visual<br>Static | Passive spatial-simultaneous |
| Hamilton et al. (2003) | Mr. Blobby | Visual<br>Spatial | Passive spatial-simultaneous<br>Passive spatial-sequential |
| Pickering & Gathercole (2001) | Static mazes<br>Dynamic mazes | Static<br>Dynamic | Passive spatial-simultaneous<br>Passive spatial-sequential |
| Miyake et al. (2001) | Forward Corsi test<br>Dot Memory task<br>Letter Rotation<br>Dot Matrix task | Short-term memory tasks<br><br>Working-memory tasks | Passive spatial-sequential<br>Passive spatial-simultaneous<br>Active visual<br>Active spatial-sequential |
| Oberauer et al. (2000; 2003) | Dot span (similar to the Forward Corsi)<br>Pattern Span (similar to the VPT)<br>Dot Span (dual)<br>Pattern span (dual)<br>Spatial working memory task<br>Pattern transformation task | Storage tasks<br><br><br><br>Storage + processing tasks | Passive spatial-sequential<br><br>Passive spatial-simultaneous<br><br>Active spatial-sequential<br>Active spatial-simultaneous<br>Active spatial-simultaneous<br>Active visual |
| Chen et al. (2003) | Item-series shapes<br>Item-series locations | Visual<br>Spatial | Passive Visual<br>Passive spatial-sequential |
| Zimmer et al. (2003) | Object locations | Visual | Passive spatial-simultaneous |
| Cornoldi and co-workers (2001, 2004, 2005) | VSWM Selective task | | Active spatial-sequential |

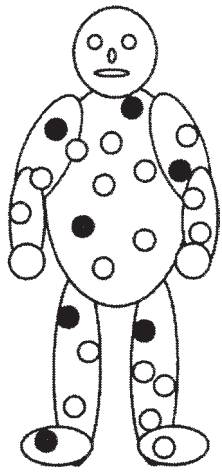


**Figure 1.** An example of stimulus derived by Hamilton, Coates and Hefferman (2003).

Pickering and Gathercole (2001) built a working memory test battery for children comprising 13 measures designed to tap the three working memory subcomponents (Baddeley 1986). To assess the phonological loop they used digits, words and non-words, and serial recall tasks. The non-words were introduced to have a short-term memory measure free from long-term memory involvement (Hulme, Maughan & Brown 1991). Other measures of the phonological loop were the non-words repetition task, in which participants hear and then attempt to repeat single, multisyllabic non-words and the words and non-words serial-recognition tasks, in which lists of items were auditorily presented twice, with the second sequence containing the same items as the first but, sometimes, with two items transposed. Children had to judge if the two lists were the same or not.

Three measures of the central executive component were included in the battery which simultaneously requested storing and processing information: the listening-recall task, the counting recall and the backward Digit Span tests. The listening-recall measure is a children's version of the task developed by Daneman and Carpenter (1980). In this task children have to judge if a series of sentences are true or false and recall the final word for each sentence. In the counting recall (Case, Kurland & Goldberg 1982), children count the number of coloured dots presented and have to then recall the tallies following a number sequence. The last central executive task is the backward digit span, in which participants recall a series of digits in reverse order (Wechsler 1974). Finally, the battery includes four tests to assess VSWM, i.e. the computerised versions of the VPT (Della Sala et al. 1997) and of the Corsi blocks task and two tests assessing memory for mazes; in the static and dynamic mazes, children view a series of two-dimensional mazes which increase in complexity across trials. In the static mazes, each figure includes a red pathway from the outside of the maze to the central figure, and children are asked to recall the route by drawing it on the cor-

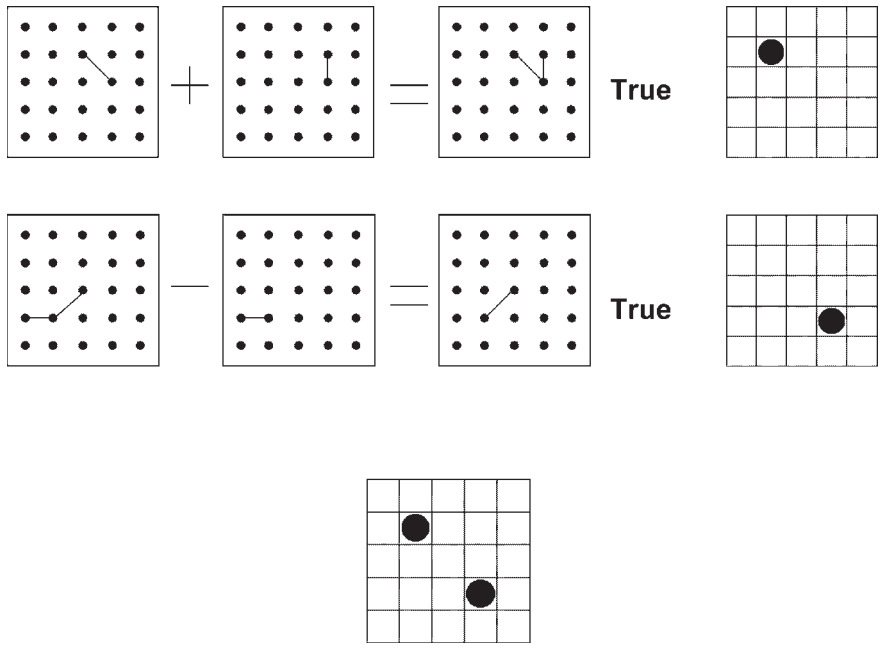



**Figure 2.** An example of the Dot Matrix task derived by Miyake et al. (2001).

responding maze; in the dynamic mazes the route is traced by the examiner's finger in full view of the child and the task consists of recalling the route in a response maze.

Other tasks used to assess VSWM were presented in a recent research by Miyake, Friedman, Rettinger, Shah and Hegarty (2001) who, examining the relationship among spatial abilities, visuospatial working memory and executive functioning, proposed a series of tests to assess simple storage-oriented tasks (short-term memory span tasks) and storage plus processing tasks (working memory span tasks). They used as short-term memory span task, a computerised version of the Corsi blocks task and the Dot Memory task, in which participants are presented with 5×5 matrices with a number of dots comprised between two and seven. After the grid presentation, participants have to recall on an answer sheet the dots' locations. The two working memory span tasks administered by Miyake et al. (2001) were the Letter Rotation and the Dot Matrix task; in the first task, participants have to decide if a capital letter is being presented in a normal or in a mirror rotation postition and remember its spatial orientation; in the Dot Matrix task each trial contains a set of to-be-verified matrix equations (for example, an addiction or a subtraction of lines into a grid of 3×3 dots) followed by a 5×5 matrix containing a dot in a particular cell (See Figure 2). The participants must verify the matrix equation and simultaneously remember the dot's location. Confirmatory factor analyses shows that both short-term and working memory span tasks involve executive functioning.

Also Oberauer and co-workers (Oberauer, Suβ, Shulze, Wilhelm, & Wittman 2000; Oberauer, Suβ, Wilhelm, & Wittman 2003) used tasks assessing storage and storage plus processing in VSWM.[2] The two storage tasks were similar to the Corsi task (the Dot task required a reproduction of locations sequentially presented) and to the VPT (the Pattern Span task required a reproduction of filled locations simultaneously presented). In one of the storage plus processing tasks (the Dot Span-dual) participants had to decide if some partially filled 3×3 matrices were symmetrical or not and then remember the presentation order of dots in different locations. The Pattern Span (dual) required remembering the positions of filled squares in a matrix and pressing different keys depending on whether an arrow appeared facing up or down in the figure. Another storage plus processing test (the Spatial working memory task) was a spatial equivalent of the reading span test (Daneman & Carpenter 1980). The task requires rotating a pattern either to the left or to the right and remembering a series of simple patterns (realized by partially filling the cells of a 3×3 matrix). Oberauer et al. (2003) also used the Pattern transformation task (Mayr & Kliegl 1993), requiring a comparison between the left and the right half of a screen presenting configurations of four or eight objects different in form (square or circle), size (small or big), border colour (black, white, grey) and colour of the entire figure (black, white, grey). Participants had to identify the feature in which only one of the objects on the right differed from its counterpart on the left. With a series of structural equation models Oberauer et al. (2003) showed that the distinction between verbal and spatial working memory was less important than the distinction between different operations in working memory, i.e. storage plus processing, coordination and supervision tasks.

Many other VSWM tasks have been proposed in the literature; for example, Chen, Hale and Myerson (2003) proposed a series of tasks to study retention intervals and information load in young and older people. Amongst the tasks used there was the Item Series-Shapes. During the study phase of this task participants are sequentially presented with two or three un-nameable shapes, whilst during the test phase they are presented with the same shapes plus a new one which participants are required to identify. In the Item Series-Locations, each trial involves the presentation of 4×5 matrices where 5 or 6 "X"s appear sequentially in different cells. In the response matrix the same set of "X"s is presented simultaneously, but one of the "X"s appears in a cell located near its original location. Participants are required to identify the "X" that is in the new location. Zimmer, Speiser and Seidler, (2003) devised a test to investigate memory for object location (the Relocation VSWM task) which consists of 9x9 matrices in which objects or artificial figures are located. Participants are required to remember the figures' locations (see Figure 3). Zimmer et al. (2003) found that the Corsi blocks and the relocation VSWM task tapped different memory mechanisms.

A task developed in our labs assessing active spatial-sequential working memory is the VSWM selective task. Different manipulations of this test have been used depending on the population involved in the studies, for example ADHD children (Cornoldi, Marzocchi, Belotti, Caroli, De Meo & Braga 2001), children with mental retardation (Lanfranchi, Cornoldi & Vianello 2004), visuospatial learning disabled

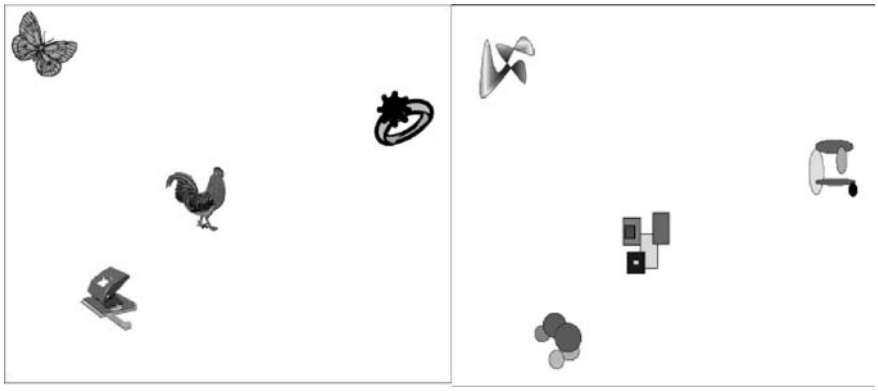


**Figure 3.** An example of the Relocation VSWM task devised by Zimmer Speiser and Seidler (2003).

children (Mammarella & Cornoldi 2005a) and older adults (Cornoldi, Bassani, Berto & Mammarella, in press). The basic procedure involves the presentation of a number of 4×4 matrices in which the experimenter sequentially points to three positions in each matrix. Participants are presented with a series of consecutive matrices. In the test phase, within an empty matrix, participants have to indicate the last position indicated by the experimenter for each matrix. The participant's secondary task is to tap on the table only in correspondence to a set of predetermined cells. Typically, results show that learning disabled children and older people manifest specific error patterns involving the previously presented information (intrusion errors) due to a difficulty in the control of irrelevant information in VSWM.

It is worth noting that some instruments reported here are based on a self-terminating procedure in that the score attributed to each participant is equivalent to the most complex series that he/she is able to correctly recall. For example in the Corsi blocks task, a participant is usually tested initially with sequences of three locations, if the performace is correct, s/he is then tested with four and if again successful with five locations. However if s/he is not able to remember five locations it is concluded that the participant's spatial span is 4. This procedure has some practical advantages: first, the test's administration time is relatively short; second, with particular groups of subjects, for example children or older-people, the participant is not annoyed or frustrated by the presentation of overly complex and ultimately useless items. Third, the experimenter can immediately attribute a score to the participant and interpret it.

## The Visuospatial Working Memory Test Battery (BEMViS)

As outlined above, many tasks have been devised to measure VSWM; however, most of them cannot be easily compared and classified. The BEMViS battery (Mammarella,

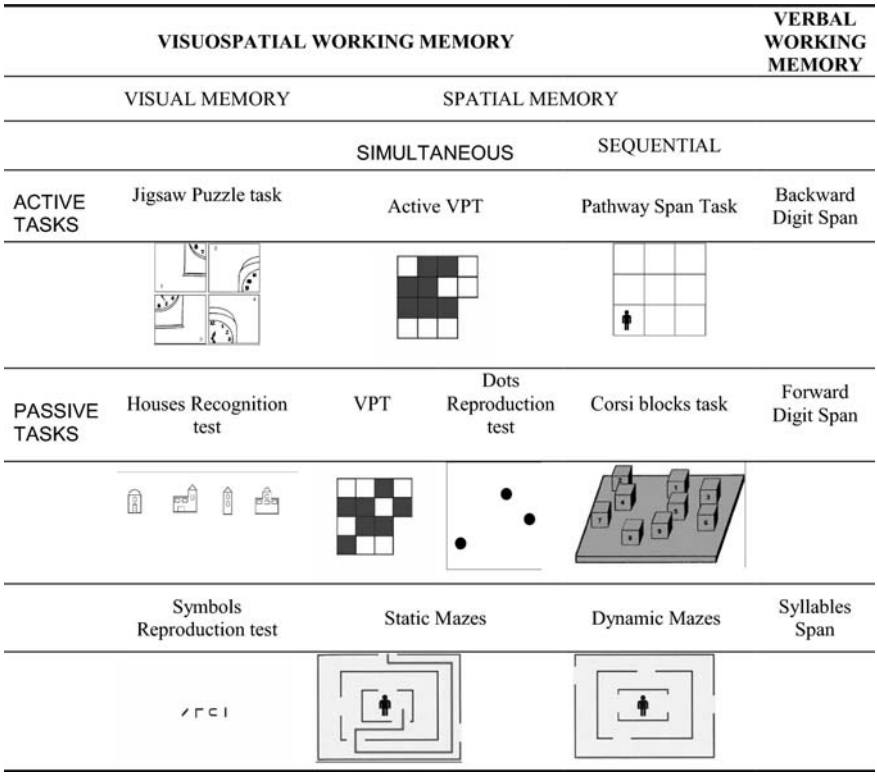



**Figure 4.** The structure of the test and of the WM components involved in BEMViS battery.

Cornoldi & Pazzaglia 2004), was devised in order to offer a more systematic tool for the examination of VSWM. The battery involves a further selection and refinement of tasks developed in our labs and already presented in preceding publications (see in particular Cornoldi & Vecchi 2003) or derived from the literature and adapted to our aims. A main advantage of the BEMViS battery is that all the tasks are clearly classified on the basis of a simple model and its administration, based on the self-terminating procedure, is easy and rapid. The battery is composed of 13 tests, with 3 control tests assessing verbal working memory (See Figure 4) and 10 VSWM tests. The measures are based on Cornoldi and Vecchi's working memory model (2003) distinguishing between active vs. passive processes (vertical continuum) and visual vs. spatial-simultaneous vs. spatial-sequential tasks (horizontal continuum). Apart from these 13 paper-pencil tests, the battery includes 6 additional computerized tasks for an in depth analysis of the more problematic areas identified in preceding tests.

Each task comprises trials of increasing levels of complexity (3 items per level) and, to achieve the next level, participants have to correctly solve at least two items out of three. Usually, tests start from the second level and each solved item receives a score equal to the level in which the item is included, so that items at the second level have a

**Table 2.** The table shows an example of scoring for the test battery. Each participant received scores equal to the sum of the three highest items solved in a particular test. In this example the participant obtained 5 + 4 + 4 = 13. The scoring was constant for all tests in the battery.

| LEVEL | Item A | Item B | Item C |
|---|---|---|---|
| 2 | RIGHT | RIGHT | / |
| 3 | RIGHT | WRONG | RIGHT |
| 4 | RIGHT (4) | RIGHT (4) | / |
| 5 | WRONG | RIGHT (5) | WRONG |

value of 2, items at the third level a value of 3, and so on. Final scores are the sum of the three most complex items solved. For example, if a participant performs successfully in two items at the third level, two at the fourth and one at the fifth, then his/her score will be 4 + 4 + 5 = 13 (See Table 2 for an example).

We will start by describing the 13 VSWM paper and pencil tests, distinguishing between visual, spatial-sequential, spatial-simultaneous and verbal tests. Successively we will describe the other 6 computerized tests.

*Visual tests*

*The House Recognition test (Passive task).* The test is classified as visual since it requires remembering well defined visual forms. More specifically, the stimuli consist of drawings of schematic houses (See Figure 4). Because the verbal label for each item is the same, verbal memory cannot offer relevant support. This task is the only one in the battery which involves a recognition procedure within a memory test for complex figures, thus implying a distinction between memory recall and recognition. In this task, at the second level, a set of two houses is shown for 2 seconds. Immediately after presentation, the participant has to recognise the target houses within a set of 4 stimuli. For each subsequent level, the number of to-be-recognised houses increases, as do the number of new houses amongst which the familiar ones are placed. More specifically the number of new houses introduced corresponds to the number of target houses used at that level. Level two will involve two to-be-recognised houses plus two new ones, level 4 will involve 4 to-be-recognised houses plus 4 new ones presented during the test phase. The level of complexity is defined as the number of houses to be recognized (from 2 to 6).

*The Signs Reproduction test (Passive task).* In this task, participants are presented with stimuli composed of a series of simple signs adapted from Cornoldi & Gruppo MT (1992). Each stimulus is displayed for 3 seconds before being removed from view and replaced by a blank response sheet. Participants are required to reproduce the signs with the same shape and direction. The level of complexity is defined by the number of to-be reproduced signs.

*The Jigsaw Puzzle task (Active task)* (adapted from Vecchi & Richardson 2000) is based on drawings derived by Snodgrass and Vanderwart (1980), and fragmented into

between two and ten numbered pieces forming a puzzle. Drawings represent common, inanimate objects with a high familiarity value and image agreement. To minimise the memory load, the pieces of each puzzle are randomly displayed in front of the participant and remain available for inspection during the entire testing period. Participants have to resolve the puzzle not by moving the pieces but by writing down (or pointing at) the corresponding number of each piece on a response sheet. The level of complexity is given by the number of pieces composing each puzzle.

*Spatial-sequential tasks*

*Dynamic Mazes (Passive task)* (adapted from Pickering, Gathercole, & Peaker 1998). Our version of the Dynamic Mazes used by Pickering and colleagues to assess dynamic memory comprises mazes of increasing difficulty in which the route to be recalled is traced by the examiner's finger in full view of the participant who must subsequently draw the route through a corresponding blank maze.

*The Corsi Blocks test (Passive task)* (adapted from Corsi 1972). In this task, as already mentioned, participants are required to reproduce a series of sequentially presented locations. In our battery we included only the forward version of the Corsi blocks task, due to the complex and not univocal implications of the backward version.

The *Pathway Span task (Active task).* Participants are required to mentally visualize a pathway followed by a little man moving on a blank matrix. The starting point is the same for each level and is positioned in the left square of the bottom row. If the task is administered to little children that do not understand left-right references, the experimenter can use points of reference in the room in which the task is being administered. At the end of a series of statements regarding directions indicated by the experimenter (i.e. forward, backward, left or right), participants have to indicate the man's final position in the matrix. The complexity of the task varies according to the size of the matrix (from $2\times2$ to $6\times6$) and the length of the pathway.

*Spatial-simultaneous tests*

*The Visual Pattern test (VPT) (Passive task)* (adapted from Della Sala et al. 1997). Participants are presented for 3 seconds with random square matrices created by filling half of the squares of a grid. The grids are of increasing size, for example in the second level, the grids include 6 squares with 3 filled cells, and in the last level 22 squares with 11 filled cells. In the presentation phase, participants memorise the filled squares; after 3 seconds, the initial stimulus is removed and participants are presented with an identical blank test matrix in which they have to indicate the previously filled squares.

*Static Mazes (Passive task)* (adapted from Pickering et al., 1998). In the Static Mazes task, participants are presented with mazes with a red line extended from the outside to the central figure. Each maze is displayed for three seconds before being removed from view and is replaced by an identical maze that does not show the route. Participants have to draw the route shown in the study item.

*The Dots Reproduction test (Passive task).* This task comprises a series of dots ordered in different locations in a blank sheet. The level of complexity ranges from a

minimum of one dot to a maximum of eight dots on a sheet. Each stimulus is displayed for three seconds before being removed from view and being replaced by a blank response sheet. The participant's task is to draw the dots in the exact location; if a dot is drawn with a diameter of more than 5 cm from the target stimulus, the trial is considered incorrect.

*The Visual Pattern Test, Active Version (VPTA) (Active task)* (adapted from Della Sala et al. 1997). The only difference between this test and the classic VPT is the active processing required for solving the task; participants are asked to reproduce the pattern in a completely blank matrix by filling the cells corresponding to the positions in a row below the row filled in the presentation matrix. For example, if in the presentation matrix the second cell in the first row is filled, the participant's task is to fill the cell in the second row (in the presentation matrices the last row is always completely blank).

*Verbal Working Memory tests*

*The Digit Span Test (forward and backward versions).* The tests involve the presentation of spoken sequences of digits for immediate serial recall. The sequences vary from 3 to 9 digits in the forward version and from 2 to 8 in the backward version (see Wechsler's procedure 1974). The forward version of this test is used to evaluate the passive processing of verbal working memory and the backward version the active one.

*The Syllables Span Test (Passive task).* In this test, participants are auditorily presented with sequences of syllables. The three trials of sequences vary in length: from two to nine syllables. The procedure is the same described for the Digit Span test. The participants' task is to listen and then to repeat the syllables in the same order. The Syllables Span Test is considered a measure of passive verbal working memory.

## Studies carried out with the use of the BEMViS battery

The first systematic use of the BEMViS battery concerned developmental groups. More specifically, two studies (Mammarella, Cornoldi & Pazzaglia 2004; Mammarella, Cornoldi & Pazzaglia, in preparation) were aimed at collecting norms for each test in a sample of children aged between 7 to 12-years old, examining the battery's internal reliability, and verifying the validity of the distinction among visual, spatial-sequential and spatial-simultaneous and between the active and passive components in VSWM. In a third study (Mammarella, Cornoldi, Pazzaglia, Toso, Grimoldi, & Vio, in press) single cases of children with visuo-spatial difficulties were analysed in order to individuate selective deficits in spatial-sequential and spatial-simultaneous components.

Results reported here are based on Mammarella et al.'s study (in preparation; see also Mammarella et al. 2004), but refers to only a part of the entire sample. 300 children (87 second-graders, 39 third-graders, 58 fourth-graders and 116 fifth-graders), were presented with all the 13 paper and pencil verbal and visuospatial working memory tests.

**Table 3.** Internal reliability on the VSWM tasks ($N$ = 300)

| | Houses | Signs | Puzzle | Dynamic | Corsi | Pathway | VPT | Static | Dots | VPTA |
|---|---|---|---|---|---|---|---|---|---|---|
| Cronbach α | .68[a] | .83° | .89 | .83 | .85 | .92 | .84 | .85 | .76[a] | .90 |

*Note*: [a] $N$ = 162 ° $N$ = 235.

In Table 3 the alpha-Cronbach values for the 10 VSWM tests are shown. Scores of the visuospatial tests were sufficiently high, ranging from α = .68 (Houses Recognition Test) to α = .92 (Pathway span task), reflecting a high degree of internal reliability within the VSWM test battery.

The structure of the VSWM was tested on the first data collected by Mammarella et al. (2004) using structural equation modelling (SEM, McDonald & Moon-Ho Ring Ho 2002). The main question asked was whether the visuospatial tests of our battery could be effectively used for testing different visuospatial components. The FIT indexes of different models were compared, paying particular attention to the comparison between a one-factor model with a unique latent variable named VSWM derived from the observed measures of the whole VSWM battery, and several two-factor models. Each of these distinguished between two of the VSWM components described in Cornoldi and Vecchi's *continuity model*. The two-factor models tested by the structural equations modelling examined the distinction between active and passive tasks (see Figure 5) and the existence of at least three separate components in the VSWM's hori-

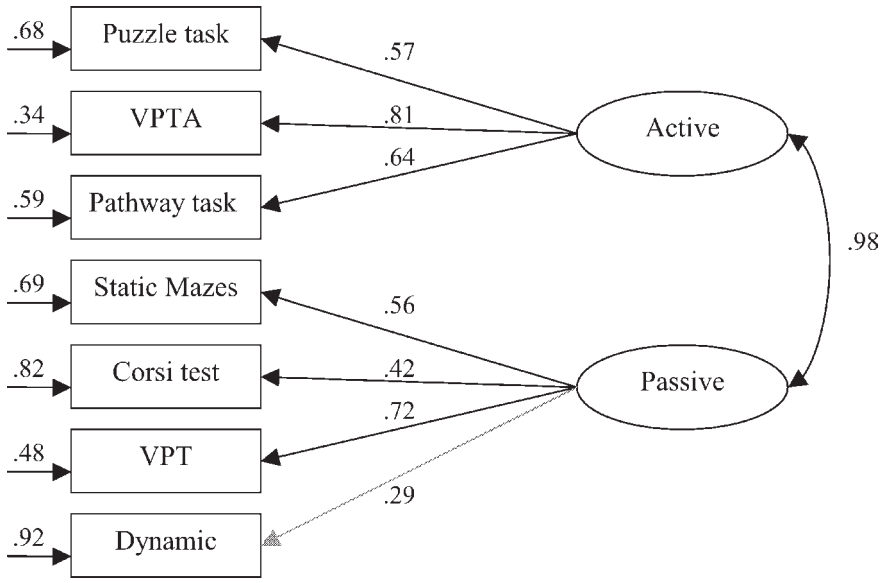



**Figure 5.** The active vs. passive model. Single-headed arrows represent standardized factor loadings. The numbers at the ends of the smaller arrows are errors terms. The double-headed arrows indicate correlations between latent variables.

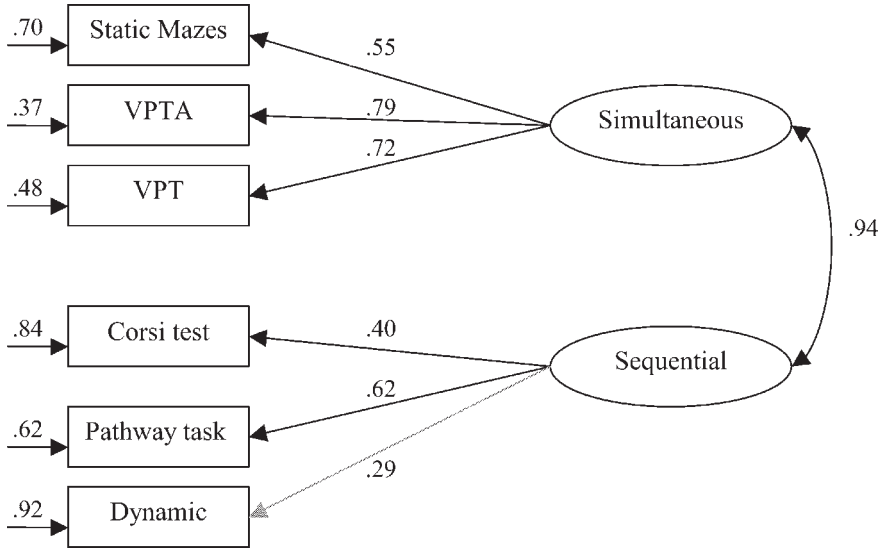



**Figure 6.** The simultaneous vs. sequential model.

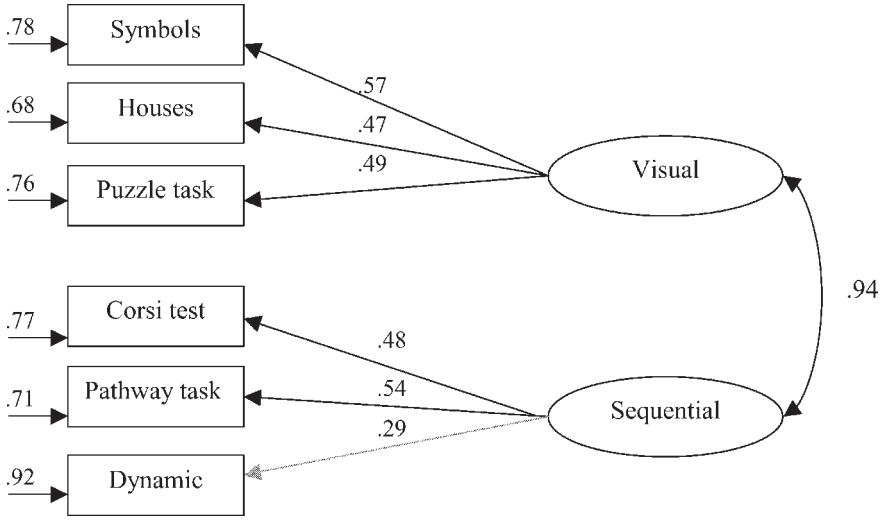



**Figure 7.** The visual vs. sequential model.

zontal dimension: simultaneous *vs.* sequential (Figure 6), visual *vs.* sequential (Figure 7), visual *vs.* simultaneous (Figure 8). Differently from the one-factor model, which had a significant $\chi^2$ value and no adequate fit indices, all the two-factor models had no significant $\chi^2$ values, indicating that the models' predictions did not deviate from the actual data patterns, and had adequate fit indices.[3]

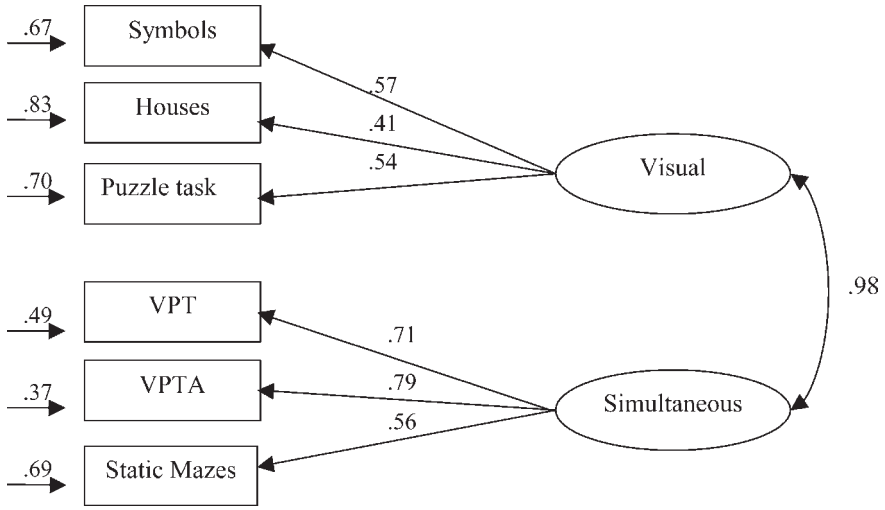



**Figure 8.** The visual vs. simultaneous model.

As already mentioned, spatial-simultaneous *vs.* spatial-sequential and visual *vs.* spatial-sequential distinctions mirror analogues distinctions, already present in the literature and, in particular, the distinction between a spatial component, involving memory for sequential pathways and movements, and a second component, defined either as visual (Logie 1995), or static (Pickering & Gathercole 2001), or spatial-simultaneous (Pazzaglia & Cornoldi 1999). Interestingly, this latter component, tapped by tasks which require the memorization of positions of items located in space, was, in our study, distinguishable from a pure visual component, measured by tasks which required memorization of drawings and differently oriented signs.

## Application of the battery to the analysis of single cases with visuospatial deficits

The BEMViS battery was administered to three non-verbal (or visuospatial) learning disabled children (for a description of these children see Rourke 1989) diagnosed on the basis of the descriptions offered by Cornoldi, Venneri, Marconato, Molin and Montinari (2003; see also Mammarella & Cornoldi (2005b).

According to Cornoldi et al. (2003), children exhibiting visuospatial learning disabilities (VSLD) typically show learning difficulties involving processing and learning of nonverbal material, a discrepancy between verbal and spatial intelligence (at least 10 IQ points) and failure in cognitive neuropsychological tests involving visuospatial abilities. A critical factor underlying VSLD children's difficulties seems to be related to deficits in visuospatial working memory (Cornoldi, Dalla Vecchia & Tressoldi 1995; Cornoldi, Rigoni, Tressoldi & Vio 1999; Mammarella & Cornoldi 2005b).

In the three cases reported by Mammarella et al. (in press), the assessment of the VSWM was based on the BEMViS battery; the results highlighted different patterns, with selective deficits in one or more of the VSWM components. A performance was considered poor if the child's score was below the mean normative score of more than 1.5 standard deviation. We identified two children with problems on spatial-simultaneous processes and one with a spatial-sequential impairment. In particular, L.P. performed 1.5 S.D. below the mean score on a series of spatial-simultaneous tasks (the two versions of the VPT, the Static Mazes and Dots Reproduction test), whereas the performance on spatial-sequential tasks (Pathway Span task, Dynamic Mazes and Corsi Blocks test) was relatively good. A similar pattern of results was observed in F.S., who obtained poor scores on three tasks assessing spatial-simultaneous memory (VPT active and classic version and Static Mazes) but did not obtain poor scores on spatial-sequential and visual tasks. On the contrary, B.L.'s performance revealed impairments on sequential tasks (Pathway span and Corsi tasks) but not on simultaneous ones.

## Tests for a more in depth assessment

A second, shorter battery is currently in preparation with the objective of creating instruments for a more in depth analysis of single cases with specific impairments detected by the first battery. This battery is also based on the distinction between the visual, spatial-sequential and spatial-simultaneous components, but only includes recognition tasks. In particular, we designed two computerised tests for each dimension: the Non-sense Shapes and the Little-fish recognition tasks, which require deciding if a series of non-sense figures (derived from Vanderplas & Garvin 1959) or the fish-shaped textures are identical or not to a previously presented series. In the Light-bulbs recognition task and in the Sequential-dots test (spatial-sequential tasks), participants are asked to recognise if the order in which the information is presented is the same in the recall phase as in the presentation phase. Finally, in the two spatial-simultaneous tasks, the Dot matrix recognition task and the Simultaneous-dots test, participants have to decide if a series of positions presented simultaneously are different to those presented in a previous phase.

In this shorter battery, scores are attributed in the same way as in the BEMViS test battery, but all the tests have the same structure, and in particular, participants are always asked to decide if a series of figures are the same or different from those previously presented. All the tests go from the second to the eighth level and each level contains 3 items. These tasks together with other tests already in use (as for example the backward Corsi blocks and the VSWM Selective-task, Cornoldi, et al. 2001) represent accurate tools for a more in depth analysis of VSWM deficits.

In conclusion, the VSWM battery together with other tests offers the possibility of an extensive assessment of the visuospatial components of working memory. The tests here presented are useful instruments for researchers and clinical psychologists because the experimenter can either administer the battery entirely or select

only certain tasks that tap a specific component. These tasks can also be employed for a diagnosis of VSWM problems in patients with brain damage or learning disabilities and, in particular, for visuospatial learning disabled children. In fact with the BEMViS battery and the additional tests it is possible to identify specific sub-types of deficits within the working memory components. For example, Cornoldi, Rigoni, Venneri and Vecchi (2000) found a double dissociation between passive storage and active processing in two VSLD children. Their results suggest that it is possible to identify selective deficits involving specific groups of tasks. Moreover, Mammarella, Cornoldi and Donadello (2003) showed that children with spina-bifida had an impaired visual memory when tested with the House Recognition test, but revealed normal scores on spatial-simultaneous (VPT) and spatial-sequential (Corsi task) tests. These results not only support a distinction between active and passive processing and between visual, spatial-simultaneous and spatial-sequential memory, but also suggest that the tests included in our battery could be useful to discriminate between specific visuospatial deficits.

## Conclusions

In conclusion, the VSWM system seems to be more complex than initially suggested. A review of the psychological instruments used for assessing VSWM and imagery showed that a unitary approach to the study of visual and spatial abilities does not exist in the literature. Although a series of instruments based on validated theoretical distinctions have been proposed revealing high discriminative power, results are not always in agreement and different approaches or theories lead to different interpretations. In our view a classification of VSWM tasks according to their active vs. passive processing request and with reference to the visual vs. spatial-simultaneous vs. spatial-sequential components could help to better understand the structure of the VSWM and to more accurately assess VSWM deficits.

## Notes

**1.** In the Burton and Fogarty (2003) study, the Mental Rotation Test, (Vanderberg & Kuse 1978) was considered as a self-report measure, in the same manner of the CAB-S Questionnaire (Hakstian & Cattel 1975), the QMI Questionnaire (Sheenan 1967), the TVIC (Richardson 1969) and the VVIQ (Marks 1973).

**2.** We reported only the tasks classified by Oberauer and co-workers (2000, 2003) as tapping visual and spatial working memory components and involving storage or storage and transformation processing.

**3.** Active vs. passive: $\chi^2(13) = 19.72$, $p = .11$, CFI = .99, RMSEA = .04, AIC = 49.72; simultaneous vs. sequential: $\chi^2(8) = 12.88$, $p = .12$, CFI = .99, RMSEA = .05, AIC = 38.88;

visual vs. sequential: $\chi^2(8) = 11.15$, $p = .19$, CFI = .99, RMSEA = .04, AIC = 37.15; visual vs. simultaneous: $\chi^2(8) = 12.31$, $p = .14$, CFI = .99, RMSEA = .04, AIC = 38.13.

## References


Baddeley, A. D., & Lieberman, K. (1980). Spatial working memory. In Nickerson, R. S. (Ed), *Attention and Performance VIII* (pp. 521–539). Hillsdale, NJ: Lawrence Erlbaum Associates.

Baddeley, A. D. (1986). *Working Memory*. Oxford: Oxford University Press.

Berch, D. B., Krikorian, R., & Huha, E. M. (1998). The Corsi block-tapping task: Methodological and theoretical considerations. *Brain and Cognition, 38,* 317–338.

Burton, L. J., & Fogarty, G. J. (2003). The factor structure of visual imagery and spatial abilities. *Intelligence, 31,* 289–318.

Carlesimo, G. A., Perri, R., Turriziani, P., Tomaiuolo, F., & Caltagirone, C. (2001). Remembering what but not where. Independence of spatial and visual working memory in the human brain. *Cortex, 37,* 519–537.

Case, R. D., Kurland, M., & Goldberg, J. (1982). Operational efficiency and the growth of short-term memory span. *Journal of Experimental Child Psychology, 33,* 386–404.

Chen, J., Hale, S., & Myerson, J. (2003). Effects of domain, retention interval, and information load on young and older adults' visuospatial working memory. *Aging Neuropsychology and Cognition, 10,* 122–133.

Cornoldi, C., Bassani, C., Berto, R., & Mammarella, N. (in press). The intrusion superiority effect in elderly visuospatial working memory. *Aging Cognition and Neuropsychology*.

Cornoldi, C., Dalla Vecchia, R., Tressoldi, P. E. (1995). Visuo-spatial working memory limitation in low visuo-spatial high verbal intelligence children. *Journal of child psychology and child psychiatry, 36,* 1053–64.

Cornoldi, C., & Gruppo M. T. (1992). PRCR-2: Prove di prerequisito per la diagnosi delle difficoltà di lettura e scrittura. Firenze: O.S.

Cornoldi, C., Marzocchi, G. M., Belotti, M., Caroli, M. G., De Meo, T., Braga, C. (2001). Working memory interference control deficits in children referred by teachers for ADHD symptoms. *Child Neuropsychology, 7,* 230–240.

Cornoldi, C., Rigoni, F., Tressoldi, P. E. & Vio, C. (1999). Imagery deficits in nonverbal learning disabilities. *Journal of Learning Disabilities, 32*, 48–57.

Cornoldi, C., Rigoni, F., Venneri, A. & Vecchi, T. (2000). Passive and active processes in visuo-spatial memory: Double dissociation in developmental learning disabilities. *Brain and Cognition, 43,* 17–20.

Cornoldi, C. & Vecchi, T. (2003). *Visuo-spatial working memory and individual differences.* Hove, UK: Psychology Press.

Cornoldi, C., & Vecchi, T. (2000). Mental imagery in blind people: The role of passive and active visuo-spatial processes. In M. Heller (Ed.), *Touch, representation, and blindness* (pp. 143–181). Oxford: Oxford University Press.

Cornoldi C., Venneri A., Marconato F., Molin A. & Montinari C. (2003), A rapid screening measure for teacher identification of visuo-spatial learning disabilities. *Journal of Learning Disabilities, 36*, 299–306.

Corsi, P. M. (1972). *Human Memory and the Medial Temporal Region of the Brain.* Unpublished doctoral dissertation, McGill University, Montreal.

Daneman, M., & Carpenter, P. A. (1980). Individual differences in working memory and reading. *Journal of Verbal Learning and Verbal Behavior, 19,* 450–466.

De Renzi, E., & Nichelli, P. (1975). Verbal and nonverbal short term memory impairment following hemispheric damage. *Cortex, 11,* 341–353.

De Ribaupierre, A., & Lecerf, T. (2006). Relationships between working memory and intelligence: Convergent evidence from a Neo-Piagetian and a Psychometric approach. *European Journal of Cognitive Psychology, 18*, 109–137.

Della Sala, S., Gray, C., Baddeley, A., Allamano, N., & Wilson, L. (1999). Pattern span: A tool for unwelding visuo-spatial memory. *Neuropsychologia, 37,* 1189–1199.

Della Sala, S., Gray, C., Baddeley, A. D. & Wilson, L. (1997). *Visual Pattern Test.* Bury St Edmunds: Thames Valley Test Company.

Denis, M., Daniel, M. P., Fontaine, S., & Pazzaglia, F. (2001). Language, spatial cognition, and navigation. In R. H. Logie & M. Denis (Eds.), *Imagery, Language and Visuo-Spatial Thinking* (pp. 137–160). New York, NY: Psychology Press

Ekstron, R. B., French, J. W., Harman, H. H., & Dermen, D. (1976). *Manual for kit of factor-referenced cognitive tests.* Princeton, NJ: Educational Testing Service.

Farah, M. J., Hammond, K. M., Levine, D. N., & Calvanio, R. (1988). Visual and spatial mental imagery: Dissociable systems of representation. *Cognitive Psychology, 20,* 439–462.

Finke, R. A., Pinker, S., & Farah, M. J. (1989). Reinterpreting visual patterns in mental imagery. *Cognitive Science, 13,* 51–78.

Garden, S., Cornoldi, C., & Logie, R. H. (2002). Visuo-spatial working memory in navigation. *Applied Cognitive Psychology, 16,* 35–50.

Hakstian, A. R., & Cattel, R. B. (1975). *Comprehensive Ability Battery.* Champaign, IL: Institute for Personality and Ability Testing.

Hamilton, C. H., Coates, R. O., & Hoffernan, T. (2003). What develops in visuo-spatial working memory development? *European Journal of Cognitive Psychology, 15,* 43–69.

Hanley, J. R., Young, A. W., & Pearson, N. A. (1991). Impairment of the visuo-spatial sketch pad. *Quarterly Journal of Experimental Psychology, 43A,* 101–125.

Hulme, C., Maughan, S., & Brown, G. D. A. (1991). Memory for familiar and unfamiliar words: Evidence for a long-term memory contribution to short-term memory span. *Journal of Memory and Language, 30,* 685–701.

Isaacs, E. B. & Vergha-Khadem, F. (1989). Differential course of development of spatial and verbal memory span: A normative study: *British Journal of Developmental Psychology, 7,* 377–380.

Juhel, J. (1991). Spatial abilities and individual differences in visual information processing. *Intelligence, 15,* 117–137.

Kessels, R. P. C., De Haan, E. H. F., Kappelle, L. J., & Postma, A. (2002a). Selective impairments in spatial memory after ischaemic stroke. *Journal of Clinical and Experimental Neuropsychology, 24,* 115–129.

Kessels, R. P. C., Kappelle, L. J., De Haan, E. H. F., & Postma, A. (2002b). Lateralization of spatial memory processes: Evidence on spatial span, maze learning, and memory for object locations. *Neuropsychologia, 40,* 1465–1473.

Kosslyn, S. M. (1980). *Image and Mind.* Cambridge, MA: Harvard University Press.

Kosslyn, S. M. (1987). Seeing and imagining in the cerebral hemisphere: A computational approach. *Psychological Review, 94*, 148–175.

Kosslyn, S. M., Koenig, O., Barett, A., & Cave, C. B. (1989). Evidences for two types of spatial representation: Hemispheric specialization for categorical and co-ordinate spatial relations. *Journal of Experimental Psychology: Human, Perception ad Performance, 15,* 723–735.

Landsdale, M. W. (1998). Modeling memory for absolute location. *Psychological Review, 105*, 351–378.

Lanfranchi, S., Cornoldi, C., & Vianello, R. (2004). Verbal and Visuospatial Working Memory deficits in children with Down syndrome. *American Journal of Mental Retardation, 6,* 456–466.

Lecerf, T., & de Ribaupierre, A. (2005). Recognition in a visuospatial memory task: The effect of presentation. *European Journal of Cognitive Psychology, 17,* 47–75.

Logie, R. H. (1995). *Visuo spatial working memory*. Hove, England UK: Lawrence Erlbaum Associates.

Logie, R. H., & Marchetti, C. (1991). Visuo-spatial working memory: Visual, spatial or central executive? In R. H. Logie & M. Denis (Eds), *Mental Images in Human Cognition* (pp. 105–115). Amterdam: North-Holland, Elsevier.

Logie, R. H., & Pearson, D. G. (1997). The inner eye and inner scribe of visuo-spatial working memory: Evidence from developmental fractionation. *European Journal of Cognitive Psychology, 9,* 241–257.

Lohman, D. F., Pellegrino, J. W., Alderton, D. L., & Regian, J. W. (1987). Dimensions and components of individual differences in spatial abilities. In S. H. Irvine & S. N. Newstead (Eds.), *Intelligence and cognition: contemporary frames of reference* (pp. 253–312). Dordrecht, Netherlands: Nijhoff.

Luzzatti, C., Vecchi, T., Agazzi, D., Cesa-Bianchi, M., & Vergani, C. (1998). A neurological dissociation between preserved visual and impaired spatial processing in mental imagery. *Cortex, 34,* 461–469.

Mammarella, I. C., & Cornoldi, C. (2005a). Difficulties in the control of irrelevant visuospatial information in children with visuospatial learning disabilities. *Acta Psychologica, 118,* 211–228.

Mammarella, I. C., & Cornoldi, C. (2005b). Sequence and Space. The critical role of backward spatial span in the working memory deficit of visuospatial learning disabled children. *Cognitive Neuropsychology, 22*, 1055–1068.

Mammarella, I. C., Cornoldi, C., & Pazzaglia, F. (2004). "*Active and Passive Components of Visuo-Spatial Working Memory: A Developmental Study in Primary School.*" Abstract of the II EWOMS (European Working Memory Symposium), Beaune. France, April, 22–24.

Mammarella, I. C., Cornoldi, C., Pazzaglia, F., Toso, C., Grimoldi, M., & Vio, C. (in press). *Impairment on spatial-simultaneous and spatial-sequential working memory in developmental disabled children*. Brain and Cognition.

Mammarella, N., Cornoldi, C., & Donadello, E. (2003). Visual but not spatial working memory deficit in children with spina bifida. *Brain and Cognition, 53,* 311–314.

Mammarella, I. C., Pazzaglia, F. & Cornoldi, C. (manuscript in preparation). *Evidences for different components in children's visuo-spatial working memory*.

Marks, D. F. (1973). Visual Imagery differences in the recall of pictures. *British Journal of Psychology, 64,* 17–24.

Mayr, U., & Kliegl, R. (1993). Sequential and coordinative complexity: Age-based processing limitations in figural transformations. *Journal of Experimental Psychology: Learning, Memory and Cognition, 19,* 1297–1320.

McDonald, R. P. & Moon-Ho Ring Ho. (2002). Principles and practice in reporting structural equation analyses. *Psychological Methods, 7,* 64–82.

Milner, B. (1971). Interhemispheric differences in the localization of psychological processes in man. *British Medical Bullettin, 27,* 272–277.

Miyake, A, Friedman, N. P., Rettinger, D. A., Shah, P., & Hegarty, M. (2001). How are visuospatial working memory, executive functioning and spatial abilities related? A latent-variable analysis. *Journal of Experimental Psychology: General. 130,* 621–640.

Oberauer, K., Suß, H. M., Shulze, R., Wilhelm, O., & Wittman, W. W. (2000). Working memory capacity – Facets of a cognitive ability construct. *Personality and Individual Differences, 29,* 1017–1045.

Oberauer, K., Süß, H. M., Wilhelm, O., & Wittman, W. W. (2003). The multiple faces of working memory: Storage, processing, supervision, and coordination. *Intelligence, 31,* 167–193.

Pazzaglia, F., & Cornoldi, C. (1999). The role of distinct components of Visuo-Spatial Working Memory in the processing texts. *Memory, 7,* 19–41.

Pickering, S. J. (2001). Cognitive approaches to the fractionation of visuo–spatial working memory. *Cortex, 36,* 457–73.

Pickering, S. J., & Gathercole, S. E. (2001). *Working Memory Test Battery for Children.* London: Psychological Corporation.

Pickering, S. J., Gathercole, S. E., Hall, M., & Lloyd, S. A. (2001). Development of memory for pattern and path: Further evidence for the fractionation of visual and spatial short-term memory. *Quarterly Journal of Experimental Psychology, 54A*, 397–420.

Pickering, S. J., Gathercole, S. E., & Peaker, M. (1998). Verbal and visuo-spatial short-term memory in children: Evidence for common and distinct mechanisms. *Memory and Cognition, 26*, 1117–1130.

Postle, B. R., Idzikowski, C., Della Sala, S., Logie, R. H., & Baddeley, A. D. (2006). The selective disruption of spatial working memory by eye movements. *Quarterly Journal of Experimental Psychology, 59*, 100–120.

Postma, A., & De Haan, E. H. F. (1996). What was there? Memory for object locations. *Quarterly Journal of Experimental Psychology, 49A,* 178–199.

Quinn, J. G., & McConnell, J. (1996). Irrelevant pictures in visual working memory. *Quarterly Journal of Experimental Psychology, 49A,* 200–215.

Raven, J. C. (1965). *Advanced Progressive Matrices, Sets I and II*. London: H. K. Lewis.

Richardson, A. (1969). *Mental Imagery.* New York: Springer.

Rourke, B. P. (1989). Nonverbal learning disabilities, the syndrome and the model. New York: Guilford Press.

Sheenan, P. W. (1967). A shortened form of Betts Questionnaires upon Mental Imagery. *Journal of Clinical Psychology, 23,* 386–389.

Smith, E. E., & Jonides, J. (1999). Storage and executive processes in the frontal lobes. *Science, 283,* 1657–1661.

Snodgrass, J. G., & Vanderwart, M. (1980). A standardized set of 260 pictures: Norms for name agreement, image agreement, familiarity, and visual complexity. *Journal of Experimental Psychology: Human Learning and Memory, 6,* 174–215.

Thurstone, L. L., & Thurstone, T. G. (1965). *Primary mental abilities.* Chicago, IL: Science Research Associates.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. S. Goodale, & R. J. W. Mansfield (Eds.), *The analysis of visual behaviour* (pp. 549–586). Cambridge, MA: MIT Press.

Vanderberg, S. G., & Kuse, A. R. (1978). Mental rotations, a group test of three-dimensional spatial visualization. *Perception and Motor Skills, 47,* 599–604.

Vanderplas, J. M., & Garvin, E. A. (1959). The association value of random shapes. *Journal of Experimental Psychology, 57,* 147–54.

Vandierendonck, A., & Szmalec, A. (2005). An asimmetry in the Visuo-Spatial demands of Forward and Backward Recall in the corsi Blocks task. *Imagination, Cognition and Personality, 23,* 225–231.

Vandierendonck, A., Kemps, E., Fastame, M. C., & Szmalec, A. (2004). Working memory components of the Corsi block task. *British Journal of Psychology, 95,* 57–79.

Vecchi, T., & Richardson, J. T. E. (2000). Active processing in visuo-spatial working memory. *Cahier de Psychologie Cognitive, 19,* 3–32.

Vecchi, T., & Richardson, J. T. E. (2001). Measures of visuo-spatial short term memory: The Knox cube imitation test and the Corsi blocks test compared. *Brain and Cognition, 46,* 291–294.

Walsh, V., Ellison, A., Battelli, L., & Cowey, A. (1998). Task-specific impairments and enhancements induced by magnetic stimulation in human visual area V5. *Proceedings of the Royal Society of London B, 265,* 537–543.

Wechsler, D. (1974) *Manual for the Wechsler Intelligence Scale for Children-Revised.* New York: Psychological Corporation.

Zimmer, H. D., Speiser, H. R., & Seidler, B. (2003). Spatio-temporal working memory and short-term object-location tasks use different memory mechanisms. *Acta Psychologica, 114,* 41–65.

CHAPTER 1.3

# Do we only remember where we left our things when we expect to need them again?

## Expectancy manipulations and object-location memory

Albert Postma and Roy P. C. Kessels

### Introduction

Remembering where we have left our things is a daily nuisance. We are regularly confronted with the task to figure out where our keys, glasses or coffee cups are placed, most typically shortly after we have used these items. This brief sketch of a daily-life problem raises the question how spatial memory, or more precisely object-location memory, works. One of the most controversial issues in spatial-memory research in the last three decades has been the question whether positions are coded automatically into memory or whether mental effort is required to commit positions to memory. According to Hasher and Zacks (1979), automatic operations work with only minimal diminishment of one's capacity to process other components of the flow of information. They occur without intention or awareness. Once initiated they are difficult to suppress, but run to completion. By contrast, effortful processes require the expenditure of attention and effort and so use a portion of a limited-capacity system. They are voluntary and conscious. The utility of automatic processing is evident in frequently occurring environmental situations, where standardised, fast and efficient (but inflexible) mental procedures are available, the use of which prevents the cognitive system from overloading by processing demands. Automatic processing may be genetically inherited. That is, the nervous system may be prewired to maximise the processing of certain types of information. Alternatively, automatic procedures can be installed by abundant amounts of practice (e.g. skilled reading).

What are the criteria by which one can decide whether a certain process is automatic or not? Hasher & Zacks give the following list (Hasher & Zacks 1979, 1984). If an attribute of an experience is coded automatically, memory for this attribute should not be affected by (a) intent (b) age (c) practice, feedback, and strategic instructions (d) individual differences, and (e) concurrent processing loads. In spatial-memory

research, intent usually is examined by having subjects study a spatial display with or without an indication that the locations of this display have to be recalled at a later point in time, i.e. under intentional or incidental learning conditions. If spatial coding works automatically, the two learning conditions should yield comparable performances. In addition, automatic processes are supposed to be innate or develop very early in life. Hence, young children should show the same pattern of results as older children. Moreover, an automatic process should be resistant to reductions in cognitive energy associated with old age, whereas obviously an effortful mechanism would not be. Regarding practice and feedback, the idea is that automatic processes already function at an asymptotic level. Hence their efficiency will not increase with more training. Furthermore, being innate, an automatic processes should not correlate with general-intelligence measures. Finally, concurrent dual-processing loads would strongly interfere with effortful coding and only minimally, if at all, with automatic operations.

Various studies have shown that intent to remember does not affect spatial memory (Andrade 1993; Ellis 1990; Ellis & Rickard 1989; Mandler et al. 1977; Von Wright et al. 1975). Others, however, have found better performance when locations were encoded intentionally (Acredelo et al. 1975; Light & Zelinski 1983; Naveh-Benjamin 1987, 1988). Age also appears to be associated with conflicting results (see below). Only sparse research has been conducted upon the topic of training (Naveh-Benjamin 1987, 1988; Postma 1997), but more work has been done on individual differences in education and intelligence. Ellis and associates (Ellis et al. 1987, 1989) demonstrated that intelligence differences as in retarded versus nonretarded subjects were not accompanied by substantial differences in spatial memory. However, Naveh-Benjamin (1987, 1988) did find such a difference between university students who were subdivided into two groups based on their intelligence. Moreover, whereas Naveh-Benjamin also reported dual-task interference to result in a lower spatial-memory performance, we have argued elsewhere that dual-task interference may have highly selective effects depending on the precise nature of both the secondary and the primary (spatial-memory) task (Postma & De Haan 1996).

It is clear that many empirical controversies surround the hypothesised automaticy of spatial memory. What may have caused these discrepancies? Possible reasons relate to the complexity and materials of the tasks used, and, most importantly here, the precise nature of the spatial-memory tasks. It can be argued that spatial memory is not a unitary construct, but instead may involve several distinct submechanisms (Shacter & Nadel 1991). In recent overviews (Postma et al. 2004; Van Asselen 2005), we have postulated that object-location memory spans three distinct processing components:[1] a) object processing b) location processing c) binding objects to locations.

In this chapter we will review to what extent these putative processing components work automatically or whether they depend on conscious effort. Our main approach will involve manipulations of expectancy: does the coding of different forms of object-location information depend on what you expect to be tested at subsequently. Or in

other words: do we only remember where we left our things when we expect to need them again?

### Verbal interference effects

Postma and De Haan (1996) started their exploration of the functional components of object location memory by using a verbal interference dual task condition. They presented 7 or 10 different items (viz letters, punctuation marks, and nonsense characters) in a $10.5 \times 10.5$ cm square frame on a computer screen for 30 seconds. Subsequently, the items disappeared from the square and had to be relocated. Three task conditions were used: one in which all items were identical, so only the exact positions had to be reconstructed; one with all different items which also had to placed in their exact positions; and finally one with different items. During the relocation phase the positions were marked by a dot, and subjects had to chose from the marked positions which belonged to a particular item. The first condition taps precise positional memory; the latter two conditions assess object-to-location binding (either to exact positions or to relative locations). Most interestingly, in their third experiment, Postma and De Haan (1996) found that verbal interference only affected the binding conditions and not remembering precise positional information in itself. This occurred when during presentation subjects had studied different items, but did not know whether during relocation only their positional memory was going to be tested (hence all previously different items were made identical) or whether one of the two binding conditions was required.

The tentative conclusion here is that apparently, some aspects run virtually automatically: our sense of where things happened appears resistant against dual-task interference even when beforehand it is not fully known that this is important. Other aspects of object-location memory, in turn, require effort and may be mediated by verbal processing. The question now is which aspect does this apply to: processing the objects or processing the object-location links.

### Verbal mechanisms in remembering objects and object-position links

Dent and Smyth (2005) devised a very elegant method to separate these two aspects. Participants attempted to remember the positions of either 3 or 5 Japanese Kanji characters, presented on a computer monitor. Following a brief interval, 2 Kanji characters were displayed and subjects had to pick the original and place it in its original location. The proportion of correct item selections showed effects of both articulatory suppression and memory load. In contrast, the conditional probability of location given a correct item selection showed only an effect of load, but not of suppression. This might

indicate that the verbal mechanisms involved in object-location memory primarily are restricted to object identity information and less to binding objects to locations.

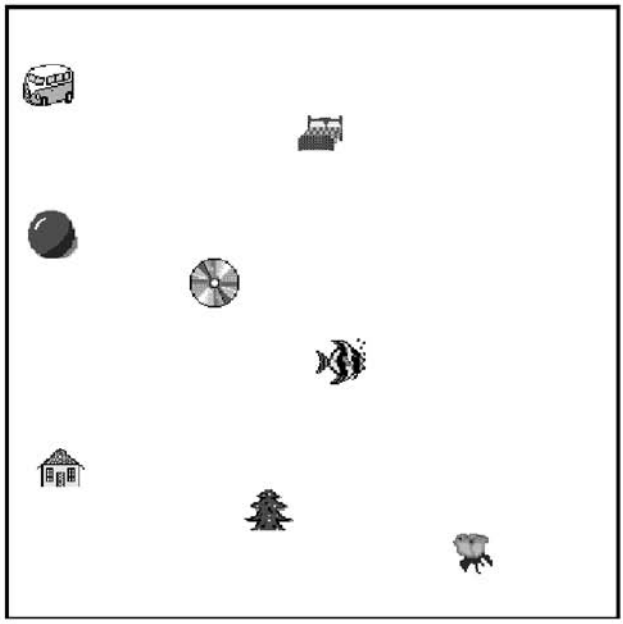
Cattaneo, Vecchi and Postma (2006) further examined the role of verbal factors in object-location memory. They were interested in the role of transformations when memorizing object locations. One of the main manipulations was to present icons during the study phase and to change them to corresponding verbal labels during relocation (see Figure 1 for an example. Not surprisingly, changing format of the items had a major impact on performance. Most importantly here, it was found that presenting icons during presentation led to a better performance than words. This picture superiority effect has been reported before for remembering items. Apparently it also extends to object-location memory situations. If we integrate this with the findings of Dent and Smyth (2005), it seems that while verbal labels might help object-location memory (in particular for processing the object identities), they do not form the sole basis in which the information is remembered. Reversely, pictorial inputs clearly outmatch strictly verbal inputs in object-location memory. In other words, if you need to remember that your keys are on the table, a picture might work better than the simple sentence "they are on the table".

Cattaneo et al. (2006) also conducted an experiment in which four words and four icons were shown together in a single display. Subsequently, either all of the items changed format or half the words and icons changed format (in both cases keeping the total number of words and icons constant). Subjects never knew which of the items would change. The findings showed evidence for a dual-coding strategy: the pictorial advantage during encoding was diminished and there was no interaction between format during coding and format during recall. Having two types of information together – pictorial and verbal – encourages dual coding. Moreover, when not knowing what exactly will happen, but being certain that some transformations may occur, it might be appropriate to adapt a deliberate dual coding strategy.

While the efficiency of certain aspects of object-location memory clearly depends on the formats of the information elements and is modulated by what one expects to happen, this does not yet directly answer the question what will happen when one does not expect anything special at all. Essentially, this is the original idea entertained in Hasher and Zacks' (1979) automaticity hypothesis: you will remember spatial locations of events even when you do not expect you need to remember them.

## Remembering locations when focusing on time

Purely incidental encoding of information is often achieved by covering up the memory requirements of a given task. For example, subjects might simply be exposed to a display of spatially located items, with no further instructions given. Next, unexpectedly an object-location recall test is given. A potential problem with this approach is that one cannot really be sure of what a subject is doing: either subjects might suspect the real nature of the test and put considerable effort in remembering the display,



PALLA CD PESCE ROSA LETTO PINO CASA BUS

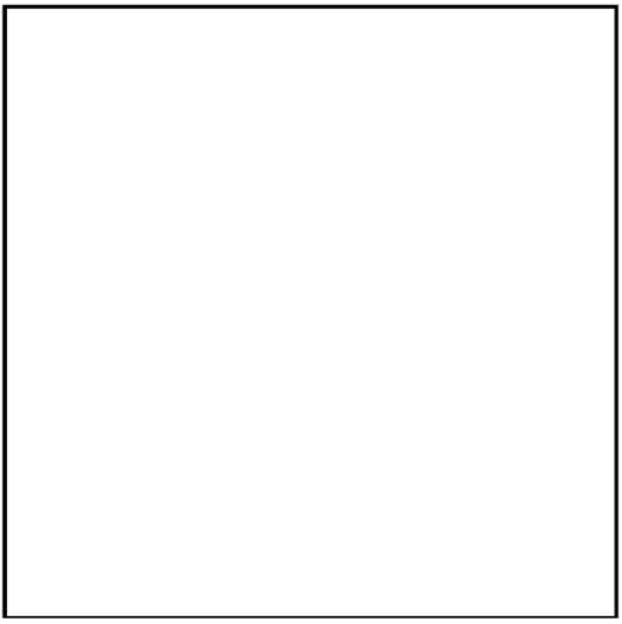


**Figure 1.** What happens when changing the format of items in an object location memory task (italian version). From Cattaneo, Postma, & Vecchi (2006).

or they might not pay attention to the various elements contained in the display at all, leading to poor memory performance, without directly addressing the question whether spatial location processing is automatic or not. That is, if certain information is not perceived in the first place, it is no surprise that it will not get into memory either.

A second manipulation of incidental encoding of particular class of information consists of making subjects focus and try to remember other features than just positions. This procedure has the advantage that the critical information elements are initially perceived and processed. In a recent study, Van Asselen, van der Lubbe and Postma (2006) presented items sequentially at different locations on a computer screen. Thus, participants received both spatial and temporal order information. Pure and mixed blocks of trials were used. In the mixed blocks participants were instructed to focus on either the spatial location or the temporal order of the stimuli, since in the majority of trials this feature was tested (expected trials). However, in some trials participants had to reproduce the other feature (unexpected trials). Moreover, a pure block was added, in which all trials included reproduction of the same feature. Inclusion of pure blocks enables us to take into account whether participants in the mixed block attended to the most likely feature. If spatial and temporal-order information are encoded in an integrated manner, then no difference should be found between performance on expected and unexpected trials. On the other hand, if temporal order information is used to encode spatial information, the difference between performance on expected and unexpected trials would be larger for the spatial task than for the temporal order task. Finally, if spatial and temporal order information are encoded separately in memory, a comparable difference between performance on expected and unexpected trials for both features would be found. Figure 2 gives an example of a test stimulus.

Importantly, as can be seen in Figure 3, more errors were made on unexpected trials than on expected trials for temporal order and spatial-information recall. These findings support the notion that neither spatial nor temporal-order information is encoded automatically into memory, nor does an automatic integration of these features take place. This is in line with the view that separate neural systems underlie spatial and temporal-order information processing in memory (Kopelman, Stanhope, & Kingsley 1997). Notice that accuracy of the unexpected trials in both the temporal order and the spatial tasks was higher than would be expected when participants were simply guessing. This indicates that subjects did encode some of the information that was not relevant for the anticipated response. This does not seem to be the result of a gradual attention division, since no difference in accuracy between the expected trials of the mixed blocks and the trials of the pure blocks was found. Moreover, no difference in accuracy between the first and the last two trials of the unexpected condition was found for all of the conditions but one. This indicates that participants did not change their strategy (from focusing only on the relevant feature to dividing attention between the two features) during a mixed block. The above-chance performance of the participants in the unexpected trials indicates that some of the information that was not attended to was processed, although not as effectively as when attention is directed to

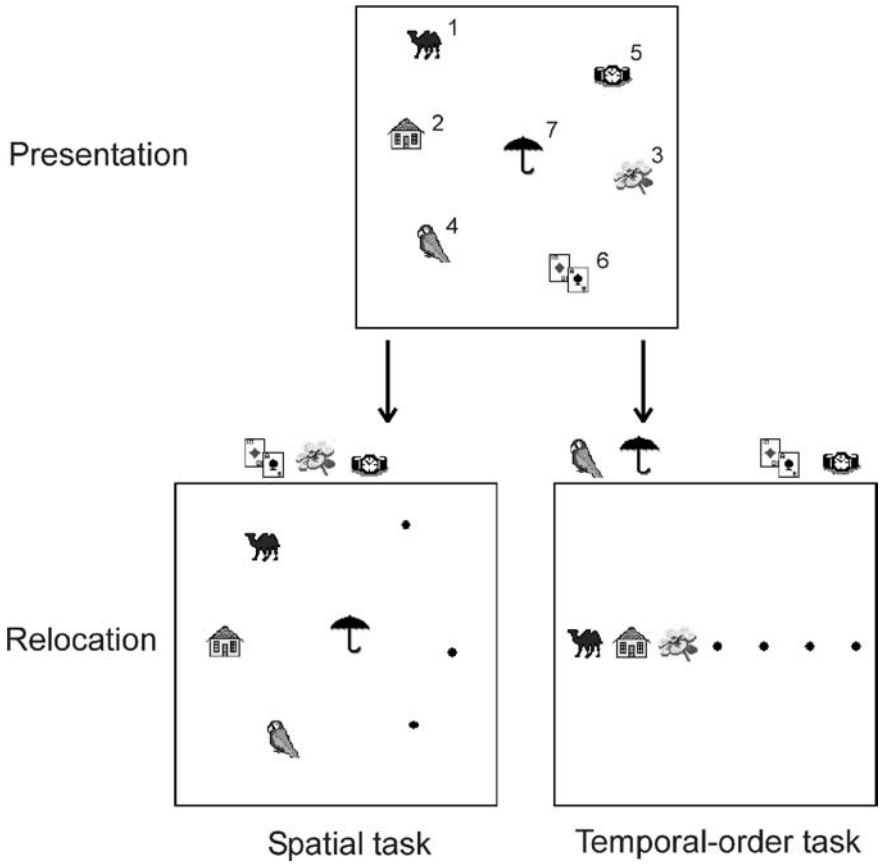



**Figure 2.** The displays during the presentation phase and the relocation phase in the spatial order and temporal order recall conditions. Notice that the digits were never shown but are used here to indicate the temporal order of the presented items.

a feature. Thus, it remains unclear what caused the above-chance performance. Some information of the irrelevant feature might have been encoded, either automatically, or through divided attention that is present in all conditions (both in the pure and mixed condition).

## Conclusions

Do we only remember where we left our things when we expect to need them again? Hasher and Zacks (1979) pleaded for an automatic coding of event and object locations into memory. The decades following their seminal paper have shown much controversy and frequent refutations of their claim. The current review likewise sug-

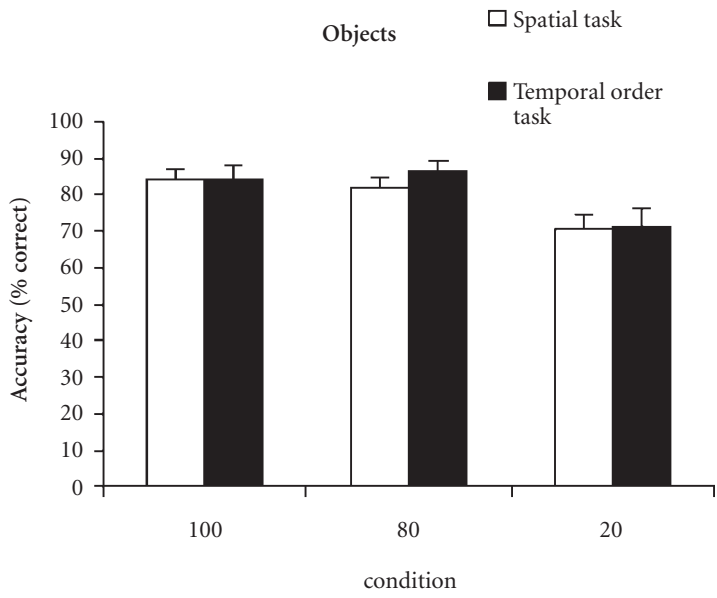



**Figure 3.** The mean error scores (+ S.E.M.) in percentages as a function of the type of feature to be recalled (i.e. spatial versus temporal) and the degree to which that was expected to be tested (100% of the trials, 80% of the trials or 20% of the trials). From van Asselen, van der Lubbe & Postma (submitted).

gests that object-location memory is not a fully automatic process. First, we showed that verbal dual tasks diminish performance. Second, we demonstrated that focusing on the temporal order of serially presented items in different locations does not yield as good a performance for recalling the locations as when focusing on the spatial order. Expectancy not only affects whether we process object locations or not, it also determines how we code different aspects of object-location information. There might be a tendency to create a dual code when both words and icons are presented together and when it is unclear which of them will change format during recall.

The good news though for the automaticity claim is that certain aspects of object-location memory appear to be processed automatically to some extent. When focusing on the temporal order information unexpected recall of spatial order is significantly above chance (albeit lower than after expected recall). Previously, it has already been suggested that the distinction between automatic and effortful coding of spatial information is rather continuous than binary. We speculate here that this continuity follows from the multi-facetted nature of object-location memory. Storing positional information per se appears to occur automatically to a substantial degree. It appears quite resistant to certain forms of interference. In turn, linking objects to locations requires more effort. Verbal interference effects indicate that this would mostly involve processing of the object identities rather than associating objects to locations. It should be noted here that other types of interference might yield a somewhat modified effect (cf.

Zimmer, Speiser & Seidler 2003). To rephrase our original question: do we automatically without special effort remember where we have left things? Sure, but it certainly helps to pay attention.

Acknowledgements

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## Note

1. Notice that we further differentiated two types of position processing and binding: one working with coordinate or exact metric positional information; the other with categorical or more relative position information.

## References

Acredelo, L. P., Pick, H. L., & Olson, M. G. (1975). Environmental differentiation and familiarity as determinants of children's memory for spatial location. *Developmental Psychology, 11*, 495–501.

Andrade, J. & Meudell, P. (1993). Is spatial information encoded automatically? *Quarterly Journal of Experimental Psychology, 46A*, 365–375.

Cattaneo, Z., Postma, A., & Vecchi, T. (2006). Gender differences in memory for object and word locations: The role of passive and active working memory components. *Quarterly Journal of Experimental Psychology, 59*, 904–919.

Dent, K. & Smyth, M. M. (2005). Verbal coding and the storage of form-position associations in visual-spatial short-term memory. *Acta Psychologica, 120*, 113–140.

Ellis, N. R. (1990). Is memory for spatial location automatically encoded? *Memory & Cognition, 18*, 584–592.

Ellis, N. R., Katz, E., & Williams, J. E. (1987). Developmental aspects of memory for spatial location. *Journal of Experimental Child Psychology, 44*, 401–412.

Ellis, N. R., & Rickard, T. C. (1989). The retention of automatically and effortfully encoded stimulus attributes. *Bulletin of the Psychonomic Society, 27*, 299–302.

Ellis, Woodley-Zanthos, P., & Dulaney, C. L. (1989). Memory for spatial location in children, adults, and mentally retarded persons. *American Journal on Mental Retardation, 93*, 521–527.

Hälbig, T. D., Mecklinger, A., Schriefers, H., & Friederici, A. D. (1998). Double dissociation of processing temporal and spatial information in working memory. *Neuropsychologia, 36*, 305–311.

Hasher, L., & Zacks, R. T. (1979). Automatic and effortful processes in memory. *Journal of Experimental Psychology: General, 108*, 356–388.

Kopelman, M. D., Stanhope, N., & Kingsley, D. (1997). Temporal and spatial context memory in patients with focal frontal, temporal lobe, and diencephalic lesions. *Neuropsychologia, 35*, 1533–1545.

Light, L. L. & Zelinski, E. M. (1983). Memory for spatial information in young and old adults. *Developmental Psychology, 19*, 901–906.

Mandler, J. M., Seegmiller, D., & Day, D. (1977). On the coding of spatial information. *Memory & Cognition, 5*, 10–16.

Naveh-Benjamin, M. (1987). Coding of spatial location information: an automatic process? *Memory & Cognition, 4*, 595–605.

Naveh-Benjamin, M. (1988). Recognition memory of spatial location information; Another failure to support automaticity. *Memory & Cognition, 16*, 437–445.

Postma, A., & De Haan, E. H. F. (1996). What was where? Memory for object locations. *Quarterly Journal of Experimental Psychology, 49A*, 178–199.

Postma, A., Kessels, R. P. C. & Van Asselen, M. (2004). The neuropsychology of object location memory. In C. Auen (Ed.), *Remembering where: Advances in understanding spatial memory*. Lawrence Erlbaum associates: Mahwah, NJ.

Schacter, D. L. & Nadel, L. (1991). Varieties of special memory: A problem for cognitive neuroscience. In R. G. Lister and H. J. Weingartner (Ed.), *Perspectives on cognitive neuroscience*. (pp. 165–185). New Yourk, NY, US: Oxford University Press.

Van Asselen, M. (2005). Neurocognition of spatial memory: Studies in patient with acquired brain damaged and healthy participants. Doctoral dissertation, Utrecht University.

Van Asselen, M. , van der Lubbe, R. H. J., & Postma, A. (2006). *Are space and time automatically integrated in episodic memor?, 14*, 232–240.

Van Asselen, M., Fritschy, E. & Postma, A. (in press). The influence of intentional and incidental learning on acquiring spatial knowledge during navigation. *Psychological Research*.

Von Wright, J. M., Gebhard, P., & Karttunen, M. (1975). A developmental study of the recall of spatial location. *Journal of Experimental Child Psychology, 20*, 181–190.

Zimmer, H. D., Speiser, H. R., & Seidler, B. (2003). Spatio-temporal working memory and short-term object location tasks use different memory mechanisms. *Acta Psychologica, 114*, 41–65.

CHAPTER 1.4

# Variations on the image scanning paradigm

## What do they contribute to our knowledge of mental imagery?

Michel Denis and Grégoire Borst

### Introduction

Research on mental imagery over the past twenty years has two interesting characteristics. The first is the genuine contribution it has made to our knowledge of this form of representation. There are now few disagreements about the empirical facts regarding mental imagery, even though the interpretation of some of them remains a matter of controversy (Kosslyn, Ganis, & Thompson 2003; Pylyshyn 2002). The second characteristic is that the study of mental imagery has not only benefited from existing experimental methods, but has also sparked the creation of new paradigms. This seems to have been especially true in the case of image scanning, a paradigm specific to the investigation of mental images that has elicited a substantial number of variants and improvements over the past twenty years or so (Denis & Kosslyn 1999).

According to Stephen Kosslyn's (1994) theory, image scanning is a process that allows people to shift their attention across visual mental images. Images are patterns within a visual buffer that functions as if it were a coordinate space. This is not an actual physical space, but a functional one that is defined by the way processes access representational structures. The visual buffer has an innately determined and fixed organization. It has a limited extent and limited resolution (which is highest at the center and decreases toward the edges). In all image representations in the visual buffer, every part of the representation corresponds to a part of the object being represented in such a way that the relative distances between the parts of the objects are preserved in the distances between the corresponding parts of the representation. Unlike verbal or propositional representations, images depict information via a semantics of resemblance. The structural analogy between images and the objects they represent confers particular functional properties on these representations. Interpretative mechanisms (that "examine" the imaged objects), and transformations (that modify their shapes) operate on these internal displays. Thus, visual mental images, and the processes that operate on them, are thought to be functionally analogous to the external objects and

the perceptual processes they simulate. This functional equivalence has been assessed using the paradigm of selective interference. Farah (1985) showed that a given letter is easier to detect if the participant has previously visualized the same letter rather than a different one. Moreover, neuroimaging studies have yielded evidence that mental imagery and visual perception activate common underlying brain structures (Le Bihan, Turner, Zeffiro, Cuénod, Jezzard, & Bonnerot 1993; Mellet, Tzourio-Mazoyer, Bricogne, Mazoyer, Kosslyn, & Denis 2000).

The phrase "image scanning" refers to the cognitive processes that operate on visual mental images when a person moves his or her attention across imagined objects. The first image scanning paradigm was designed to investigate the spatial properties of images (Kosslyn 1973). In the original experiment, participants memorized drawings of elongated objects (such as a tower). They were then asked to visualize one of the objects and to focus at one of its end (for example, the bottom of the tower). Lastly, participants heard the name of a feature on the object (e.g., a flag), and they had to look for it. Participants were not instructed to scan their image, but were simply told to focus on the original location until the probe was delivered, and then to focus on the named part or feature (if they could see it on the imaged object). They pressed one button when they had focused on the named part, and another button if they failed to find it. The critical finding was that response times increased linearly with increasing distances from the focus point to the named part of the object. This finding was taken as evidence that distance, as traversed by image scanning, is genuinely represented in visual mental images.

A variant of the original image scanning paradigm was later designed by Kosslyn, Ball, and Reiser (1978). The key feature of this new paradigm was that there were no intervening objects between focus and probes. In a learning phase, participants memorized a map of an island containing seven landmarks (such as a rock, a beach, etc.). The map of the island was designed in such a way that the distances between all pairs of landmarks were different. In the test phase, at the beginning of each trial, the participants heard the name of one of the seven landmarks. They were instructed to form an image of the entire island, and to focus mentally on the named landmark. Shortly thereafter, the name of a second object was displayed. If the second object was one of the landmarks located in the island, participants were to scan to it by following mentally a little spot and to press a button when the spot reached it. In half of the trials, the second object named was not one of the seven landmarks, and in these trials the participants were instructed to press a different button. As in the original experiment, the participants took longer to scan greater distances, and scanning times increased linearly with increasing distances. Kosslyn et al. (1978) interpreted this finding as evidence that mental images incorporate the metric information present in the original stimulus.

## Wider implications of the findings of image scanning experiments

In the first image scanning experiments, the tasks involved rather simple visual images (Kosslyn 1973). The subsequent experiments involved more complex images, in which a large number of different distances had to be scanned (Kosslyn et al. 1978). What these experiments had in common was that the participants had to perform a mental inspection of images acquired during the experimental session. Images of configurations of which the internal distances were already coded when the experiment began were not used, so that the response times would not be affected by prior knowledge, in particular, by declarative knowledge about the distances involved.

However, in at least one study, configurations of objects already present in the participants' long-term memory were scanned. In this study, Jolicoeur and Kosslyn (1985) used statements that asserted that an object or an animal had some specific visible property. In a preliminary experiment, participants had rated these statements on the basis of whether a mental image had to be used to decide whether they were true or false. Two sets of object-property pairs were then contrasted: those that were reported to require imagery to evaluate and those that reportedly did not. The objects were elongated either horizontally or vertically when viewed in the usual orientation, and the property was always located at one end of the object. The high-imagery items included "*A goat has curved horns*" and "*A pineapple has pointed leaves*", whereas the low-imagery items included "*A chimp has two eyes*" and "*A submarine has a metal propeller*". The participants in the main part of the experiment were invited to form an image of an object or animal (e.g., a goat) and to focus mentally on one end of it. They then heard a property that was formulated as an adjective-noun pair (e.g., "*curved horns*"), and were asked to decide whether the object had this property. While they were carrying out this task, the participants were instructed to create an image of the object, and to focus on the specified location. In half the trials, the property concerned was at the end on which the participant was focusing, and in the other half, it was at the opposite end. The data showed that for the items that had previously been rated as requiring imagery, less time was needed when the participants focused on the end where the property was located than when they were focused on the other end. In contrast, for the items that had previously been rated as not requiring imagery, the time was the same for both locations. In addition, response times were longer for items that required imagery than for those that did not. The participants apparently engaged in simulating scanning only for those items that required imagery to evaluate. Admittedly, in this experiment, the scanned distances did not strictly speaking involve any "metric" determination. However, they did suggest that the distance between a focused point and a property to be checked does affect the response times.

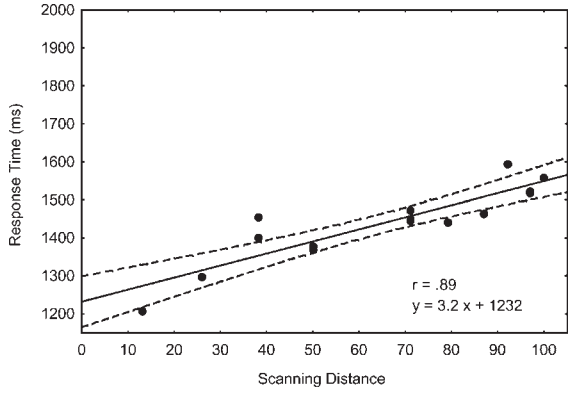
Whether they are drawn from the episodic or long-term memory, the images used in the conventional scanning experiments are constructed by reviving previous perceptual experience in some form. Images are thought to include features that are derived from previous perceptual episodes. In fact, this situation limits the investigation of image scanning to "reproductive imagery", and therefore overlooks many forms of im-

agery, such as the creation of novel images that are not directly traceable to immediate or recent sensory experience. Pioneer research has highlighted the distinction between the so-called "memory images" and "imagination images" (Holt 1964; Vinacke 1952), but the creative facet of mental imagery has been (and still is) largely ignored by contemporary research on imagery. "Creative imagery" can be, of course, investigated for the properties that are specific to it and make it distinct from purely reproductive imagery. However, there is room for investigating whether any features are shared by both forms. In particular, would images that a person has constructed in a novel manner, from an endogenous process or by using instructions provided by another person, for instance an experimenter, display metric properties?

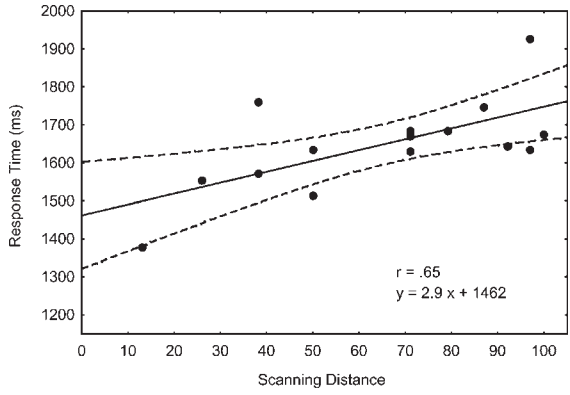
To find out, it is necessary to create a situation in which a person builds the image of a complex object or spatial configuration from a verbal description in such a way that metric information is included in that representation. If this person is then invited to scan that image, will this metric be detected? In other words, can images exhibit metric properties without the representation having been constructed from a perceptual experience directly involving metric information?

This is the program that was assigned to the research initiated by the experiments of Denis and Cocude (1989). These experiments contrasted a situation where scanning is executed on an image of a geographical map (as did Kosslyn et al. 1978), with another situation where it is executed on an image of this map, which has been constructed by processing a verbal description. The configuration was that of a circular island, with landmarks located on its periphery. The description located each landmark at a metrically defined point using the conventions of aerial navigation (e.g., "*The lighthouse is located at one o'clock*"). In this way, the locations were made quite explicit, although no information was provided about the distances separating each pair of landmarks.

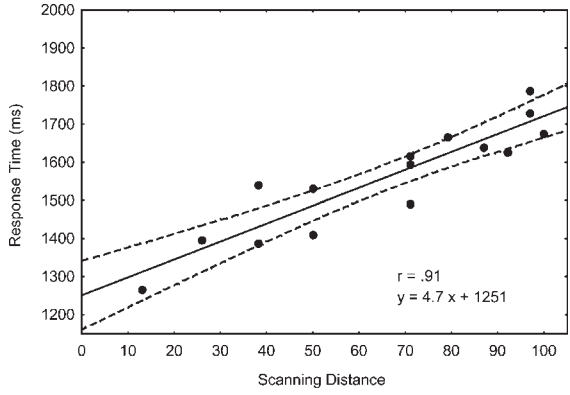
The participants, who learned the map under conditions similar to those used by Kosslyn et al. (1978), displayed the typical increase in time with increased distance scanned (Figure 1a). What was new was the fact that when the participants scanned images formed from the verbal description, the same pattern appeared, reflected by a positive correlation coefficient between times and distances. In the first study, however, this coefficient was lower than that found for the participants using the map, and the absolute scanning times were also longer (Figure 1b). To check whether this was a genuine effect or simply reflected the fact that the structural qualities of the image had been insufficiently consolidated during the learning phase, further experiments were conducted in which the participants were allowed more time to learn the description and construct the corresponding visual image. It turned out that with additional learning opportunities (six learning trials instead of three), the scanning performance of participants using the description was very similar to that following perceptual learning (Figure 1c). Thus, with a moderate rate of learning, an image constructed from a verbal description may fail to attain the structural coherence and metric validity of a perceptually based image, but with additional learning, the image may become cognitively indistinguishable from an image derived from perception. This effect attests that




(a) After map learning




(b) After description learning (three learning trials)




(c) After description learning (six learning trials)

**Figure 1.** Response time as a function of the distance scanned: (a) after map learning; (b) after description learning (three learning trials); (c) after description learning (six learning trials) (Denis & Cocude 1989). In this figure, distances are expressed in terms of their ratios to the diameter of the circular island.

the referential validity of an image (i.e., its ability to reflect accurately the set of objects it refers to) is not an all-or-nothing property, but results from a stepwise process.

The study carried out by Denis and Cocude (1989) was the first to demonstrate that mental images constructed from verbal descriptions have metric properties, and that this is reflected by the fact that the same chronometric pattern of image scanning is found as when images are based on perceptual inputs. The special value of this finding was to make it obvious that such images ultimately contain more information than the explicit information conveyed by the descriptions. In particular, images not only contain information regarding the locations of the landmarks, but they also contain information about the relative distances between landmarks, even though the descriptions have not provided any information about this. The representational property inherent in visual imagery explains this important characteristic of linguistically based images. When the individual locations of parts of a representation are encoded in an image, their relative positions are displayed and are immediately available to mental inspection.

Further studies were designed to test the sensitivity of image scanning to experimental variations that would make it more difficult for the participants to construct a coherent, integrated image from a verbal description. For instance, the particular order of the sentences that make up the description was thought to affect the construction of visuo-spatial representations, and hence their availability for retrieval. Denis and Cocude (1992) investigated whether well-structured representations could be constructed from poorly structured descriptions. To do this, the description was modified by presenting the same set of sentences in a random sequence, rather than the regular clockwise sequence originally used. This was intended to create a cognitively unfriendly context that would make it more difficult to establish spatial connections between the landmarks. In fact, the analysis of response times in the subsequent scanning task did not suggest that the mental images had a coherent internal structure. Response times were much longer than in the control condition, and no significant correlation was found between scanning times and distances. However, after more exposures to the description, the scanning times became shorter, and a significant positive correlation was eventually found between times and distances. These findings support the view that the structure of a description affects the internal structure of images, and thus interferes with the mental operations subsequently performed on these images. A poorly structured description does not prevent the image from reaching a coherent structure wherein metric information is represented, but it does have a cognitive cost in the form of requiring further processing and the allocation of additional resources.

The construction of visual images from a verbal description was investigated again in a subsequent experiment, which tested a model intended to account for the gradual process of image elaboration, and the progressive increase in image accuracy as learning proceeds. The model proposed by Denis, Gonçalves, and Memmi (1995) posited that the location of a landmark mentioned in a description is not best represented as a sharp point in the mental image, but rather as a region around this point. The region

corresponds to the range of the possible locations of a landmark at a given stage of learning. Learning a description and the stepwise construction of a visuo-spatial representation consist of progressively narrowing each "region of uncertainty" associated with a landmark to its exact location. The size of these regions is thought to vary inversely with the degree of image elaboration. The closer the image is to its ultimate step of elaboration, the more restricted the regions of uncertainty.

The experiment involved repeating the same sequence of events three times: exposure to the description twice, followed by an image scanning test. The results confirmed that there was no time/distance correlation at all for the first scanning test, which means that no metric information was yet present in the image under construction. In addition, response times were exceptionally long. Two more exposures changed the situation significantly. The chronometric patterns revealed that the image now contained more accurate metric information. The fact that the image was more readily available was also reflected by significantly shorter scanning times. The impact of the process was still more marked after the last two exposures to the description. Scanning times and correlation coefficients indicated further improvement in the internal structure of the image. The model of image accuracy was confirmed by a mathematical calculation of the regions of uncertainty, revealing that the size of these regions decreased steadily from test to test.

Lastly, Denis and Cocude (1997) examined the sensitivity of image scanning to descriptions in which differing emphasis was given to the various landmarks. For instance, the description of some landmarks not only contained information about their locations, but also provided a short narrative containing many concrete details likely to attract the participants' attention, making the landmark concerned more salient. The scanning data showed, however, that there was no difference between the times for scanning towards a salient landmark and those for scanning towards a secondary, unimportant one. The time/distance correlation coefficients were virtually identical in both cases. The locations of landmarks appeared to be the only factor governing scanning times in this task. Further experimental attempts to alter the salience of landmarks in material learned from verbal descriptions did not produce any measurable representational biases.

In the same set of experiments, Denis and Cocude (1997) collected evidence that image scanning is highly sensitive to individual characteristics. The participants in image scanning experiments were split into two groups: those who scored above the median score in a test of visuo-spatial abilities (the Minnesota Paper Form Board; cf. Likert & Quasha 1941), and those who scored below the median. This was done in order to compare people who had the greatest aptitude for generating and manipulating visual images with those less prone to imaging. The results showed that the participants with the highest visuo-spatial capacities produced the typical image scanning results, while in sharp contrast, the participants with the least imaging abilities showed no evidence that their images had any consistent structural properties. Their scanning times were much longer than those of their counterparts, and there was no relationship at all between times and distances. Thus, individual visuo-spatial capaci-

ties did predict people's ability to generate metrically accurate images, even when these images had been constructed from verbal descriptions.

To summarize, visual perception is not the only source of analog representations. We have reviewed experiments in which variations on the scanning paradigm have provided genuinely new information. First, language has been shown to be able to create images with intrinsic properties that are not essentially different from those of perception-derived images. Newly created images are not unstructured patterns. They possess a structure that is similar to the structure of representations arising from visual perception. Note, however, that the assessment of the equivalence of images generated from perception and from descriptions is restricted to their geometrical properties. Other properties, such as clarity or vividness, may be expressed differently in perceptually and verbally based images. Second, scanning studies extended to language-based images have shown that mental images are constructed stepwise. Before reaching its final structure, a newly created image passes incrementally through earlier states where its metric structure is not evident. By measuring scanning times, the experimenter can gauge the progress during which the structural qualities of an image firm up, from a starting state where this structure is absent, to an end state where it is fully achieved. Variations on image scanning have thus proven to be a useful source of new information about the intimate structure of visual mental images.

## Two contrasting scanning processes

Following Kosslyn's original studies, other researchers criticized the experimental procedures and paradigms used in research on imagery. The main objection was that the results are so contaminated by the experimental situation as to be irrelevant to the properties of imagery (Mitchell & Richman 1980). One formulation of this criticism focused on experimenter expectancy effects. The participants are thought to deduce the investigator's expectations, and to modify the timing of their responses in order to fit in with the experimenter's expectations (Intons-Peterson 1983). Another criticism had nothing to do with the experimenter's expectations, but centered on the notions of task demands and tacit knowledge (Pylyshyn 1973). According to this objection, the results of the scanning experiments simply reflect the tacit knowledge that participants have about visual processes. Pylyshyn (1981) argued that imagery processes are cognitively penetrable, because they can be altered by the participants' beliefs, goals, expectations, or knowledge. However, several empirical studies have refuted the idea that people would be able to predict the results of image scanning experiments (Denis & Carfantan 1985; Goldston, Hinrichs, & Richman 1985). It is true nevertheless that all these counter-explanations of the scanning effect claim that the results of the scanning experiments do not tell us anything about the nature of the mental representations that underlie imagery, but simply reflect how participants (either consciously or unconsciously) regulate their responses during the experiment.

Such criticisms were actually very useful in that they forced imagery researchers to improve the design of their experiments. Ideally, studies must fulfill three conditions in order to protect image scanning from undesirable effects such as those mentioned above. First, the responses given by the participants must not be biased by prior knowledge. Second, no explicit imagery instructions should be given to the participants. Third, the participants should not be able to infer that the experimenter is interested in the relationship between scanning time and distance. Finke and Pinker (1982) were the first to design an image scanning paradigm that met all three conditions. In their experiments, the participants first memorized a pattern of four dots. This pattern was then replaced by an arrow in an unpredictable position in a blank field. The participants were to decide as quickly as possible whether the arrow was pointing to a location previously occupied by one of the dots. The participants were not instructed at any time to form or scan visual mental images. However, the results revealed a strong linear relationship between response times and the distances separating the tip of the arrow and a target dot, very much like the relationship found in the experiments based on the original paradigm. These findings could not be explained by experimenter expectancy effects, or by task demands. They were confirmed in subsequent experiments (Finke & Pinker 1983; Pinker, Choate, & Finke 1984), and were taken as further evidence that scanning does reflect the spatial structure of image representations.

Since then, the process of image scanning has been investigated using a variety of further experimental paradigms (Dror & Kosslyn 1994; Kosslyn, Margolis, Barrett, Goldknopf, & Daly 1990; for a review, see Denis & Kosslyn 1999). All of these tasks were implicitly assumed to tap into the same image scanning process by which people shift their attention across objects in visual mental images. However, this implicit assumption is open to question. The concept of image scanning as a single or dual mental process was therefore investigated in a set of experiments (Borst, Kosslyn & Denis, in press). These experiments were designed to find out whether scanning should be divided into (at least) two distinct subtypes. Our hypothesis was that one aspect of scanning consists of simulating a move from one location to another, whereas the other consists of extrapolating the location of a target point. The paradigm devised by Kosslyn et al. (1978) may be seen as primarily eliciting an image scanning process that involves simulating a *movement* between two points. In contrast, the paradigm used by Finke and Pinker (1982) would imply a scanning process that enables people to extrapolate the *location* of a point.

Three experiments were conducted in order to investigate this hypothesis. One major constraint was that the same group of participants perform image scanning tasks based upon the two paradigms using the same materials (i.e., the same number of targets and the same set of distances). In order to compare the participants' performance in the two tasks, we defined a set of measures of the image scanning process. We took the correlation between scanning times and distances into account, and we also analyzed the slopes of the best-fitting lines and the intercepts at the ordinate of the best-fitting lines (two indices which are not often taken into account in scanning experiments). We wanted to find out whether the same chronometric patterns would

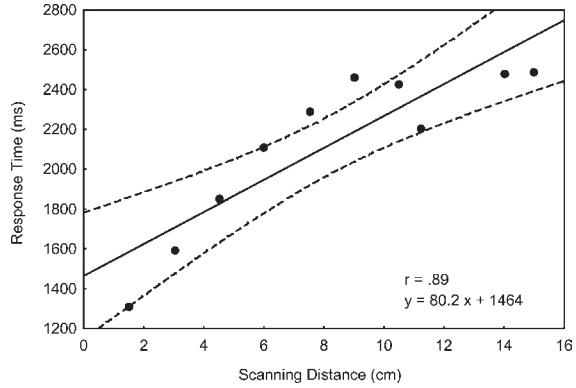
appear in these indices in both paradigms. To do this, we determined whether parameters were correlated in the two paradigms. Would participants who scanned quickly in one paradigm also scanned quickly in the other? Furthermore, if the same underlying process is being tapped into, we would expect to find high levels of correlation between the slopes of the time/distance regression lines. In contrast, if different processes are involved, we would not expect to find such correlations.

In the first experiment, the participants performed the two scanning tasks based on the same spatial materials. In order to compare the results obtained in the two tasks, we matched every aspect of the two procedures. First, to circumvent the problem resulting from the fact that the materials in the original Kosslyn et al. (1978) and Finke and Pinker (1982) experiments involved different numbers of points, we created a single pattern with the same number of points to be used in both tasks. We used the same configuration of dots, as well as the same set of inter-dot distances. Because each participant did two scanning tasks, rather than using two different patterns, we used a configuration in one task and a version rotated through 180° in the other task.

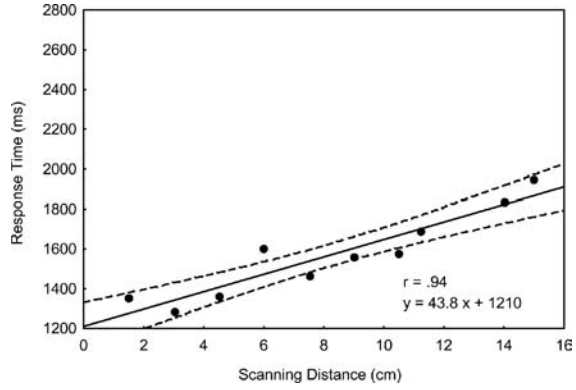
The stimulus configuration contained five dots of different colors. In the Kosslyn et al. task (hereafter referred to as the KBR task), the participants had to scan mentally between the 10 possible pairs of the five dots of one pattern. In the Finke and Pinker task (hereafter referred to as the FP task), the participants had to decide whether an arrow was pointing at one of the previously seen dots. In both tasks, we recorded response times.

In both tasks, response times increased linearly with increasing distances (Figure 2). The close relationship between response times and distances in the two paradigms provided evidence that mental images incorporate metric information contained in the spatial display they evoke. Despite the fact that the same pattern of time/distance correlation was found in both paradigms, the individual performance of the participants differed in the two tasks, which was revealed by the weak correlations found between the two scanning tasks for all three statistical indices (time/distance correlation coefficients, slopes, and intercepts of the best-fitting lines). We interpreted this lack of correlation as strongly suggesting that the two paradigms involve distinct image scanning processes. These findings challenged the concept of a single scanning process, and led us to conclude that image scanning was more complex than the participants' just moving their attention across an imagined configuration of objects.

In a second experiment, we investigated the nature of the two types of image scanning process. In particular, we thought that in the KBR task, the participants would primarily be performing transformational processes when scanning, whereas in the FP task they would rely on attentional processes. In the KBR task, where the participants moved a small spot between two points, a transformation applied to the content of the visual buffer. On the other hand, in the FP task, when participants had to decide whether an arrow was pointing to the location of a previously seen dot, most of them reported that they mentally "projected" the line of the arrow and checked whether it reached one of the targets, a process that may primarily involve attention.




(a) KBR task




(b) FP task

**Figure 2.** Response time as a function of the distance scanned: (a) KBR task; (b) FP task (Borst, Kosslyn, & Denis in press).

In order to investigate this hypothesis, we added two new tasks to those used previously, namely, a mental rotation task (Cooper & Shepard, 1973), and a visual search task (Treisman & Gelade 1980). We selected these two tasks because one (mental rotation) involves transformational processes, whereas the other (visual search) involves attentional processes. In the mental rotation task, participants had to decide whether a letter was displayed in its normal version or as a mirror image, regardless of its orientation in the picture plane. The usual finding is that response times increase with how far the letter has been rotated from the standard upright position, which suggests that the image is mentally rotated. In the visual search task, the participants had to decide whether a letter printed in a specific color (i.e., the target) was present in a pattern including the same letter printed in different colors and some other letters in the same color (distractors). It is generally assumed that this task involves the participants moving their attention over the pattern, and this seems to be confirmed by the fact that a linear relationship is found between the number of distractors and the response times.

We reasoned that if a transformational process lies at the heart of the KBR task, we should find a correlation between the slopes of the best-fitting lines and those in the mental rotation task, but not with those in the visual search task. However, this prediction is based on the assumption that the translation operated in scanning involves at least some of the processes used in rotation. Conversely, if an attentional process lies at the heart of scanning in the FP task, then the slopes of the best-fitting lines in this task should match those in the visual search task, better than those in the mental rotation task.

As in the first experiment, we did not find any relationship between the measures of the scanning processes in the two scanning paradigms. This finding, like those of the first experiment, supported the hypothesis that there were (at least) two distinct image scanning processes. Our findings showed that the KBR task did not correlate with the mental rotation task, indicating that the transformational process involved in the KBR task seems to be distinct from a rotational process. We concluded that the image scanning process in the KBR task is probably closer to a translation operation. In the FP task, the various measures of process efficiency (time/distance correlation coefficients, slopes, and intercepts) were correlated with those of the visual search task. This finding was to be expected if attentional processes play a key role in the FP task. We interpreted it as evidence for the functional equivalence between imagery processes and the perceptual operations they are thought to mimic.

The lack of correlation between the two scanning paradigms may not inform us about the scanning process, but other aspects of the paradigms. At first glance, one might be concerned that having to discriminate between targets and non-targets in the FP task would affect the speed of scanning. In the third and last experiment, we investigated whether this possible bias could account for the lack of correlation between the two image scanning tasks. In order to investigate this alternative interpretation, we varied the difficulty of discriminating between targets and distractors in the FP task. In the first two experiments, subtle discrimination was required from the participants (which made the task very difficult). In the new experiment, we added two higher levels of discriminability (which made the task easier). For each of the three resulting levels of discriminability (low, medium, high), the participants performed exactly the same task, that is, they had to decide whether an arrow was pointing towards the location that had been occupied by one of the previously viewed dots. The difficulty of the task was determined by the angle by which the arrow missed any of the dots: the greater the angle, the easier the task.

The results for the KBR task replicated the typical findings: there was a strong linear relationship between response times and distances. In the FP task, the original results were replicated for all three levels of discriminability. This was not surprising for the low level of discriminability (which was the level used in the original Finke and Pinker experiment), but we found that the time/distance correlation was also confirmed at the two higher levels of discriminability. Thus, regardless of the difficulty of the task, the participants seemed to form a mental image of the pattern and then mentally scan the distances between the tip of the arrows and the target points even

though they were not explicitly instructed to do so. We also found that the speed of the scanning process depended on the difficulty of discriminating between the target and distractor points, which was revealed by the fact that the slopes of the best-fitting lines were steeper when the difficulty was greater.

These findings confirmed that the two scanning paradigms involved different processes. In fact, even when the impact of the discriminative component of the task was varied, the scanning processes still remained unrelated to each other. Thus, the lack of correlation between the chronometric measures of scanning found in the two scanning tasks was unlikely to be a consequence of the discriminative process taking place as in the FP paradigm. The dissociation cannot therefore be attributed to discrimination, and must instead be viewed as an essential difference between the scanning processes elicited by the two tasks.

To summarize, the results of the three experiments converged to demonstrate that different scanning processes are involved in the two classical image scanning paradigms. The main conclusion was that there are two distinct types of image scanning: (a) a scanning process involving a simulation of a *movement* between two points (the KBR paradigm), where people incrementally transform the content of the visual buffer until they reach the target; this sort of scanning involves a transformational process, which is distinct from the transformation used in mental rotation; and (b) a scanning process involving the *localization* of a target point (the FP paradigm), in which people shift their attention window along a straight line from the tip of the arrow to the target point; this sort of scanning undoubtedly involves attentional processes.

### Scanning along straight or complex paths

Studies of the visual inspection of complex linear structures converge to show that the shape of the path followed by visual scanning affects scanning times. The same effect is also likely to operate in mental imagery. For instance, Reed, Hock, and Lockhead (1983) asked participants to scan images of various linear configurations. Their results showed that the configuration of the pattern did influence the scanning speed. Diagonal lines were scanned more quickly than spirals, and spirals were scanned more quickly than mazes. For all three patterns, however, Reed et al. (1983) found consistent linear increases in scan times with increasing distance.

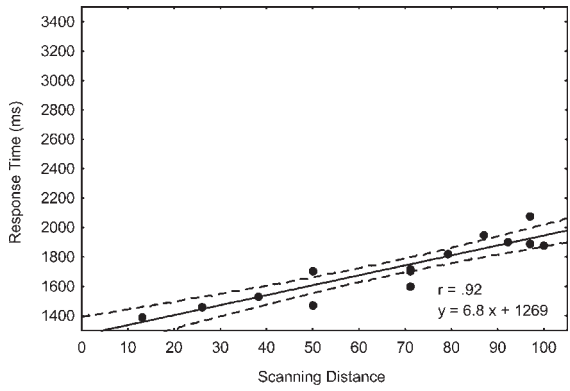
The effect of various linear structures on scanning times explains why research on image scanning has devoted so much effort to controlling the paths followed by the participants during the mental inspection of distances across configurations. In most experiments, this control involved having the participants explore distances extending along straight lines. This makes sense if the aim is to record "pure" correlational measures, that is, checking that the metric data used in the computations have not been affected by undesirable deviations from linear scanning on the part of the participants. When the material is open to variants of straight-line exploration, the instructions

insistently ask the participants to follow straight lines while exploring the imaged configuration (e.g., Borst et al. 2005; Denis & Zimmer 1992; Kosslyn et al. 1978). Post-experimental questionnaires also ask participants to say whether they felt that they have followed the instructions, and any participants who declare that they have not complied with the instructions (in particular, those who have deviated from straight line scanning) are excluded from the analyses.

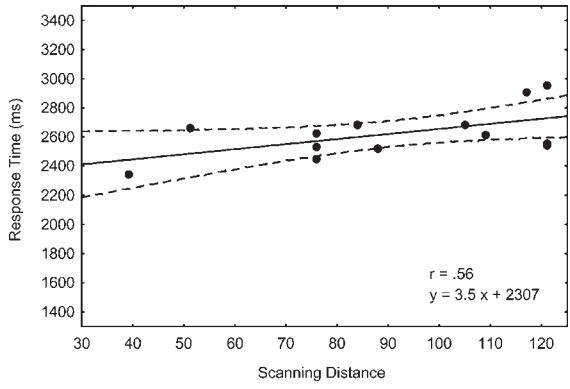
This is a good, rigorous method. However, once the basic data are established using this method, one is left wondering whether they would be confirmed in situations where the route being scanned itself deviates from linearity. In particular, in the type of experiment performed by Denis and Cocude, one can imagine a participant invited to perform image scanning between, say, the harbor and the lighthouse, and then immediately from the lighthouse to the beach. Would the participant scan along the two interconnected segments in a single (additive) scanning process? Would the two individual scanning times, i.e. from the harbor to the lighthouse and from the lighthouse to the beach, simply be added to each other in a single scanning episode? If this is the case, the total time would simply be the sum of the two individual scanning times.

Denis and Cocude (1995) conducted an experiment in which participants learned the island configuration used in their previous experiments and which was based on the same verbal description. The participants then carried out a scanning task in which their response times for all the individual inter-landmark distances were calculated, resulting in the computation of a time/distance correlation coefficient. They were then invited to perform the same type of scanning along the distances of two interconnected segments, which involved having to reorientate the scanning line at the end of the first segment, and correlation coefficients were calculated between response times and the two-segment distances. Would these latter coefficients exhibit the same pattern as those calculated during the scanning of single-segment distances?

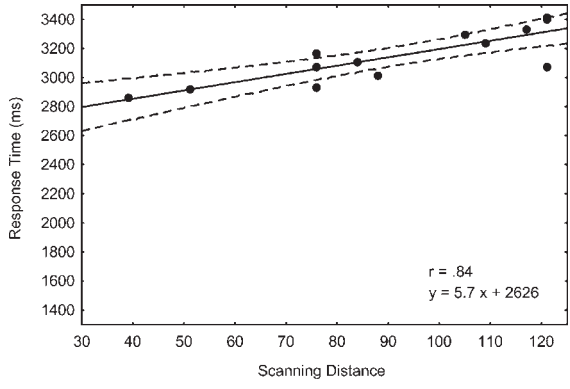
The results showed, first, that scanning times for single segments were positively correlated with distance, a confirmation of the classic finding (Figure 3a). In the two-segment scanning trials, this correlation was also found to be significant, although it was somewhat lower, reflecting more "noise" in the scanning process (Figure 3b). Not surprisingly, the average absolute times were longer for the second type of trials. However, what we were trying to find out was whether this situation reflected a purely additive phenomenon. For each pair of segments, we therefore added the times that had been taken for each of the two segments. These theoretical values are shown in Figure 3c. The analysis showed that the actual times taken for the two-segment scanning trials were in fact significantly shorter than these theoretical times. The meaning of this difference, however, remained unclear. Adding the individual times for two one-segment scanning episodes probably overestimated the total duration since the scanning process was triggered twice. The triggering time is reflected by the intercept of the regression lines at the ordinate; consequently, the value of the intercept is counted twice. For this reason, we made a further computation in which the intercept of every individual participant in the one-segment trials was subtracted from the sum of the two one-segment scanning times. This considerably reduced the theoretical times,




(a) One-segment scanning trials

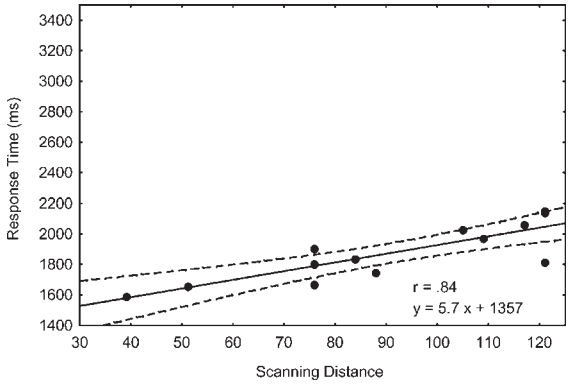



(b) Two-segment scanning trials




(c) Theoretical data for two-segment scanning

**Figure 3.** Response time as a function of the distance scanned: (a) one-segment scanning trials; (b) two-segment scanning trials; (c) theoretical data for two-segment scanning; (d) corrected theoretical data for two-segment scanning (Denis & Cocude 1995). In this figure, distances are expressed in terms of their ratios to the diameter of the circular island.




(d) Corrected theoretical data for two-segment scanning

**Figure 3.** (*continued*)

which in fact became even shorter than the actual two-segment scanning times (Figure 3d). We cannot therefore account for the two-segment scanning trials by simply adding two one-segment episodes.

One- and two-segment trials also differed in other respects. The value of the intercept was significantly higher for two-segment than for one-segment scanning. In theory, the intercept should not have been affected by the fact that more distances were included as experimental items. The fact that we did find this difference shows that the participants treated the two conditions not as variants of the same experimental situation, but as two different tasks. Obviously, the task involving a reorientation of the scanning process took longer to prepare. Another time indicator that was found to differ in the one- and two-segment trials was the slope of the regression line, which was significantly steeper in the one-segment than in the two-segment trials. This suggests that the strategy involved in one-segment scanning took longer to cover each further increment of distance.

The analysis of individual time measures revealed a complex pattern of correlations. Not surprisingly, there was a significant positive correlation between one- and two-segment scanning in terms of overall scanning times. People who were quick at scanning single segments were also quicker at scanning two interconnected segments. This is probably a non-specific effect, simply reflecting the fact that people who respond quickly in one task tend to do so in all tasks. Similarly, the slopes of the regression lines, although they had different absolute values, were positively correlated. In other words, the participants who needed more time for every new increment of scanned distance in one-segment trials also needed more time for each new increment in two-segment trials. Furthermore, the intercepts of the regression lines were not significantly correlated, which means that people who were fast at implementing the scanning process under standard conditions were not necessarily as quick at implementing two-segment scanning. This is further indication that the two-segment condition is not simply a quantitative variant of the one-segment one. Different strate-

gies are likely to be implemented, depending on whether the participants anticipate a single scanning shift or some reorientation during the scanning process. Lastly, individual time/distance correlations were statistically unrelated in the two conditions. This means that if a participant exhibits a strong time/distance correlation in one condition, this does not mean that he or she will demonstrate the same scanning performance in the other condition. Again, this absence of a significant relationship supports the concept that the two conditions call for different strategies (not necessarily different processes). Thus, the overall pattern of correlations offered a subtle combination of differences and similarities between the original condition and the two-segment variant examined here.

The data reported above result from variations on the strict version of the image scanning paradigm, involving two-dimensional configurations designed in the context of experimental setting. One may wish to consider more realistic environments, which involve paths that "naturally" depart from strict linearity. If people are asked to perform image scanning along more or less distorted routes, and if the size of non-straight distances is entered in the computations, should one still expect the same time/distance correlations to be demonstrated as before?

Quite a few studies have investigated the scanning of distances along "natural" routes, such as streets in urban environments. In one of these studies (Mellet, Bricogne, Tzourio-Mazoyer, Ghaëm, Petit, Zago, Etard, Berthoz, Mazoyer, & Denis 2000), the participants studied a city map, with seven landmarks represented in the form of colored dots. After learning the map, the participants were invited to follow mentally the street segments that connected two named dots. This implied that the participants would perform image scanning by following the specific pattern of the streets. Scanning was sometimes linear, when the two dots were located on the same street, and sometimes curved when they were located on two successive non-collinear segments. When a total of nine distinct distances were taken into account, a highly significant correlation coefficient was found between times and segment lengths.

In a further study (Mellet, Bricogne, Crivello, Mazoyer, Denis, & Tzourio-Mazoyer 2002), participants learned the verbal descriptions of two environments (a leisure park and a village). The two texts provided determinate descriptions, which referred to unambiguous topological relations, but no information was provided about the distances separating the landmarks. In particular, the relative lengths of the streets remained unspecified. As a consequence, the participants built representations of the same overall structure, but with various relative sizes. This was made evident in the sketch maps that the participants drew after the experiment. From these sketch maps, we computed the distances that each participant had inscribed in his or her representation between every pair of landmarks. Because there was a high degree of variability among participants as regards the distances separating the landmarks, distances were standardized as the ratio of their absolute values to the half-perimeter of the map drawn by each participant. Before drawing the map, the participants carried out an image scanning task. The specific feature, as in the previously mentioned experiment, was that scanning along the distance separating two landmarks sometimes departed from a straight line. For each

individual protocol, time/distance correlation coefficients were computed. The results showed that for most participants, the response times were positively correlated with the scanned distances.

The experiments reported above attest to the value of assessing the consistency of the scanning results when scanning follows non-linear routes. Evidence was obtained that a context in which individual variability occurs in the representation of distances is not detrimental to the demonstration of the scanning effect, but more importantly that the effect is robust enough to be confirmed in variants of the paradigm where scanning departs from straight lines. These findings further illustrate the wide range of situations involving the process.

## Conclusion

In their review of the image scanning literature, Denis and Kosslyn (1999) pointed out that this process has developed from being a single topic in itself, to being a tool than can be used to address other topics. Kosslyn's (1973; Kosslyn et al. 1978) initial research focused on the methods and the basic phenomenon, and provided evidence that scanning taps into the structural properties of the representations underlying the experience of imagery. Further experiments have been conducted to rule out alternative explanations and have confirmed the concept that mental images are indeed analog representations. The value of these further investigations has been to make researchers more confident about using image scanning for other scientific purposes. In this chapter, we have reviewed some of these purposes, in particular those that focus on the interface between language and imagery, on the transformational vs. attentional components of the scanning process, and on the new situations created when scanning involves more than a single straight segment. Image scanning is now more firmly established as a key process in mental imagery. It can provide a reliable basis for further investigation of how the human mind works.

## References

Borst, G., Kosslyn, S. M., & Denis, M. (in press). Different cognitive processes in two image scanning paradigms. *Memory and Cognition*.

Cooper, L. A., & Shepard, R. N. (1973). The time required to prepare for a rotated stimulus. *Memory and Cognition, 1*, 246–250.

Denis, M., & Carfantan, M. (1985). People's knowledge about images. *Cognition*, *20*, 49–60.

Denis, M., & Cocude, M. (1989). Scanning visual images generated from verbal descriptions. *European Journal of Cognitive Psychology*, *1*, 293–307.

Denis, M., & Cocude, M. (1992). Structural properties of visual images constructed from poorly or well-structured verbal descriptions. *Memory and Cognition*, *20*, 497–506.

Denis, M., & Cocude, M. (1995). Multi-segment image scanning. Unpublished study.

Denis, M., & Cocude, M. (1997). On the metric properties of visual images generated from verbal descriptions: Evidence for the robustness of the mental scanning effect. *European Journal of Cognitive Psychology*, *9*, 353–379.

Denis, M., Gonçalves, M.-R., & Memmi, D. (1995). Mental scanning of visual images generated from verbal descriptions: Towards a model of image accuracy. *Neuropsychologia*, *33*, 1511–1530.

Denis, M., & Kosslyn, S. M. (1999). Scanning visual mental images: A window on the mind. *Current Psychology of Cognition*, *18*, 409–465.

Denis, M., & Zimmer, H. D. (1992). Analog properties of cognitive maps constructed from verbal descriptions. *Psychological Research*, *54*, 286–298.

Dror, I. E., & Kosslyn, S. M. (1994). Mental imagery and aging. *Psychology and Aging*, *9*, 90–102.

Farah, M. J. (1985). Psychophysical evidence for a shared representational medium for mental images and percepts. *Journal of Experimental Psychology: General*, *114*, 91–103.

Finke, R. A., & Pinker, S. (1982). Spontaneous imagery scanning in mental extrapolation. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *8*, 142–147.

Finke, R. A., & Pinker, S. (1983). Directional scanning of remembered visual patterns. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *9*, 398–410.

Goldston, D. B., Hinrichs, J. V., & Richman, C. L. (1985). Subjects' expectations, individual variability, and the scanning of mental images. *Memory and Cognition*, *13*, 365–370.

Holt, R. R. (1964). Imagery: The return of the ostracized. *American Psychologist*, *19*, 254–264.

Intons-Peterson, M. J. (1983). Imagery paradigms: How vulnerable are they to experimenters' expectations? *Journal of Experimental Psychology: Human Perception and Performance*, *9*, 394–412.

Jolicoeur, P., & Kosslyn, S. M. (1985). Is time to scan visual images due to demand characteristics? *Memory and Cognition*, *13*, 320–332.

Kosslyn, S. M. (1973). Scanning visual images: Some structural implications. *Perception and Psychophysics*, *14*, 90–94.

Kosslyn, S. M. (1994). *Image and brain: The resolution of the imagery debate*. Cambridge, MA: The MIT Press.

Kosslyn, S. M., Ball, T. M., & Reiser, B. J. (1978). Visual images preserve metric spatial information: Evidence from studies of image scanning. *Journal of Experimental Psychology: Human Perception and Performance*, *4*, 47–60.

Kosslyn, S. M., Ganis, G., & Thompson, W. L. (2003). Mental imagery: Against the nihilistic hypothesis. *Trends in Cognitive Sciences, 7*, 109–112.

Kosslyn, S. M., Margolis, J. A., Barrett, A. M., Goldknopf, E. J., & Daly, P. F. (1990). Age differences in imagery abilities. *Child Development*, *61*, 995–1010.

Le Bihan, D., Turner, R., Zeffiro, T. A., Cuénod, C. A., Jezzard, P., & Bonnerot, V. (1993). Activation of human primary visual cortex during visual recall: A magnetic resonance imaging study. *Proceedings of the National Academy of Sciences of the United States of America*, *90*, 11802–11805.

Likert, R., & Quasha, W. H. (1941). *Revised Minnesota Paper Form Board (Series AA)*. New York: The Psychological Corporation.

Mellet, E., Bricogne, S., Crivello, F., Mazoyer, B., Denis, M., & Tzourio-Mazoyer, N. (2002). Neural basis of mental scanning of a topographic representation built from a text. *Cerebral Cortex*, *12*, 1322–1330.

Mellet, E., Bricogne, S., Tzourio-Mazoyer, N., Ghaëm, O., Petit, L., Zago, L., Etard, O., Berthoz, A., Mazoyer, B., & Denis, M. (2000). Neural correlates of topographic mental exploration: The impact of route versus survey perspective learning. *NeuroImage*, *12*, 588–600.

Mellet, E., Tzourio-Mazoyer, N., Bricogne, S., Mazoyer, B., Kosslyn, S. M., & Denis, M. (2000). Functional anatomy of high-resolution visual mental imagery. *Journal of Cognitive Neuroscience*, *12*, 98–109.

Mitchell, D. B., & Richman, C. L. (1980). Confirmed reservations: Mental travel. *Journal of Experimental Psychology: Human Perception and Performance*, *6*, 58–66.

Pinker, S., Choate, P. A., & Finke, R. A. (1984). Mental extrapolation in patterns constructed from memory. *Memory and Cognition*, *12*, 207–218.

Pylyshyn, Z. W. (1973). What the mind's eye tells the mind's brain: A critique of mental imagery. *Psychological Bulletin*, *80*, 1–24.

Pylyshyn, Z. W. (1981). The imagery debate: Analogue media versus tacit knowledge. *Psychological Review*, *88*, 16–45.

Pylyshyn, Z. W. (2002). Mental imagery: In search of a theory. *Behavioural and Brain Sciences, 24*, 157–237.

Reed, S. K., Hock, H. S., & Lockhead, G. R. (1983). Tacit knowledge and the effect of pattern configuration on mental scanning. *Memory and Cognition*, *11*, 137–143.

Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology, 12*, 97–136.

Vinacke, W. E. (1952). *The psychology of thinking*. New York: McGraw-Hill.

CHAPTER 1.5

# The use of transcranial magnetic stimulation in spatial cognition

Massimiliano Oliveri, Giacomo Koch, Sara Torriero, and Carlo Caltagirone

## Introduction

The study of selective disorders of spatial cognition such as the unilateral neglect syndrome can help to characterize the specific forms of neural activity that underlie our phenomenological consciousness, either in terms of the dynamic properties and topographic distribution or of the temporal order of succession of this neural activity.

The power of transcranial magnetic stimulation (TMS) to disrupt and modulate the neural activity in focal brain regions has provided researchers in this field a promising tool to empirically test specific neuropsychological models and constructs of spatial cognition and of its deficits (Walsh & Cowey 1998).

We will review a series of studies, which exemplify three of the major potential contributions of TMS to the study of spatial cognition: the transient disruption of focal cortical activity to establish the causal role and the timing of the contribution of a given cortical region in a behavior; the application of TMS to the study of functional brain connectivity; the application of TMS to human patients with contralesional space perception deficits to examine the compensatory cortical plasticity that occurs in response to a lesion.

## TMS studies of spatial extinction

Among the multiple deficits of perception and exploratory behavior that constitute the neglect syndrome, extinction of contralesional sensory stimuli is a cardinal sign indicating an attentional disorder (Bisiach & Vallar 2000). Patients with extinction can perceive a single contralesional stimulus but are unaware of the same stimulus when another is presented simultaneously on the ipsilesional side. Extinction, like neglect, is more frequent after right hemisphere damage (Vallar et al. 1994) and it has been interpreted as the result of a pathological attentional bias toward the right space, due

to the disinhibition of the healthy (i.e. left) hemisphere following the release of the reciprocal inhibition from the affected one (Kinsbourne 1977, 1994).

In this field, a group of studies used TMS to transiently disrupt the cortical activity of focal brain areas in normal subjects in order to replicate the effects of neurological lesions. The first demonstration of attentional, "extinction-like", effects of TMS was provided by Pascual-Leone et al. (1994), applying repetitive TMS (rTMS) trains at 25 Hz frequencies over parietal, occipital and temporal cortices during a visual attentional task. The main results showed that rTMS to the right and left parietal cortices induced selective extinction of contralateral visual stimuli during simultaneous double stimulation. By contrast, rTMS of the occipital cortex interfered with detection of contralateral visual stimuli both in single and bilateral presentation modalities.

In the tactile domain, using the same "virtual lesion" approach by applying TMS to the somatosensory cortex, Cohen et al. (1991) showed that TMS could induce suppression of perception of a threshold stimulus to the contralateral hand.

Subsequent studies have looked at the role of interhemispheric interactions in tactile attention. Seyal et al. (1995) tested the theory that extinction reflects a pathological orienting of attention toward the right side in a group of healthy subjects carrying out a tactile detection task with the thumb of the hand ipsilateral to the site of TMS (right). Single-pulse TMS delivered to the right parietal cortex 50 ms prior to the delivery of the electrical stimulus to the thumb resulted in increased sensitivity to cutaneous stimulation compared to baseline or frontal TMS trials. These findings were interpreted as the result of a TMS-induced transient disruption of the ipsilateral parietal cortex, resulting in disinhibition of the contralateral (i.e. left) parietal cortex during the sensory discrimination task. This study provides an elegant example of how the effects of TMS are not limited to the target site but involve other anatomically correlated regions, even of the contralateral hemisphere (Ilmoniemi et al. 1997).

Another example of how TMS can provide chronometric information to the causal role of parietal and frontal cortices to tactile attention tasks is a study of Oliveri et al. (1999a). They used single-pulse TMS of the left/right parietal and frontal cortices during unimanual or bimanual tactile discrimination tasks. The main results showed that TMS of the right parietal cortex interfered with the detection not only of contralateral but also of ipsilateral stimuli. These effects were mainly evident during bimanual discrimination tasks, thus reproducing a contralateral or ipsilateral tactile extinction. Regarding the timing of the effects, the contribution of the right parietal cortex was critical between 20 and 40 ms after tactile stimulation, suggesting the involvement of late cortical events for both contralateral and ipsilateral space attention mechanisms. This pattern of time-effects can also explain the conflicting conclusions about ipsilateral sensory processing between this study and that of Seyal et al. (1995). In fact, it is conceivable that the processing of ipsilateral sensory stimuli can be facilitated via transcallosal effects only provided that TMS is delivered before the sensory stimuli, or that its effects last enough to produce contralateral hemisphere disinhibition. By contrast, when TMS is delivered after sensory stimulation, its effects

could appear too late to allow expression of a disinhibition effect, and the colliding suppression effects on ipsilateral somatosensory ascending volleys are prevalent.

In addition to disrupt cortical function, TMS can be used to modulate the excitability of a specific cortical region and even to facilitate task performance. Studies using a paired-pulse protocol (Kujirai et al. 1993) allowed detailed investigations of intracortical excitatory and inhibitory interactions in the human motor cortex. In this protocol, a TMS pulse delivered at subthreshold level to elicit a motor evoked potential (MEP) influences the response to a subsequent suprathreshold TMS pulse. Depending on the interstimulus interval (ISI), the effect of the first conditioning pulse may be either inhibitory (short ISIs of 1–4 ms) or excitatory (longer ISIs of 7–15 ms). This method allows to study selective neurophysiological changes in the motor cortex in physiological as well as in pathological conditions (Chen et al. 1998; Liepert et al. 2000; Ziemann et al. 1996).

Mechanisms underlying the neurophysiological counterparts of perceptual processes have been more difficult to investigate, especially because the dependent measures based on subjects' reports are often variable and thus not easy to quantify and control. The first attempt to use paired-TMS in this direction is provided by a study of Oliveri et al. (2000a), in which paired-TMS was applied over the right posterior parietal cortex to investigate the presence of a pattern of excitatory/inhibitory interactions during tactile perceptual tasks in healthy subjects. Fifteen healthy volunteers performed a tactile discrimination task from the left thumb. Electrical stimuli were followed after 30 ms by paired-TMS pulses, with a conditioning stimulus (70% of motor threshold) followed at various interstimulus intervals (ISI: 1, 3, 5, 10, 15 ms) by a suprathreshold (130% of motor threshold) stimulus. The main results showed a pattern of excitatory and inhibitory interactions during the tactile perceptual process: paired-TMS pulses disrupted tactile detection (as compared to single-pulse TMS alone) when delivered 1 ms apart, and facilitated it when delivered 5 ms apart. These findings provide the first example of selective modulation of cortical excitability by paired-TMS outside motor areas.

In a recent study (Koch et al. 2005) these findings were replicated in the visual domain. When applied at an interval of 150 ms from the presentation of threshold unilateral or bilateral visual dots, paired-TMS of the right posterior parietal cortex with ISI of 3 ms interfered with contralateral visual perception compared with single-pulse TMS; on the other hand, paired-TMS with ISI of 5 ms facilitated contralateral visual perception compared with single-pulse TMS.

These findings argue for the existence of a supramodal pattern of excitatory and inhibitory interactions in the right posterior parietal cortex during spatial attentional tasks. An intriguing question for both basic and clinical research in this field is whether it is possible to induce lasting changes in spatial attentional abilities using TMS. Future studies could investigate the presence of specific alterations of these interactions in patients with sensory attentional disorders. We will address this topic in the following section of the chapter.

### Suppression of extinction with TMS in patients with unilateral brain damage

The role of interhemispheric interactions in spatial attention can be explored by applying TMS to patients with extinction or neglect disorders, therefore analyzing the compensatory cortical plasticity that occurs in response to a lesion. An example of this approach is a study in which single-pulse TMS was applied over the unaffected hemisphere of right- (RBD) and left-brain-damaged (LBD) patients, during unimanual and bimanual tactile discrimination tasks (Oliveri et al. 1999b). TMS of the left frontal cortex at 110% of motor threshold intensity significantly reduced contralesional extinction rates during bimanual stimulation in RBD group, while it was ineffective in the LBD group, as well as during unimanual stimulation. This work represents the first example of the application of TMS in human patients to improve a cognitive function. The results show that, as in the animal models of neglect (Lomber & Payne 1996), transient disruption of one hemisphere restores the distribution of attention to the contralesional side of space, thereby improving neglect phenomena. These findings support the model of the hemispheric imbalance, implying a disinhibition of the healthy hemisphere as a possible physiological basis of the right hyperattention in the neglect syndrome. Moreover, the findings extend previous observations about hemispheric asymmetries in the processing of somatosensory stimuli. It is also worth noting that only contralateral extinctions, primarily produced by deficits at the attentional level, were influenced by left hemisphere TMS, whereas the perception of contralesional unimanual stimuli was not influenced. This suggests that the contralateral deficits ameliorated by TMS-disruption of the healthy hemisphere have an attentional component.

A further step in this direction was the direct demonstration of an imbalance of excitatory/inhibitory interactions in the unaffected hemisphere of brain-damaged patients in trials with extinction of contralesional stimuli. Oliveri et al. (2000b) showed that improvement of extinction is maximized when paired-TMS pulses with ISIs that selectively enhance intracortical inhibitory mechanisms are applied over the unaffected hemisphere. The authors applied paired-TMS with ISIs known to target inhibitory (1 ms) or excitatory (10 ms) interneurons over the left parietal and frontal cortex in eight RBD patients with tactile extinction, during bimanual tactile discrimination tasks. The aim of the study was to combine the interfering mechanism of action of single-pulse TMS with distinct facilitatory/inhibitory effects on task performance due to the modulatory actions of the preceding conditioning stimulus. In fact, paired-TMS had distinct effects on contralesional extinction depending on the ISI and on the time of application: at the ISI of 1 ms, there was an improvement in extinction rate greater than that induced by single-pulse TMS; at the ISI of 10 ms there was a worsening of extinction, with a complete reversal of the effects of single-pulse TMS. Moreover, TMS effects were different in the parietal vs. frontal cortex depending on the time of TMS application: the effect on parietal cortex appeared significantly earlier (20–30 ms after tactile stimulation) than the effect on the frontal cortex, reaching its maximum

40 ms after tactile stimulation, as already demonstrated in the previous study (Oliveri et al. 1999b).

These results provide an example of how TMS can also be useful to test the chronometry of spatial attention, thanks to its time-resolution beyond the power of neuroimaging studies. Moreover, the findings confirm that the ability to activate intracortical inhibitory and excitatory circuits extend outside of the motor cortex, suggesting the possibility to selectively modulate the excitability disorders underlying higher cognitive functions.

At this aim, in a study using paired-TMS, Oliveri et al. (2002) have tested the hypothesis that the pattern of inhibitory/excitatory interactions sub-serving right tactile perception is dynamically altered in the unaffected (left) parietal cortex of RBD extinction patients. The rationale behind the study was that the relative hyper-activation of the left hemisphere would be selectively evident during bimanual stimulation, due to the imbalanced inter-hemispheric competition for attention resources, which is selectively present in this stimulation condition. The authors analyzed the effects of paired-TMS pulses, delivered at 1 ms ISI over the left parietal cortex, on right (i.e. ipsilesional) tactile detection, comparing the patients' performance with that of a control group of healthy subjects. The critical comparison was between the TMS-effects on right tactile detection during unimanual right (a non-extinction condition) vs. bimanual (when contralesional extinction emerged) stimulation tasks.

The paradigm of paired-TMS consisted of a subthreshold conditioning stimulus (CS) followed by a suprathreshold test stimulus (TS) at 1 ms ISI. The CS intensity was 70% of motor threshold, while the TS intensity was 130% of motor threshold. The TS was delivered at 30 ms delay following the onset of the tactile stimulus.

Single-pulse TMS to the left parietal cortex similarly disrupts right tactile perception in both patients and controls in either unimanual or bimanual detection tasks. The effects of paired-TMS with 1 ms ISI on right tactile perception are different in RBD patients vs. controls depending on the stimulation condition (i.e. unimanual vs. bimanual). In the control subjects, paired-TMS disrupts right tactile perception more than single-pulse TMS during both unimanual and bimanual stimulation, as previously demonstrated (Oliveri et al. 2000); in RBD patients, the interfering effect of paired-TMS on right perception is not more present during bimanual stimulation, and it is even reversed in sign. On the other hand, when patients are tested with unimanual right stimulation, paired-TMS to the left parietal cortex has the same disrupting effect as in normal subjects.

In addition, the results confirm previous findings (Oliveri et al. 1999b, 2000b), showing that both single-pulse and paired-TMS of the left (undamaged) hemisphere ameliorate left tactile extinctions of RBD patients, the effect of paired-TMS with 1 ms ISI being significantly greater than that of single-pulse TMS. These findings illustrate how the dysfunction of a specific pattern of neural activity can be responsible for the selective lack of awareness of personal space in humans.

Interestingly, the basic mechanism of disruption of contralateral tactile perception by single-pulse TMS is intact in RBD patients during both unimanual and bimanual

stimulation tasks. What it is altered in the left parietal cortex of RBD patients is the interaction between conditioning and test magnetic shocks, which, by analogy with the motor cortex, probably reflects the excitability of intrinsic interneuronal GABAergic and glutamatergic circuits. However, it is worth noting that any inference of cortical excitation and inhibition starting from behavioral data is speculative at present. Data from the motor cortex suggest that inhibition and facilitation are generated by cortical elements, such as cortico-cortical connections, oriented parallel to the surface of the brain. The activation of such fibers by CS during paired-TMS induces release of glutamate, which activates both excitatory and inhibitory interneurons, leading to local increases in cerebral blood flow (CBF), as detected with neuroimaging recordings. Consistent with these data, a recent study using Positron Emission Tomography showed an increase of CBF with paired-TMS at both inhibitory and excitatory ISIs between CS and TS (Strafella & Paus 2001). By extension, one can speculate that a reduced intracortical inhibition is likely to determine a reduced metabolic activation, as studied with functional magnetic resonance imaging (fMRI), in the corresponding cerebral regions. In other words, the lack of inhibitory effects of paired-TMS in the left parietal cortex of RBD patients during bimanual stimulation could represent the physiological counterpart of the reduced activity of the left hemisphere observed with fMRI or event-related-potentials during extinction, as compared with non-extinction, conditions (Marzi et al. 2000; Rees et al. 2001; Vuilleumier et al. 2001).

## TMS studies of visual spatial neglect

A number of studies have demonstrated that TMS can be useful not only in the study of extinction but also of visual neglect. The studies that reversibly interfered with the activity of posterior parietal cortical areas in humans and animals have reproduced deficits similar to those reported by patients with contralesional neglect (Chambers et al. 2004a; Hilgetag et al. 2001; Muri et al. 2002; Rushworth et al. 2001; Wardak et al. 2004).

One of the most common ways to test visual neglect is the line bisection task, in which the subjects are asked to mark the center of a line, or the Landmark task, in which the subjects are asked to judge the relative length of the two segments of pre-bisected lines (Harvey & Milner 1995).

Fierro et al. (2000) first tested the hypothesis that parietal rTMS can induce a transitory visuospatial neglect in healthy subjects, by using a modified version of the Landmark task. They applied rTMS trains of 10 stimuli at 25 Hz over right or left posterior parietal cortices of 11 normal subjects performing a visuo-spatial task, requiring judgments about the symmetry of prebisected lines. Visual stimuli consisted of symmetrically or asymmetrically (right-elongated or left-elongated) transected lines, tachistoscopically presented for 50 ms on a computer monitor. Right parietal rTMS induced a significant rightward attentional bias in symmetry judgments as compared with basal and sham rTMS conditions, counteracting a physiological leftward bias,

described in the literature as pseudoneglect (Jewell, McCourt 2000). These findings provide the first evidence of a (relative) contralateral neglect induced by a transitory "virtual" lesion of the right parietal cortex in healthy subjects. The results are in good accordance with the notion that the right hemisphere contains representations of both hemispaces and therefore its lesions are most responsible for space perception deficits. In addition, together with the results of Pascual-Leone et al. (1994), showing a transient visual extinction after both right and left parietal rTMS, they support the idea of non-identical anatomo-functional mechanisms underlying neglect and visual extinction (Vallar et al. 1994).

Using a similar paradigm, Bjoertomt et al. (2002) applied rTMS over the right posterior parietal cortex, the right and left dorsal occipital cortex and the right ventral occipital cortex in the attempt to disentangle the role of these cortical areas in the perception of near vs. far space. rTMS of the parietal cortex induced a significant shift to the right in the perceived midpoint for lines located in the near space, whereas rTMS of the right ventral occipital lobe interfered with bisection judgments of lines located in the far space. These results reproduce in healthy subjects the dissociation between neglect in near and far space that has been described in patients with different right hemisphere lesions (Halligan & Marshall 1991). This dissociation supports the hypothesis that there is a dorsal/near – ventral/far space segregation of processing in the visual system reflecting the behavioral goals of the two visual streams.

Another study has explored the effects of rTMS-trains delivered over the right parietal and frontal cortices on line-bisection judgments, in the attempt to disambiguate perceptual and response factors in the visuospatial impairment due to rTMS (Brighina et al. 2002). One prevalent view suggests prevalence of perceptual-related factors in neglect following parietal damage and of motor-related factors in neglect following frontal damage (Bisiach et al. 1990). The authors have employed a task of judgment of asymmetrically prebisected lines, requiring subjects to make a binary forced-choice decision ("right" / "left") according to two different response types: A and B. With response type A, subjects had to name the side of the longer segment, and with response type B the side of the shorter segment of the prebisected line. The authors have then evaluated separately the perceptual component (tendency to judge the left segment as shorter and the right segment as longer) and the response component (tendency to name the same side of the line in the two response conditions) of the attentional bias induced by rTMS. The main results showed that both parietal and frontal rTMS gave rise to left visuospatial neglect, which in both cases appeared to be mainly due to perceptual factors. These findings are in accord with those of a functional imaging study (Fink et al. 2000), showing that right prefrontal cortex and right posterior parietal cortex are activated in healthy subjects performing line bisection judgments. In addition, these results support those of another study (Bisiach et al. 1998), according to which a definitely response-related neglect is more likely to occur following lesions of sub-cortical structures, a target that appears outside the actual spatial resolution of TMS.

Similarly to what observed in TMS studies of extinction, TMS offers a good tool to investigate the chronometry of activation of parietal and frontal cortices during visuospatial attentional task. An example of this application is provided by a study in which single-pulse TMS was applied over right posterior parietal and frontal sites at various time intervals (150ms, 225ms, 300 ms) from the presentation of prebisected lines (Fierro et al. 2001). Subjects had to indicate which line segment appeared longer. There was a relative transitory rightward bias when parietal TMS was delivered 150 ms after visual stimulus presentation. Frontal stimulation induced no effect on visuospatial perception with the time intervals explored. These effects are concordant with data from ERP studies, suggesting that spatial attention exerts a gain control of sensory information flow in the visual pathways between 80 and 200 ms after stimulus onset, peaking at 150–160 ms over parietal areas (Hillyard et al. 1998).

*rTMS effects on spatial imagery*

rTMS has been recently employed also for testing the neural correlates of spatial imagery in both healthy subjects and patients with spatial neglect following right hemispheric damage.

Experimental paradigms using numbers are useful for testing the models of spatial imagery. The metaphor of "mental number line" suggests that low numbers are represented in the left-side and higher numbers in the right-side mental space (Dehaene et al. 1990). Consistent with this hypothesis, patients with right hemispheric damage and contralesional neglect are compromised in tasks of line bisection using numbers, with a rightward error similar to that observed in similar tasks using physical lines (Zorzi et al. 2001).

Oliveri et al. (2004) have investigated whether the numerical distance between two numbers could look different depending on the side of space where the task takes place. They asked a group of healthy subjects to judge whether the numerical distance between a middle number and two left- or right-sided outer numbers tachistoscopically presented on a computer monitor was bigger/smaller in the right or in the left side. The performance in baseline trials was compared with that in trials following rTMS of the right and left posterior parietal cortex. The task was thus performed in three main blocks, randomized across subjects: 1) baseline; 2) following right parietal rTMS; 3) following left parietal rTMS, separated by a 30- to 60-minute rest period in order to allow for the effects of rTMS to vanish out. Leftward/rightward biases were evaluated (leftward bias: left/equal response in the case of numerical distance bigger in the right side or left response in the case of bisectable triplets; rightward bias: right/equal response in the case of numerical distance bigger in the left side or right response in the case of bisectable triplets).

The results show that healthy subjects tend to overestimate the numerical distances in the left side of space. rTMS of the right posterior parietal cortex selectively counteracts this leftward bias, whereas left parietal rTMS does not affect subjects' performance. This behavior is indicative of a left-sided attentional bias for internally

generated spatial images (Heilman et al. 2004) that appears to be consistent with the pseudoneglect observed with external physical stimuli.

The reason for this left spatial bias is unknown, but several studies have shown that objects that receive more attention appear to have a greater magnitude than objects that receive less attention. In addition, each hemisphere attends primarily to body-centered contralateral hemispace. Thus, based on these magnitude-attention postulates, one explanation of pseudoneglect would be that when performing spatial tasks with either external or "internal" stimuli, subjects have to make spatial computations; because the right hemisphere is dominant for performing spatial computation, subjects activate their right hemisphere more than their left hemisphere. This asymmetric hemispheric activation then leads to a left-sided attentional bias with deviation to the left on a line bisection task. An alternative hypothesis suggests that the right hemisphere is dominant for attention and has a stronger attentional bias to left space than does the left hemisphere toward right space.

However, other investigators asked normal subjects to image half objects, and subjects were more likely to image the right than left side of the objects (Shuren et al. 1996). If attentional dominance were the only factor to induce a spatial imagery bias, these subjects should have imaged the left side of objects. Lesion (Bowers et al. 1991) and functional imaging studies (Farah 1989) have revealed that object imagery is mediated by the left hemisphere, and thus imaging objects may activate the left hemisphere, inducing a right-sided imagery bias, but spatial imagery may activate the right hemisphere and induce a left-sided bias. The finding by Oliveri et al. that repetitive transcranial magnetic stimulation of the right parietal lobe is associated with a reduction of representational (imagery) pseudoneglect provides further evidence to support the postulate that normal people have an leftward attentional bias for stimuli presented in their environment and images activated in their brain that is mediated by an attentionally dominant right parietal lobe.

*The anatomy of visual spatial neglect: Evidence from TMS*

Although the limited spatial resolution does not make TMS the best technique for addressing the topic of anatomical localization in cognitive neuroscience, recently this technique provided interesting findings on the anatomy of visual neglect. In fact, recent anatomo-clinical correlation studies have extended the right hemisphere lesion sites associated with left unilateral spatial neglect to the superior temporal gyrus (STG) (Karnath et al. 2001) and the right angular and parahippocampal gyri (Mort et al. 2003), in addition to the traditional posterior-inferior-parietal localization of the responsible lesion. A critical component for the anatomical correlates of the neglect syndrome is represented by the tasks used to assess neglect: these include target cancellation assessments (Karnath et al. 2001; Vallar et al. 1986), and batteries including both line bisection and target cancellation tests (Doricchi et al. 2003; Leibovitch et al. 1998; Mort et al. 2003). However, right-brain-damaged patients may show a rightward error in line bisection without other manifestations of spatial unilateral neglect, such as defective visuo-motor exploration, as assessed by cancellation tasks (Halligan

& Marshall 1992; Marshall & Halligan 1995). This dissociation suggests that the ability of setting the mid-point of a horizontal line may have a neural basis different, at least in part, from the brain regions involved in visuo-motor exploration. Taking into account these considerations, a recent rTMS study tested the contribution of posterior parietal vs. superior temporal cortex in tasks related to the two traditional neglect paradigms (Ellison et al. 2004). The main results revealed dissociation between the two brain regions depending on the cognitive task used. rTMS of the posterior parietal cortex disrupted performance in the landmark task, as previously demonstrated (Fierro et al. 2000), while no such effects were obtained with rTMS of the STG. On the other hand, rTMS of the STG selectively disrupted performance in a difficult exploratory search task through feature items though not for conjunction items.

These results suggest that the detection of neglect is likely to be highly dependent on the task used. Indeed, they show that patients with damage to the right posterior parietal cortex should manifest deficits in processing of both the landmark and hard conjunction tasks, while patients with right STG lesions should be more likely to have deficits in difficult exploratory single-feature search.

Another study (Chambers et al. 2004b) used rTMS to determine which cortical sub-regions in the right hemisphere control strategic attention in vision and touch. Neuroimaging evidence (Macaluso et al. 2002) suggests that spatial orienting is controlled by a single supramodal attention system in the posterior parietal cortex. Chambers et al. examined a group of healthy subjects with a covert orienting task, in which a central arrow predicted the location of a subsequent visual or somatosensory target. rTMS trains at 10 Hz frequency were delivered over different brain regions (angular gyrus, supramarginal gyrus, STG, superior parietal lobe) of the right hemisphere during either cue or target presentation.

Results show that rTMS of the supramarginal gyrus interfered with orienting to visual but not somatosensory targets. These findings do not support the hypothesis of a supramodal system controlling spatial attention, and are rather consistent with the view that spatial orienting is mediated by modality-specific processes that are activated in synchrony (as suggested by neuroimaging studies) but are anatomically independent.

### Suppression of visual neglect with TMS in patients with unilateral brain damage

Similarly to what reported in the section regarding extinction, some studies have documented a role for TMS in the recovery from visual neglect. Such studies are based on the role of interhemispheric influences in neglect behavior of brain-damaged patients. As already demonstrated in the TMS studies on tactile extinction (Oliveri et al. 1999b, 2000b), it is in fact presumable that an asymmetrical hemispheric competition, with a disinhibition of the unaffected hemisphere, plays a major role in determining neglect-like behavior. In this scenario, Oliveri et al. (2001) have applied rTMS over the unaffected hemisphere of 2 LBD and 5 RBD neglect patients during the performance

of prebisected lines length judgment task. They documented for the first time that in humans, as in the animal model (Lomber & Payne 1996), transient disruption of the healthy hemisphere might restore spatial attention and improve visuospatial neglect in both right- and left-brain-damaged patients. These results are promising regarding a possible application of rTMS for inducing long-lasting changes of cortical excitability, which could be useful for the rehabilitation of neglect patients.

This kind of application could be particularly true when using rTMS parameters able to induce long-term changes of cortical excitability. Brighina et al. (2003) have applied rTMS trains of 900 stimuli at 1 Hz frequency over the left parietal cortex of left neglect patients every other day for two consecutive weeks. This procedure is known to induce a depression of cortical excitability of the stimulated area that extends beyond the cessation of the rTMS train. In fact, rTMS induced a significant improvement of visuospatial performance that remained quite unchanged 15 days after the cessation of the rTMS "treatment" and was extended to a variety of tasks (landmark task, line bisection, clock drawing).

Although the limited number of patients tested does not allow drawing definite conclusions, these results leave room to the possibility that rTMS might represent a complementary rehabilitative treatment in visuospatial neglect, especially in the light of the recent demonstration of even longer effects on cortical excitability of the "theta burst stimulation" procedure, using high frequency (50 Hz) rTMS trains (Huang et al. 2004).

## Conclusions

We have reviewed a number of studies, using single-pulse, paired- and rTMS and different experimental paradigms, which show how this technique can be of fundamental importance in elucidating the neurophysiological mechanisms of space representation and of its deficits (i.e. extinction and neglect). In addition, some of these studies open the way to the possible application of TMS not only as a research method, but also as a tool for inducing long-lasting brain excitability changes, which can be useful for the treatment of various neurological disorders.

## References

Bisiach, E. & Vallar, G. (2000). Hemineglect in humans. In F. Boller & F. Grafman (Eds.), *Handbook of neuropsychology*, 1 (pp. 459–502). Amsterdam: Elsevier.

Bisiach, E., Geminiani, G., Berti, A., & Rusconi, M. L. (1990). Perceptual and premotor factors of unilateral neglect. *Neurology, 40,* 1278–1281.

Bisiach, E., Ricci, R., Lualdi, M., & Colombo, M. R. (1998). Perceptual and response bias in unilateral neglect: Two modified version of the Milner landmark task. *Brain and Cognition, 37,* 369–386.

Bowers, D., Blonder, L. X., Feinberg, T., & Heilman, K. M. (1991). Differential impact of right and left hemisphere lesions on facial emotion and object imagery. *Brain, 114,* 2593–2609.

Brighina, F., Bisiach, E., Piazza, A., Oliveri, M., La Bua, V., Daniele, O., & Fierro, B. (2002). Perceptual and response bias in visuospatial neglect due to frontal and parietal repetitive transcranial magnetic stimulation in normal subjects. *Neuroreport, 13* (18), 2571–2575.

Brighina, F., Bisiach, E., Oliveri, M., Piazza, A., La Bua, V., Daniele, O., & Fierro, B. (2003). 1 Hz repetitive transcranial magnetic stimulation of the unaffected hemisphere ameliorates contralesional visuospatial neglect in humans. *Neurosci Lett, 336,* 131–133.

Bjoertomt, O. Cowey, A., & V. Walsh (2002). Spatial neglect in near and far space investigated by repetitive transcranial magnetic stimulation. *Brain, 125,* 2012–2022.

Chambers, C. D., Payne, J. M., Stokes, M. G., & J. B. Mattingley (2004a). Fast and slow parietal pathways mediate spatial attention. *Nat Neurosci, 7,* 217–218.

Chambers, C. D., Stokes, M. G., & Mattingley, J. B. (2004b). Supramodal control of spatial attention in parietal cortex. *Neuron, 44,* 925–930.

Chen, R., Tam, A., Butefisch, C., Corwell, B., Ziemann, U., Rothwell, J. C., & L. Cohen (1998). Intracortical inhibition and facilitation in different representations of the human motor cortex. *Journal of Neurophysiology, 80,* 2870–2881.

Cohen, L. G., Bandinelli, S., Sato, S., Kufta, C., & Hallett, M. (1991). Attenuation in detection of somatosensory stimuli by transcranial magnetic stimulation. *Electroencephalogr Clin Neurophysiol, 81*, 366–376.

Dehaene, S., Dupoux, E., & Mehler, J. (1990). Is numerical comparison digital? Analogical and symbolic effects in two-digit number comparison. *J ExpPsychol Hum Percept Perform, 16,* 626–641.

Doricchi, F., & Tomaiuolo, F. (2003). The anatomy of neglect without hemianopia: A key role for parietal-frontal disconnection? *Neuroreport, 14,* 2239–2243.

Ellison, A., Schindler, I., Pattison, L. L. & A. D. Milner (2004). An exploration of the role of the superior temporal gyrus in visual search and spatial perception. *Brain, 127,* 2307–2315.

Farah, M. J. (1989). The neural basis of mental imagery. *Trends Neurosci, 12,* 395–399.

Fierro, B., Brighina, F., Oliveri, M., Piazza, A., La Bua, V., Buffa, D., & Bisiach, E. (2000). Contralateral neglect induced by right posterior parietal rTMS in healthy subjects. *NeuroReport, 11,* 1519–1521.

Fierro, B., Brighina, F., Piazza, A., Oliveri, M. & E. Bisiach (2001). Timing of right parietal and frontal cortex activity in visuo-spatial perception: A TMS study in normal individuals. *Neuroreport, 12* (11), 2605–2607.

Fink, G. R., Marshall, J. C., Shah, N. J., Weiss, P. H., Halligan, P. W., Grosse-Ruyken, M., Ziemons, K., Zilles, K., & H. J. Freund (2000). Line bisection judgments implicate right parietal cortex and cerebellum as assessed by fMRI. *Neurology, 54,* 1324–1331.

Halligan, P. W., & Marshall, J. C. (1991). Left neglect for near but not far spacein man. *Nature, 350,* 498–500.

Halligan, P. W., & Marshall, J. C. (1992). Left visuo-spatial neglect: A meaningless entity? *Cortex, 28,* 525–535.

Harvey, M., & D. Milner (1995). An investigation of hemispatial neglect using the landmark task. *Brain and Cognition, 27,* 59–78.

Heilman, K. M., Jeong, Y., & Finney, G. R. (2004). Spatial cognition (editorial). *Neurology, 63,* 1994–1996.

Hilgetag, C. C., Theoret, H., & Pascual-Leone, A. (2001). Enhanced visual spatial attention ipsilateral to rTMS-induced 'virtual lesion' of human parietal cortex. *Nat Neurosci, 4,* 953–957.

Hillyard, S. A., & Anllo-Vento, L. (1998). Event-related brain potentials in the study of visual selective attention. *Proc. Natl. Acad. Sci. USA, 95,* 781–787.

Huang, Y. Z., Edwards, M. J., Rounis, E., Bhatia, K. P., & Rothwell, J. C. (2004). Report Theta Burst Stimulation of the Human Motor Cortex. *Neuron, 45,* 201–206.

Ilmoniemi, R. J., Virtanen, J., Ruohonen, J., Karhu, J., Aronen, H. J., Naatanen, R., Katila, T. (1997). Neuronal responses to magnetic stimulation reveal cortical reactivity and connectivity. *Neuroreport, 8,* 3537–3540.

Karnath, H-O., Ferber, S., & Himmelbach, M. (2001). Spatial awareness is a function of the temporal not the posterior parietal lobe. *Nature, 411,* 950–953.

Kinsbourne, M. (1977). Hemi-neglect and hemisphere rivalry. In E. A. Weinstein & R. P. Friedland (Eds.), *Hemi-inattention and hemisphere specialization* (Adv Neurol 18) (pp. 41–49). New York: Raven Press.

Kinsbourne, M. (1994). Mechanisms of neglect: Implications for rehabilitation. *Neuropsychol Rehabil*, *4*, 151–153.

Koch, G., Oliveri, M., Torriero, S., & Caltagirone, C. (2005). Modulation of excitatory and inhibitory circuits for visual awareness in the human right parietal cortex. *Exp Brain Res, 160* (4), 510–516.

Kujirai, T., Caramia, M. D., Rothwell, J. C., Day, B. L., Thompson, P. D., Ferbert, A., Wroe, S., Asselman, P., & Marsden, C. D. (1993). Corticocortical inhibition in human motor cortex *The Journal of Physiol, 471,* 501–519.

Leibovitch, F. S., Black, S. E., Caldwell, C. B., Ebert, P. L., Ehrlich, L. E., & Szalai, J. P. (1998). Brain-behavior correlations in hemispatial neglect using CT and SPECT: The Sunnybrook Stroke Study. *Neurology, 50,* 901–908.

Liepert, J., Storch, P., Fritsch, A., & C. Weiller (2000). Motor cortex disinhibition in acute stroke. *Clinical Neurophysiology, 111,* 671–676.

Lomber, S. G., & Payne, B. R. (1996). Removal of two halves restores the whole: Reversal of visual hemineglect during bilateral cortical or collicular inactivation in the cat. *Vis Neurosci, 13,* 1143–1156.

Macaluso, E., Frith, C., & Driver, J. (2002). Supramodal effects of covert spatial orienting triggered by visual or tactile events. *J Cogn Neurosci*, *14,* 398–401.

Marshall, J. C., & Halligan, P. W. (1995). Within- and between-task dissociations in visuo-spatial neglect: A case study. *Cortex, 31,* 367–376.

Marzi, C. A., Girelli, & M., Miniussi, C. et al. (2000). Electrophysiological correlates of conscious vision: Evidence from unilateral extinction. *J Cogn Neurosci, 12* (5), 869–877.

Mort, D. J., Malhotra, P., Mannan, S. K., Rorden, C., Pambakian, A., Kennard, C. et al. (2003). The anatomy of visual neglect. *Brain 126,* 1986–1997.

Muri, R. M., Buhler, R., Heinemann, D., Mosimann, U. P., Felbinger, J., Schlaepfer, T. E., & Hess, C. W. (2002). Hemispheric asymmetry in visuospatial attention assessed with transcranial magnetic stimulation. *Exp Brain Res 143,* 426–430.

Oliveri, M., Rossini, P. M., Pasqualetti, P., Traversa, R., Cicinelli, P., Palmieri, M. G., Tomaiuolo, F. and Caltagirone, C. (1999a). Interhemispheric asymmetries in the perception of unimanual and bimanual cutaneous stimuli. A study using transcranial magnetic stimulation. *Brain 122,* 1721–1729.

Oliveri, M., Rossini, P. M., Traversa, R., Cicinelli, P., Filippi, M. M., Pasqualetti, P., Tomaiuolo, F. and Caltagirone, C. (1999b). Left frontal transcranial magnetic stimulation reduces contralesional extinction in patients with unilateral right brain damage. *Brain 122,* 1731–1739.

Oliveri, M., Caltagirone, C., Filippi, M. M., Traversa, R., Cicinelli, P., Pasqualetti, P., & Rossini, P. M. (2000a). Paired-transcranial magnetic stimulation protocols reveal a pattern of inhibition and facilitation in the human parietal cortex. *Journal of Physiology, 529,* 461–468.

Oliveri, M., Rossini, P. M., Filippi, M. M., Traversa, R., Cicinelli, P., Palmieri, M. G., Pasqualetti, P., & C. Caltagirone (2000b). Time-dependent activation of parieto-frontal networks for directing attention to tactile space. A study with paired transcranial magnetic stimulation pulses in right-brain-damaged patients with extinction. *Brain, 123,* 1939–1947.

Oliveri, M., Bisiach, E., Brighina, F., Piazza, A., La Bua, V., Buffa, D., & Fierro, B. (2001). rTMS of the unaffected hemisphere transiently reduces contralesional visuospatial hemineglect. *Neurology, 57* (7), 1338–1340.

Oliveri, M., Rossini, P. M., Filippi, M. M., Traversa, R., Cicinelli, P., & C. Caltagirone (2002). Specific forms of neural activity associated with tactile space awareness. *Neuroreport, 13* (8), 997–1001.

Oliveri, M., Rausei, V., Koch, G., Torriero, S., Turriziani, P., & Caltagirone, C. (2004). Overestimation of numerical distances in the left side of space. *Neurology, 63,* 2139–2141.

Pascual-Leone, A., Gomez-Tortosa, E., Grafman, J., Always, D., Nichelli, P., & Hallett, M. (1994). Induction of visual extinction by rapid-rate transcranial magnetic stimulation of parietal lobe. *Neurology, 44*, 494–498.

Rees, G., Wojciulik, E., & Clarke, K. et al. (2001). Unconscious activation of visual cortex in the damaged right hemisphere of a parietal patient with extinction. *Brain, 123,* 1624–1633.

Rushworth, M. F. S., Ellison, A., & V. Walsh (2001). Complementary localization and lateralization of orienting and motor attention. *Nat Neurosci, 4,* 656–661.

Seyal, M., Ro, T., & Rafal, R. (1995). Increased sensitivity to ipsilateral cutaneous stimuli following transcranial magnetic stimulation of the parietal lobe. *Ann Neurol, 38,* 264–267.

Shuren, J. E., Greer, D., & Heilman, K. M. (1996). The use of hemi-imagery for studying brain asymmetries in image generation. *Neuropsychologia 1996, 34,* 491–492.

Strafella, A. P., & T. Paus (2001). Cerebral blood flow changes induced by paired-pulse transcranial magnetic stimulation of the primary motor cortex. *J Neurophysiol, 85,* 2624–2629.

Vallar, G., & Perani, D. (1986). The anatomy of unilateral neglect after right hemisphere stroke lesions. A clinical CT/Scan correlation study in man. *Neuropsychologia, 24,* 609–622.

Vallar, G., Rusconi, M. L., Bignamini, L., Geminiani, G., & Perani, D. (1994). Anatomical correlates of visual and tactile extinction in humans: A clinical and CT scan study. *J Neurol Neurosurg Psych*, *57*, 464–470.

Jewell, G., & McCourt, M. E. (2000). Pseudo-neglect: A review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia. 38,* 93–110.

Vuilleumier, P., Sagiv, N., & Hazeltine, E. et al. (2001). Neural fate of seen and unseen faces in visuospatial neglect: A combined event-related functional MRI and event-related potential study. *Proc. Natl. Acad. Sci. USA, 98* (6), 3495–3500.

Walsh, V., & A. Cowey (1998). Magnetic stimulation studies of visual cognition. *Trends Cogn Sci, 2,* 103–110.

Wardak, C., Olivier, E., & Duhamel, J.-R. (2004). A deficit in covert attention after parietal cortex inactivation in the monkey. *Neuron, 42,* 501–508.

Zorzi, M., Priftis, K., & Umiltà, C. (2003). Brain damage: Neglect disrupts the mental number line. *Nature, 417,* 138–139.

Ziemann, U., Rothwell, J. C. & M. C. Ridding (1996). Interaction between intracortical inhibition and facilitation in human motor cortex. *Journal of Physiology, 496,* 873–881.

SECTION II

# Models and components of imagery and visuo-spatial processes

CHAPTER 2.1

# Neural bases and cognitive mechanisms of Human Spatial Memory

Panagiota Panagiotaki and Alain Berthoz

## Introduction

In the present chapter we discuss two distinct but interconnected subjects concerning the study of human spatial memory: a) the neural mechanisms subserving spatial memory tasks and b) the cognitive mechanisms encoding and retrieving sensory information received during a spatial experience such as navigation.

## Part A

*Neural bases of Spatial Memory: Neurophysiological and neuropsychological evidences*

Since Brenda Milner (1971) suggested the involvement of the hippocampal region and parts of the parietal cortex in the dynamic aspects of spatial memory, many studies demonstrated the importance of hippocampus for the processing and memorisation of multisensory information concerning a spatial experience.

The effort in understanding the neural basis of spatial orientation and the memory of routes has focused on the different cognitive strategies required for establishing relations between our body and the environment (Berthoz 2000).

Hippocampus is activated mainly by visual, olfactory, and acoustic inputs (Berthoz 2000). Moreover, the vestibular inputs provide substantial information for the creation of hippocampal spatial representations, in concert with the visual inputs (Stackman & Herbert 2002; Stackman et al. 2002). These types of sensory information are necessary for encoding the spatial experience, and then representing it cognitively in two ways; on one hand the egocentric – 'route' like – coding, where the point of reference is the observer himself, and on the other hand the allocentric coding or survey or mapping strategies used during tasks, in which humans mentally remember a path by mental navigation, where the reference point is external to the observer (Ghaem et al. 1997; Berthoz 2000).

According to the map theory of O'Keefe & Nadel (1978), hippocampus encodes spatial information in an allocentric cognitive map, which is necessary for the recognition of absolute locations in space. The hippocampal region can be activated in both types of tasks, egocentric and allocentric, based on the idea that hippocampus is responsible for encoding newly received spatial information both of an egocentric and allocentric representation. Once this information stored in the long-term memory, hippocampus is activated by the retrieval of the allocentric-stored pattern (Maguire et al. 1997; Burgess et al. 2001), while parahippocampus by the egocentric pattern (Maguire et al. 1997), especially by landmarks and spatial views (Maguire et al. 2001; Rosenbaum et al. 2004).

Hippocampal spatial activation is not bilaterally equally distributed. Studies on patients with selective hippocampal lesions, either on the right (r-H) or the left hemisphere (l-H), displayed proofs, in which only the r-H patients failed to perform spatial allocentric tasks (Parslow et al. 2005), while the l-H patients showed a performance similar to that of control subjects for allocentric tasks. Convergent to the latter data in PET scan and f-MRI scan present right hippocampal activation when survey strategy is involved (Mellet et al. 2000).

While hippocampal formation subserves the allocentric strategy, the parahippocampal formation is mostly involved in the egocentric encoding, based on the observer's point of view (routing) (Hartley et al. 2003). PET scan study (Ghaem et al. 1997) demonstrated that during recalling of landmarks a bilateral activation of the middle hippocampal regions, left inferior temporal gyrus, left hippocampal regions, precentral gyrus and posterior cingulate gyrus were observed. In case of a route recalling and subjects' movements along it, there was a bilateral activation of the dorsolateral cortex, posterior hippocampal areas, posterior cingulate gyrus, supplementary motor areas, right middle hippocampal areas, left precuneus, middle occipital gyrus, fusiform gyrus and lateral premotor area. When substracted between these two conditions the activated areas were reduced to left hippocampus, precuneus and insula. These results indicated an overlapping but also a separate activation of brain areas involved in the cartographic and static aspects of 'topographic' memory. Additionally, a bilateral activation of the entorhinal and parahippocampal cortex is observed during 'route-type' navigation (egocentric strategy). Yet, these areas are silent during a map exploration (allocentric strategy). This 'behaviour' agrees with the role of the parahippocampus in the topographical processes (Habib et Sirigu 1987). In other words, we observe a dissociation of the mechanisms used for the allocentric tasks (mapping) that would include mainly the right hippocampus, and the mechanisms subserving the egocentric tasks (routing) that would implicate the bilateral parahippocampal formation. Moreover, the results demonstrate an activation of the posterior cingulate gyrus during a task of mental navigation, but not during map exploring. A possible interpretation for this result would be that cingulate gyrus intervenes to the transformation of the mental simulation (imaging) in a proper route representation.

The multiple fibre projections from hippocampus to parahippocampal sulcus suggest the intense collaboration (effective connectivity) of these two areas on memory

aspects. Aguirre et al. (1996) supported the dynamic role of hippocampus together with the parahippocampus, during topographic encoding and recalling. This activation converged with the clinical image of topographical disorientation of patients with lesions to the parahippocampal cortex. Furthermore, the innovative method of recording neurons in the hippocampal and parahippocampal area of hippocampal epileptic patients (Ekstrom et al. 2003) showed that the hippocampal place cells responded on the view of spatial locations, while the parahippocampal cortex responded in the view of landmarks. It is important to underline that in this study, an activation of the wider area of frontal and temporal cortex was correlated with navigational goals; suggesting that the effect of 'navigational goal' was correlated with the firing of specific place-cells on humans, meaning that the presence of a goal in a spatial context may modulate the firing of specific place-cells.

The understanding of the contribution of hippocampus and the parahippocampal formation to spatial memory is not well established yet. In spite of the plethora of studies supporting, on one hand, the correlation between the allocentric strategy and hippocampus, and, on the other hand, the egocentric strategy and the parahippocampus, other works question this localization. In the case study of spatial disorientation due to a lesion on the right mediotemporooccipital lobe including the parahippocampal sulcus, a deficit of the allocentric representation and of visuospatial encoding and recalling was observed (Nyffeler et al. 2005). This result suggests that the parahippocampal area may subserve both egocentric and allocentric visual functions. It is, though, important to mention that these observations are based on a single case study with a lesion not perfectly localized. Nevertheless, an increased connectivity between left hippocampus and left parahippocampus was demonstrated during the recalling of memorized autobiographic episodes in healthy humans (Maguire et al. 2000).

Importantly, parahippocampus is activated bilaterally when coding large-scale environments or buildings; however, the activation is restricted to the right parahippocampal formation for their retrieving from the long-term memory (Maguire et al. 2001). Right parahippocampus is also activated in the recalling of familiar landmarks that are strongly related with a specific spatial context (Rosenbaum et al. 2004). Additionally, right parahippocampal area together with right posterior parietal and posteriodorsal medial parietal cortex are activated during the retrieving of spatial context (Burgess et al. 2001).

Despite the aforementioned works supporting the idea that parahippocampal cortex is the responsible area for the encoding and recognition of landmarks, there are other studies suggesting the activation of hippocampal formation in case of observation of landmarks during virtual reality (VR) experiments. Yet, these landmarks are used for the recognition of an encoded environment and for defining the subjects' orientation in it. This behavioral observation accords with the evidences from studies in rodents, where hippocampus is activated during the encoding of a location (Hartley et al. 2004).

From the above studies, we observe that a considerable ambiguity is raised on the matter of the precise role of hippocampal and parahippocampal cortex to spatial mem-

ory. A possible explanation for this ambiguity would be that these two areas present an important synergistic activity in the matter of spatial representation, as well as that there could be other cortical areas that may subserve the topographic encoding in alteration or in collaboration with the mediotemporal cortex (Redish & Touretzky 1997; Aguirre et al. 1996). Indeed, the parietal and frontal structures involved in "spatial neglect" are also found to be involved in the egocentric orientation tasks of subjective midline detection (Berthoz 2000).

The question on the precise role of hippocampus and parahippocampus in the human spatial memory is also extended on the issue of hemispheric laterality. Numerous studies give evidences of the bilateral activation of hippocampus for encoding allocentric information, and of parahippocampal sulcus for the encoding of the egocentric information, whereas the activation is limited in the right hemisphere when retrieving encoded spatial information (Burgess et al. 2001; Committeri et al. 2004; Ekstrom et al. 2003; Nyffeler et al. 2005). Yet, in other studies an important activation of the left hippocampus and parahippocampus is observed for the same spatial behaviour (Ghaem et al. 1997; Maguire et al. 2000; Pine et al. 2002).

A plausible interpretation to conciliate the aforementioned evidences was given by Lambrey et al. (2003). In an experiment performed in VR, healthy subjects, right Medial-Temporal Lobe (RMTL) patients, and Left Medial-Temporal Lobe (LMTL) patients had to navigate in a virtual maze, which contained a distinct object in every crossroad (chair, ladder, etc.). The pathway to follow was designated by green-coloured walls, while red-coloured walls indicated wrong directions. Subjects navigated five times in the maze and after each navigation were drawing the travelled path with their eyes closed and named the landmarks in the order they thought that they had appeared. The results showed that all subjects could recall the landmarks seen during navigation, but LMTL produced significantly more errors in their correct sequence compared to healthy subjects, while RMTL patients had an intermediate performance between the control group and LMTL. LTML patients had a relative worse performance comparing to control subjects in memorising the association between a seen landmark and the corresponding direction to take in the crossroad. The interpretation deriving from this study is that both right and left median-temporal lobes are involved in spatial memory but in two different ways: while right median-temporal lobe would subserve survey (allocentric) spatial encoding, the left median-temporal lobe would be essentially involved in route (egocentric) encoding. This hippocampal activation. The authors suggest that left median-temporal lobe would be involved in sequential aspects of encoding and recalling (associative learning, route memory), and the right median-temporal lobe would be correlated to inferential aspects of memory (spatial inference, survey spatial encoding).

Although hippocampus and parahippocampus are considered as essential neural structure for spatial memory, the contribution of the prefrontal area to spatial encoding is also of great importance. In the previous years, several studies mentioned the prefrontal cortex as a basic module of spatial memory despite the existence of many other works not confirming this opinion. The results of more recent neuro-imaging

studies (PET and fMRI) proposed that the activation of the prefrontal cortex is due to the process-specific functions (e.g. encoding, recognition, and recalling) (Leung et al. 2005; Makino et al. 2004) and not to the context-specific function (e.g. spatial memory vs. non-spatial memory). This idea comes in accordance with the model of working memory by Baddeley (1996), in which the prefrontal lobe is considered to subserve the central executive mechanism.

Nonetheless, the evidences of the latest studies assist us to understand not only the precise and distinct role of each brain region, such as hippocampus and parahippocampus, or cingulate gyrus, subserving the spatial memory, but also the cooperative and overlapping activation of these areas in complex spatial tasks (Kesner & Rogers 2004). For example, in the fMRI study of Committeri et al (2004), the neural correlates of three different types of spatial coding were compared. The different types were: viewer-centered, which allows an egocentric coding, object-centered and landmark-centered that both lead to an allocentric coding. The results of this study showed that the retrosplenial and ventromedial occipito-temporal cortex were involved in the landmark-centered condition and, particularly the ventrolateral occipito-temporal cortex was involved in the object-centered condition, whereas the egocentric coding (viewer-centered) activated mainly the dorsal stream and the connected frontal regions. This work demonstrated on one hand the distinct neural substrates activated for egocentric and allocentric tasks, and on the other hand the strong synergistic activity from different cortical areas in order to perform accurate spatial tasks in a complex environment: for egocentric tasks the activation of the parietal and frontal premotor areas, while for allocentric tasks the parietal-frontal, ventromedial occipito-temporal and retrosplenial regions. These networks are involved in the dynamic aspects of spatial memory, for which the term 'topokinetic memory' was proposed by Berthoz (1997).

In addition to neurophysiological and neuropsychological studies, cognitive and computational models are also engaged in the discussion about the activation of brain areas involved in spatial encoding and retrieval. Gerstner & Abbott (1997) proposed a computational model, where, during activation, hippocampal place cells created target-dependent maps indicating the direction towards a specific target in the represented environment. Another model of place cells of the hippocampal areas CA3-CA1 suggested the combination of egocentric and allocentric spatial information during navigation in order to build a uniform and fixed representation of the navigated environment (Arleo & Gerstner 2000). On the other hand, Burgess et al. (2001) proposed the modeling of neuronal populations from the medial temporal and parietal lobes. In this model the added element is the combination of episodic memory properties (real-life events) of egocentric character, activating the parietal part of the model, along with the allocentric spatial information retrieved from the long-term memory and activating the medial temporal part of the model.

Jacobs & Schenk (Jacobs 2003) suggested a cognitive model of the spatial properties of hippocampal formation. According to their Parallel Map Theory (PMT) different sub-areas of hippocampal formation process in two distinct ways the information

of cognitive mapping. PMT is based on the homologies of medial temporal region that modulate the spatial memory on reptiles and mammals. Instead of one cognitive map, we can find two components of the cognitive map, the 'bearing map' and the 'sketch map', that once integrated together, they can create a novel map, otherwise the integrated (cognitive) map. The bearing map derives from a multicoordinate grid map, while the sketch map is rather the representation of topographical data received from the memory of positions of single landmarks. In other words, the authors propose here the creation of a 'complete-cognitive' map modulated by diverse hippocampal structures, and which contains both allocentric (bearing map) and egocentric (sketch map) information. Nevertheless, for the present PMT is mainly based on evidences on mammals but not expanded on human evidences.

**Part B**

*Multisensory information during spatial navigation and spatial encoding of the traveled pathway* (Panagiotaki et al., under submission, preliminary account)
In Part A we described the current state of the art on neural bases subserving human spatial memory. In addition to the study of these neurophysiological mechanisms, it is important to investigate the processing of different types of sensory information encoded during a spatial experience. In the second part of the current chapter we discuss the issue of integration of different types of sensory inputs received during spatial navigation.

Sensory information (visual, vestibular, proprioceptive, somatosensory, auditive) information is necessary for spatial navigation on humans. In Part A, we discussed the involvement of specific brain regions to the encoding of visual and non visual information to spatial memory.

Visual inputs – and particularly optic flow – contribute to visual control of locomotion (Bakker et al. 1999; Warren et al. 2001), to postural control (Golomer et al. 1999; Israël et al. 1993), to body movement perception (Berthoz 1993; Farrell et al. 1998), as well as to distance estimation and coding visual landmark as reference points to navigation/into space (Spiers et al. 2001). The vestibular system is important for preserving a stable external image during locomotion due to the vestibular-ocular reflex (VOR) (Baloh & Halmagyi 1996: 16), and VOR's interaction with the visual inputs provides information for humans' position and movement in space especially in superior cerebral levels (Collewijn 1989a; Probst et al. 1985; Berthoz 1993). Vestibular, proprioceptive and somatosensory information interact together during active or passive navigation (Israël et al. 1997), as well as during body's orientation through space (Melvill Jones et al. 2000). Additionally, proprioceptive information is combined together with visual information for the coordination of movement in space (Gentilucci et al. 1994). Importantly, it is suggested that proprioceptive information has an important role to postural position and spatial orientation (Lackner 1988).

In some cases, only one type of the aforementioned information may be sufficient to spatial navigation. Nonetheless, several studies give evidence of the necessity of multisensory integration to pertain an optimal perception of the external world and of human's interaction with it. Moreover, studies on the issue of multisensory adaptation showed a calibration of sensory systems' coordination after introducing a sensory conflict. Sensory adaptation between visual and vestibular system (Viaud-Delmon et al. 1999; Siegler et al. 2000), as well as between somatosensory and visual system (Weber et al. 1998), or vestibular and somatosensory system (Gordon et al. 1995) has been reported in the goal of 'resolving' a sensory inconsistency of perceiving the external world during passive or active spatial navigation. Moreover, vestibulo-ocular adaptation might occur due to mechanisms of mental imagery in the absence of external cues (Melvill Jones et al. 1984); cognitive mechanisms like mental imagery could influence the allocentric perception of space, thus suggesting eventual top-down processes to multisensory interaction. Jointly, there are evidences of the importance of inter-individual differences in performance during sensory adaptation on humans (Ivanenko et al. 1998).

Nevertheless, it is not yet clear how all these different types of sensory information are combined together in order to produce the final consistent encoding and recall of the spatial experience. A hypothesis attempting to give answers on this matter is the 'multisensory integration' (van Beers et al. 1999; Telban, et al. 2001) according to which inputs from different sensory modalities are processed in a way to produce a 'mean' weighting encoded to spatial memory, thus providing a unique sensory input finally encoded for a particular spatial experience. However, recent studies support the hypothesis of 'selection of sensory information' instead of a sensory weighting during encoding (Lambrey et al. 2002). They demonstrated that information from different sensory modalities is encoded to spatial memory without been processed to a mean final encoded input, and the type of information recalled depended on the nature of each task (e.g. for designing a travelled path subjects were based more to their visual information, while for reproducing by their whole-body movement, they were based mainly on the proprioceptive information).

Further to these studies, we discuss here an experiment presenting results addressing a basic question in order to examine the integration of inputs of different sensory modalities; we examine whether the presence of a sensory conflict could influence the recall of a memorised travelled path in case of non-association of the conflict with the pathway's initial learning and encoding.

In other words, we are interested in understanding whether the different sensory inputs concerning a spatial navigation are encoded in a form of a mean output or each sensory input is memorised separately, but in relation with the other inputs in a spatial frame concerning the specific spatial experience. In order to give an answer to the above questions, we have set a paradigm of spatial navigation and memorisation in virtual reality. In our experiment, subjects navigated passively and memorised trajectories in a virtual environment, where we have introduced artificial sensory conflict between visual and non-visual information.



**Figure 1.** Views of three different virtual corridors used during the Experiment 1 and 2.

*Experimental set-up*

Participants were interacting with an immersive virtual environment by the use of a monocular Head mounted display (Kaiser Electro Optics' ProView™60, Carlsbad, CA).

An electromagnetic system (Flock of Birds, Burlington, VT) was measuring the subjects' head orientation on the horizontal plane. The head angular position was estimated by a movement tracker (Ascension Technology Corporation), and was sent to an image generator (O2, Silicon Graphics), which was transmitting the adjusted to the movement image back to the display. Thus, when subjects rotated themselves, had the impression to rotate in the VR environment. The virtual environment consisted of 6 virtual corridors, composed by four straight segments and connected by three angles (45°, 90°, and 135°) in random order and direction. Another corridor, consisting of 8 straight segments and 7 right angles was used as the 'interference corridor' (see Figure 1).

The sensorimotor conflict was realised by inserting a variable factor g between virtual (visual) rotation and real (proprioceptive) rotation. When g was equal to 1, real rotation was equal to virtual rotation. Thus, we were able to obtain different values of sensorimotor conflict according to g values. Two types of conflict were used for the experiment; a) visual rotation < proprioceptive rotation, and b) visual rotation > proprioceptive rotation.

The aim of this study was to examine whether the reproduction of a learned rotation could be influenced by a sensorimotor conflict non associated with its learning. In order to test our second hypothesis, we introduced the dependent variable 'Congruency between Experimental and Interference corridor', having two levels: a] 'Congruent', where the conflict gain g of the 'Experimental' and the 'Interference' corridor had the same value (e.g., for both of them body rotation > visual rotation), and b] 'Incongruent', where the conflict gain of the 'Interference was the inverse of the Experimental corridor's gain (e.g., if for 'Experimental' corridor, body rotation > visual rotation, then for 'Interference' corridor visual rotation > body rotation).

*Experimental procedure*

Participants navigated twice an experimental corridor (Navigation 1 and 2) and memorised their trajectory. After the second navigation they navigated the 'Interference corridor' without memorising their trajectory. Finally, they reproduced (Reproduction

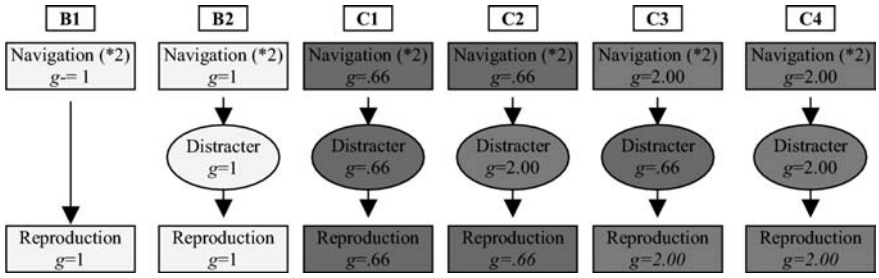



**Figure 2.** The experimental conditions as obtained by the combination of the variable of 'conflict gain' and of 'congruence of the distracter corridor'. B1 & B2 are baselines, while C1-C4 the tests.

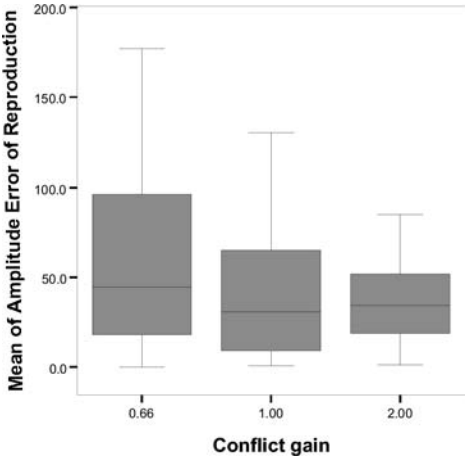



**Figure 3.** The amplitude error of reproduction during the three conflict values, g = .66 (body rotation > visual rotation), g = 1.00 (body rotation = visual rotation) and g = 2.00 (visual rotation > body rotation).

Task) with their eyes closed the memorised trajectory of the experimental corridor (Navigation 1 and 2). Eighteen healthy volunteers participated (10 men). Participants' mean age was 26.41 years (S.D. = 3.554). All participants gave their written informed consent to participate in the study. During the experiment, all participants were adapted to conflict condition, by navigating successfully through the corridors, and then proceeded to reproduction.

The results showed a significant influence of the sensorimotor conflict to subjects' angular reproduction ($F(1,53) = 1.134$, $p = .000$). The pair-wise comparison showed that subjects tended to produce significant more errors when the body rotation was bigger than the visual rotation during learning phase.

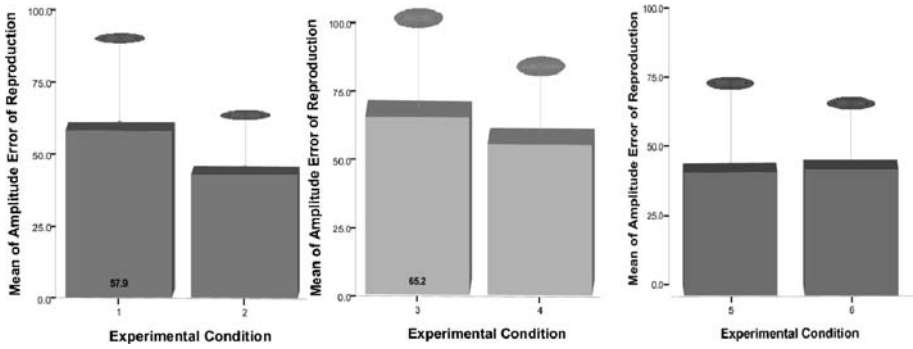



**Figure 4.** The interference corridor had no effect to the angular reproduction of the memorised trajectories: in this figure results for the Baselines B1 and B2, and the Tests C1, C2, C3 and C4.

Importantly, we found no significant influence of the interference conflict to the angular reproduction of the memorised path ($F(1,53) = 1.134$, $p = .292$). These results are illustrated on Figure 3.

During the learning phase of the experiment (Navigation 1 & 2), behavioural observations showed that subjects were well adapted to sensory conflict while navigating in each corridor. All subjects were able to perform the learning tasks by controlling successfully their movement in all conflict values.

Interestingly, half of the subjects did not become aware of the sensorimotor conflict, even if the discrepancy between the 'expected' visual angle and the manipulated proprioceptive angle was significant; subjects managed to adjust their movement during this conflicting navigation. This result is in accordance with previous studies on sensory adaptation (Gordon et al. 1995; Ivanenko et al. 1998; Melvill Jones et al. 1984; Siegler et al. 2000; Viaud-Delmon 1999), where an adaptation occurs after introducing a sensory conflict between sensory information; most of these studies suggest that the role of adaptation is to maintain the stability of locomotion during navigation (Gordon et al. 1995).

Yet, the question of the non-awareness remains. An interesting interpretation for this phenomenon derives from the study of Varraine et al. (2002), where, even when subjects managed to adjust themselves in case of sensory conflict, still this was not a necessary condition for becoming aware of it. These authors proposed an 'inertia effect of awareness', according to which subjects remained unaware of a sensory increase (resistance) during an important period of time (>6sec) when their intended movement has a constant velocity and the sensory conflict increases also in a linear way. This 'online feedback' may be the reason for being unaware even during large modification of the initial sensory information value.

In our study, the results revealed that the angular reproduction of memorized trajectory was influenced by the conflict associated with its navigation and learning {1} (see also Lambrey et al. 2002). This result converges with our initial study providing

strong evidences that a sensory conflict associated with a trajectory's learning, influences its memorisation and recalling (Lambrey et al. 2002). Nevertheless, our results indicate that introducing a sensory conflict non-associated with the memorization of a specified travelled path does not influence the recall of the latter {2}. Observations {1} and {2} allow us to conclude that a sensory conflict is related to -and thus encoded together with- the precise sensory information that concerns the same spatial experience, e.g. a navigated path. This suggests that the sensory information concerning a spatial experience would be encoded in a form of spatial context, which would enable to preserve its encoded information intact from other impertinent information, thus ensuring the best possible recall and reproduction of the memoried path. We underline that this interpretation does not concern mere sensory adaptation (Ivanenko et al. 1998; Viaud-Delmon et al. 1999; Siegler et al. 2000). There are two main differences between the present study and previous ones; to begin with, the duration of the conflict on sensory adaptation studies lasted more than 40–45 minutes using a passive movement, focusing mainly on primary cerebral mechanisms, such as the VOR. Secondly, these experiments did not implicate either memorization or recall of the navigated paths, as a consequence to their initial aim to study the aforementioned mechanisms. On the other hand, in the present study we introduced conflicts of short duration ($\approx$ 90sec), not sufficient to create conditions of sensory adaptation. Additionally, the main task of the current study is the memorisation of navigated trajectories; it is evident that the nature of this task implicates higher cognitive mechanisms, like spatial memory; in that way, subjects' performance could not be attributed in purely low-level cognitive mechanisms, like study VOR.

In a previous Lambrey et al. (2002) discussed the hypothesis that one of the two conflicting cues may be dominant according to the sensory context, which can be considered as a certain type of non-linearity. At first sight, the present findings do not support this hypothesis, since no trace of non-linearity in multisensory interaction was found when considering the data averaged across the 10 sessions. Nonetheless, when distinguishing three phases in the experiment (sessions before being aware of the conflict, during awareness, and after being aware), evidences of non-linearity were detected during the day that subjects became aware of the conflict. In detail, there was a significant linear tendency in Visual subjects before and after becoming aware of the conflict, but not during the day they became aware of the sensorimotor discrepancies. Equally, there was a significant non-linear trend in Non-visual subjects during the day they became aware of the conflict. The current results do not allow determining the cause of this non-linearity nor the mechanism that could evoke it. An eventual explanation to this non-linearity would be that it signals the moment of the subject's re-weighting (e.g. changing perceptive strategy) as well as the moment that the subject becomes aware of the sensory conflict. Nevertheless, new experiments are necessary in order to verify the nature of this non-linearity.

## Instead of epilogue

In the present chapter we presented the latest theories, approaches and evidences of the study in human spatial memory in two axes. In our first axis we resume the current state of the art concerning the neural bases subserving the function of the spatial memory in humans, and on the other hand the cognitive mechanisms that are involved in the processing, encoding and retrieval of the sensory information of a spatial experience, such as navigation.

Currently there is a plethora of findings concerning the activation of specific neural mechanisms during spatial encoding. The hippocampal formation – particularly of the right hemisphere – is activated during the encoding and retrieving of allocentric tasks, but is also activated by vestibular inputs. The parahippocampal sulcus is involved in egocentric tasks, and is also activated during the retrieving of visual landmarks and visual scenes. Additionally, the neuroimaging techniques (fMRI, PET) reveal wider brain networks activated in complex spatial tasks including the parietal and prefrontal cortex for allocentric tasks and the ventromedial occipito-temporal and retrosplenial areas for egocentric areas questions.

Nonetheless, crucial about the precise contribution of the areas involved in spatial memory, still remain unanswered and strengthened by contradictory evidences, such as: which is the exact role of hippocampus and parahippocampus in the different ways of spatial encoding (egocentric, allocentric); how the performance of these areas is differentiated according to the hemispheric laterality; what is the added contribution of the prefrontal 'central executive' mechanism to working spatial memory and the encoding of allocentric and egocentric information?

Furthermore, in the present chapter, we discussed the cognitive mechanisms for encoding multi-sensory information during navigation. We hypothesized the role of a 'spatial-context mechanism' during encoding multi-sensory information, which would be useful in order to preserve the encoded sensory information concerning a particular navigating experience, from being altered or deteriorated by other irrelevant perceived sensory input. To verify, eventually, this hypothesis it would be necessary to investigate deeper two specific aspects; first, the diverse types of sensory information encoded in such spatial contexts, as well as the way they would interact with sensory information encoded in other spatial contexts, in the frame of wider and more complex spatial navigations. Secondly, to examine in which way sensory information is encoded in such a spatial context; is there a pre-selection of the most 'valid' type of information during the learning and encoding phase, or all relevant information is encoded in the spatial context related to this experience, and remains available for eventual recall, according to the specific conditions and nature of this recall?

We believe that future studies on these directions will provide significant information on the neurophysiological and cognitive mechanisms of spatial memory.

## References


Aguirre, G. K., Detre, J. A., & D'Esposito, M. (1996). The parahippocampus subserves topographical learning in man. *Cerebral Cortex, 6*, 823–829.

Arleo, A., & Gerstner, W. (2000) Spatial cognition and neuro-mimetic navigation: A model of hippocampal place cell activity. *Biological Cybernetics, 83*, 287–299.

Baddeley, A. (1996). The fractionation of working memory. *Proceedings of the National Academy of Sciences, 93*, 13468–13472.

Bakker, N. H., Werkhoven, P. J., & Passenier, P. O. (1999). The effects of proprioceptive and visual feedback on geographical orientation in virtual environments. *Presence, 8*, 36–53.

Baloh, R. W., & Halmagyi, G. M. (1996). *Disorders of the Vestibular System*. Oxford University Press, New York.

Beers, van, R. J., Sittig, A. C., & Gon, van, der, J. J. D. (1999). Integration of proprioceptive and visual position-information: An experimentally supported model. *Journal of American Physiology*, 1355–1364.

Berthoz, A. (1997). Parietal and hippocampal contribution to topokinetic and topographic memory. *Philosophical Transactions of Royal Society of London, 352*, 1437–1448.

Berthoz, A. (2000). *The brain's sense of movement*. Cambridge, MA: Harvard University Press.

Burgess, N., Becker, S., King, J. A., & O'Keefe, J. (2001). Memory for events and their spatial context: Models and experiments. *Philosophical Transactions of Royal Society of London, Biological Sciences, 29*, 1493–1503.

Burgess, N., Maguire, E. A., Spiers, H. J., & O'Keefe, J. (2001). A temporoparietal and prefrontal network for retrieving the spatial context of lifelike events. *NeuroImage, 14*, 439–453.

Collewijn, H. (1989a). The vestibulo-ocular reflex: An outdated concept? *Prog Brain Research, 80*, 197–209.

Committeri, G., Galati, G., Paradis, A.-L., Pizzamiglio, L., Berthoz, A., & LeBihan, D. (2004). Reference Frames for Spatial Cognition: Different Brain Areas are Involved in Viewer-, Object-, and Landmark-Centered Judgments About Object Location. *Journal of Cognitive Neuroscience, 16*, 1517–1535.

Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Isham, E. A., Newman, E. L., & Fried, I. (2003). Cellular networks underlying human spatial navigation. *Nature, 425*, 184–187.

Farrell, M. J., & Robertson, I. H. (1998). Mental rotation and the automatic updating of body-centered spatial relationships. *Journal of Experimental Psychology: Learning, Memory and Cognition, 24* (1), 227–233.

Gentilucci, M., Jeannerod, M., Tadary, B., & Decety, J. (1994). Dissociating visual and kinesthetic coordinates during pointing movements. *Experimental Brain Research, 102*, 359–366.

Gerstner, W., & Abbott, L. F. (1997). Learning navigational maps through potentiation and modulation of hippocampal place cells. *Journal of Computational Neuroscience, 4*, 79–94.

Ghaem, O., Mellet, E., Crivello, F., Tzourio, N., Mazoyer, B., Berthoz, A., & Denis, M. (1997). Mental navigation along memorized routes activates the hippocampus, precuneus, and insula. *Neuroreport, 8*, 739–744.

Golomer, E., Crémieux, J., Dupui, P., Isableu, B. & Ohlmann, T. (1999). Visual contribution to self-induced body sway frequencies and visual perception of male professional dancers. *Neuroscience Letters, 267*, 189–192.

Gordon, C. R., Fletcher, W. A., Melvill Jones, G. M. & Block, E. W. (1995). Adaptive plasticity in the control of locomotor trajectory. *Experiment Brain Research, 102*, 540–545.

Habib, M., & Sirigu, A. (1987). Pure topographical disorientation: A definition and and anatomical basis. *Cortex, 23*, 73–85.

Hartley, T., Maguire, E. A., Spiers, H. J., & Burgess, N. (2003). The well-worn route and the path less traveled: Distinct neural bases of route following and wayfinding in humans. *Neuron, 37*, 877–888.

Hartley, T., Trinkler, I., & Burgess, N. (2004). Geometric determinants of human spatial memory. *Cognition, 94*, 39–75.

Hillis, J. M., Ernst, M. O., Banks, M. S., & Landy, M. S. (2002). Combining sensory information: Mandatory fusion within, but not between, senses. *Science, 298* (5598), 1627–1630.

Israël, I., André-Deshays, C., Charade, O., Berthoz, A., Popov, K., & Lipshits, M., (1993). Gaze control in microgravity. 2. Sequences of saccades toward memorized visual targets. *Journal of Vestibular Research, 3*, 345–360.

Israël, I., Grasso, R., Georges-François, P., Tsuzuku, T., & Berthoz, A. (1997). Spatial memory and path integration studied by self-driven passive linear displacement. I. *Basic properties. Journal of Neurophysiology*, 77, 3180–3192.

Ivanenko, Y. P., Viaud-Delmon, I., Siegler, I., Israel, I., & Berthoz, A. (1998). The vestibulo-ocular reflex and angular displacement perception in darkness in humans: Adaptation to a virtual environment. *Neuroscience Letters, 241*, 167–170.

Jacobs, R. A. (2002). What determines visual cue reliability? *Trends of Cognitive Science, 6* (8), 345–350.

Jacobs, F. J. (2003). The evolution of the cognitive map. *Brain, Behavior and Evolution, 62*, 128–139.

Kesner, R. P., & Rogers, J. (2004). An analysis of independence and interactions of brain substrates that subserve multiple attributes, memory systems, and underlying processes. *Neurobiology of Learning and Memory, 82*, 199–215.

Lackner, J. R. (1998). Some proprioceptive influences on the perceptual representation of body shape and orientation. *Brain, 111*, 281–297.

Lambrey, S., & Berthoz, A. (2003). Combination of conflicting visual and non-visual information for estimating actively performed body turns in virtual reality. *International Journal of Psychophysiology, 50* (1–2), 101–115.

Lambrey, S., Samson, S., Dupont, S., Baulac, M., & Berthoz, A. (2003). Reference frames and cognitive strategies during navigation: Is the left hippocampal formation involved in the sequential aspects of route memory? *International Congress Series, 1250*, 261–274.

Lambrey, S., Viaud-Delmon, I., & Berthoz, A. (2002). Influence of a sensorimotor conflict on the memorization of a path traveled in virtual reality. *Cognitive Brain Sciences, 14* (1), 177–186.

Leung, H. C., Gore, J. C., & Goldman-Rakic, P. S. (2005). Differential Anterior Prefrontal Activation during the Recognition Stage of a Spatial Working Memory Task. *Cerebral Cortex* (e-publishing ahead).

Lutz, A., Lachaux, J. P., Martinerie, J., & Varela, F. J. (2002). Guiding the study of brain dynamics by using first-person data: Synchrony patterns correlate with ongoing conscious states during a simple visual task. *Proc National Academy of Sciences of USA, 99* (3), 1586–1591.

Makino, Y., Yokosawa, K., Takeda, Y., & Kumada, T. (2004). Visual search and memory search engage extensive overlapping cerebral cortices: An fMRI study. *NeuroImage, 23*, 525–533.

Maguire, E. A., Frackowiak, R. S., & Frith, C. D. (1997). Recalling routes around London: Activation of the right hippocampus in taxi drivers. *Journal of Neurosciences, 17*, 7103–7110.

Maguire, E. A., Frith, C. D., & Cipolotti, L. (2001). Distinct Neural Systems for the Encoding and Recognition of Topography and Faces. *NeuroImage, 13*, 743–750.

Maguire, E. A., Mummery, C. J., & Buchel, C. (2000). Patterns of hippocampal-cortical interaction dissociate temporal lobe memory subsystems. *Hippocampus, 10*, 475–482.

Mellet, E., Briscogne, S., Tzourio-Mazoyer, N., Ghaem, O., Petit, L., Zago, L., Etard, O., Berthoz, A., Mazoyer, B., & Denis, M. (2000). Neural correlates of topographic mental exploration: The impact of route versus survey perspective learning. *NeuroImage, 12*, 588–600.

Melvill Jones, G. M., Berthoz, A., & Segal, B. (1984) Adaptive modification of the vestibulo-ocular reflex by mental effort in darkness. *Experimental Brain Research, 56*, 149–153.

Melvill Jones, G. M., Galiana, H. L., Weber, K. D., Fletcher, W. A., & Block, E. W. (2000). Complex podokinetic (PK) response to post-rotational vestibular stimulation. *Archives Italiennes de Biologie, 138*, 99–105.

Milner, B. (1971). Interhemispheric differences in the localization of psychological processes in man. *British Medicin Bulletin, 27*, 272–277.

Nyffeler, T., Gutbrod, K., Pflugshaupt, T., Wartburg, v. R., Hess, C. W., & Muri, R. M. (2005). Allocentric and egocentric spatial impairments in a case of topographical disorientation. *Cortex, 41*, 133–143.

O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford, Oxford University Press.

Panagiotaki, P., Lambrey, S., & Berthoz, A. Multisensory-Information Interaction during spatial navigation and encoding: Evidences for a top-down procedure. (Under submission)

Parslow, D. M., Morris, R. G., Fleminger, S., Rahman, Q., Abrahams, S., & Recce, M. (2005). Allocentric spatial memory in humans with hippocampal lesions. Acta *Psychologica, 118*, 123–147.

Pine, D. S., Grun, J., Maguire, E. A., Burgess, N., Zarahn, E., Koda, V., Fyer, A., Szeszko, P. R., & Bilder, R. M. (2002). Neurodevelopmental Aspects of Spatial Navigation: A Virtual Reality fMRI Study. *NeuroImage, 15*, 396–406.

Probst, T., Straube, A., & Bles, W. ( 1985). Differential effects of ambivalent visual-vestibular-somatosensory stimulation on the perception of self-motion. *Behavioural Brain Research, 16*, 71–79.

Redish, A. D. & Touretzky, D. S. (1997). Cognitive maps beyond the Hippocampus. *Hippocampus, 7*, 15–35.

Rosenbaum, R. S., Ziegler, M., Winocur, G., Grady, C. L., & Moscovitch, M. (2004). "I have often walked down this street before": fMRI studies on the hippocampus and other structures during mental navigation of an old environment. *Hippocampus, 14*, 826–835.

Siegler, I., Viaud-Delmon, I., Israël, I., & Berthoz, A. (2000). Self-motion perception during a sequence of whole-body rotations in darkness. *Experimental Brain Research, 134*, 66–73.

Spiers, H. J., Burgess, N., Hartley, T., Vargha-Khadem, F., & O'Keefe, J. (2001). Bilateral hippocampal pathology impairs topographical and episodic memory but not visual pattern matching. *Hippocampus, 11*, 715–725.

Stackman, R. W., Clark, A. S., & & Taube, J. S. (2002). Hippocampal representations require vestibular input. *Hippocampus, 12*, 291–303.

Stackman, R. W. & Herbert, A. M. (2002). Rats with lesions of the vestibular system require a visual landmark for spatial navigation. *Behavioural Brain Research, 128*, 27–40.

Telban R. J., & Cardullo, F. M. (2001). An integrated model of human motion perception with visual-vestibular interaction. http://www-sdb.larc.nasa.gov/aiaa-2001-4249.html .

Varraine, E., Bonnard, M., & Pailhous, J. (2002). The top down and bottom up mechanisms involved in the sudden awareness of low level sensorimotor behavior. *Cognitive Brain Research, 13* (3), 357–361.

Viaud-Delmon, I., Ivanenko, Y. P., Berthoz, A., & Jouvent, R. (1999). Sex, Lies and Virtual Reality. *Nature Neuroscience, 1* (1), 15–16.

Viaud-Delmon, I., Ivanenko, Y. P., Grasso, R., & Israël, I. (1999). Non-specific directional adaptation to asymmetrical visual-vestibular stimulation. *Cognitive Brain Research, 7*, 507–510.

Warren, Jr, W. H., Kay, B. A., Zosh, W. D., Duchon, A. P. & Sahuc, S. (2001). Optic flow is used to control human walking. *Nature Neuroscience, 4* (2), 213–216.

Weber, K. D., Fletcher, W. A., Gordon, C. R., Melvill Jones, G., & Block, E. W. (1998). Motor learning in the "podokinetic" system and its role in spatial orientation during locomotion. *Experimental Brain Research, 120* (3), 377–85.

CHAPTER 2.2

# Working memory, imagery and visuo-spatial mechanisms

Zaira Cattaneo, Maria Chiara Fastame, Tomaso Vecchi, and Cesare Cornoldi

## Introduction

The notion of Visuo-Spatial Working Memory (VSWM) refers to a series of mechanisms and processes that are of critical importance for human cognition. The current chapter will analyse the structure and articulation of VSWM in view of Cornoldi and Vecchi's (2003) WM model, highlighting how the system is connected to perception, imagery and consciousness and describing how it is compatible with other approaches to WM.

The first section will illustrate the notion of WM, starting from its very roots represented by the WM model as originally developed by Baddeley and Hitch (1974). We will focus the reader's attention particularly on the "ancestor" of VSWM, i.e. Baddeley's visuo-spatial sketchpad, which – in the last few years – has raised growing interest within the psychological community. In our discussion, we will refer to the important contributions of many researchers (e.g., Logie 1995) and to the different research fields (e.g., studies on congenital blindness, genetic syndromes, developmental studies, neuroimaging studies, etc. . .) which have helped in further specifying and defining the functioning and architecture of WM in general and of VSWM in particular.

Specifically, we will illustrate Cornoldi and Vecchi's (2003) VSWM model, that assumes a "continuous" view of the WM system in which the different components – individuated by Baddeley (1986) – are not strictly separate but successfully interact in carrying out different cognitive activities.

A specific section will be dedicated to mental imagery, regarded in Cornoldi and Vecchi view (2003) as a peculiar function of the VSWM system. Furthermore, we will underline how the VSWM and the perceptual system partially share common functional properties, but we will also provide consistent evidence in favor of a functional independence between the two systems.

Furthermore, we will consider alternative approaches to WM that regard the WM system as an activated part of long term memory: in two different sections we will briefly summarize such theoretical accounts, trying to highlight the similarities

and differences with Cornoldi and Vecchi's model. In particular, we will explain why Cornoldi and Vecchi (2003) consider such LTM approaches to WM as misleading.

Finally, a last section will offer a short insight into one of the most complex but also most fascinating issue in cognitive sciences: the notion of consciousness. In particular, we will try to explain how awareness can be related to the WM system, and to VSWM in particular.

## Models of Working Memory (WM)

Many studies have been investigating the nature of WM since Baddeley and Hitch (1974) proposed their innovative model of short-term memory. The originality of Baddeley and Hitch's theory consists of refuting the assumption of a temporary unitary storage capable only of retaining stimuli for a few seconds: rather, the authors conceive short-term memory as a more complex multiple-component structure (i.e., WM), that can both temporarily retain and simultaneously process a limited amount of information allowing the execution of different daily life activities, such as mental calculation, reading, decision making and comprehension (Baddeley 1986). From this perspective, WM is thought of as a limited-resource cognitive system, fractionated (in the original version of the model) into a supervisory component, the Central Executive (CE) and two subsidiary (also called "slave") systems, the Phonological Loop (PL) and the Visuo-Spatial Sketch Pad (VSSP) (Baddeley & Hitch 1974). The CE is mainly an amodal control component that monitors the activities carried out by the two slave systems supervising information processing; furthermore, it serves to focus or switch attention and to recover mental representations from long-term memory (Baddeley 1996; Baddeley & Logie 1999). The PL and the VSSP are domain-specific systems: the former is specialised in storing and manipulating verbal material, the latter is devoted to the storage and manipulation of both visual (e.g., shape, colour, texture) and spatial (e.g., location or movement of an object) stimuli acquired through the peripheral perceptual systems or recovered from long-term knowledge. A further function of the VSSP is to carry out mental imagery tasks, i.e. the subsystem can generate and operate on mental representations even in the absence of a corresponding visuo-spatial perceptual experience (this topic will be discussed in more detail later on in this chapter).

Several studies have investigated whether the two slave systems work in synergy or whether they are selectively activated on the basis of the nature of the task to be carried out. Strong evidences from a tradition of studies adopting a dual-task paradigm (e.g., Brooks 1967, 1968; Logie, Zucco, & Baddeley 1990) and from empirical observations of brain-damaged patients (e.g., Baddeley, Papagno, & Vallar 1988; Baddeley 1993) suggest that the PL and VSSP are functionally independent: hence, the involvement of either one of the two slave systems does not necessarily require the intervention of the other. An important example of the functional independence of these two systems comes from a clinical case of an undergraduate student who performed poorly

in tasks involving the PL (e.g., forward serial recall of words), whereas the functioning of his VSSP fell into the range of normality (Baddeley 1993). Conversely, Hanley, Young and Pearson (1991) reported the case of a middle-aged woman presenting evident deficits in visuo-spatial functions but a preserved PL capacity. The hypothesis of a functional independence between the slave systems is further corroborated by the pattern of WM performance observed in a variety of genetic syndromes. For example, the Down syndrome's cognitive phenotype seems to be characterised by a deficit in the capacity to process phonological stimuli whereas the VSSP functioning is mostly preserved (e.g., Hodapp, Evans, & Grey 1999; Jarrold & Baddeley 1997; Lanfranchi, Cornoldi, & Vianello 2004; Seung & Chapman 2004). In contrast, individuals with Williams syndrome present an evident impairment of visuo-spatial WM processes, whereas their verbal domain is better preserved (e.g., Jarrold, Baddeley, & Hewes 1998, 1999; Wang & Bellugi 1994).

Further studies have selectively focused on one of the slave systems, trying to answer specific questions: for example, research has investigated whether the PL's structure is unitary or fragmented. Neuropsychological evidence (see Baddeley 1986) supports a distinction within the PL between passive and active functions: the verbal WM would consist of a phonological store, responsible for the passive storage of information, and a subvocal rehearsal mechanism (i.e., the articulatory loop), that actively refreshes the mnestic traces in order to avoid their decay. A further critical function of the articulatory substructure is the capability to translate visually presented verbal stimuli into a corresponding acoustic/phonological format (Logie & Baddeley 1990).

If for a long time cognitive psychologists had been primarily interested in assessing the architecture and functioning of verbal WM, giving less attention to the VSSP, starting from the end of the past century the VSSP has started attracting growing interest. Alternative models of WM have been developed, that differ to a greater or lesser extent from Baddeley's original view (Baddeley & Hitch 1974). In particular, on one side some authors share the idea of a unitary WM system (e.g., Anderson, Reder, & Lebiere 1996; Engle, Cantor, & Carullo 1992), whilst on the other several authors emphasize the fragmentary nature of the memory system (e.g., Logie 1995; Cornoldi & Vecchi 2000, 2003; Shah & Miyake 1996). Amongst the latter, it has been suggested that, due to the similarity between the two slave systems, also the VSSP could be fractionated into passive and active functions (e.g., Baddeley & Logie 1999; Logie 1986, 1995; Cornoldi & Vecchi 2000, 2003). For instance, Logie (1995) has suggested a functional distinction between the visual and spatial WM components: in his view, the visuo-spatial WM system is composed of a "visual cache", devoted to passively retain non-verbal information (resembling the function of the phonological store), and of a "inner scribe", a spatial structure responsible for actively refreshing, processing, manipulating and integrating visuo-spatial information (resembling the activity of the articulatory loop). According to Logie (1995), visual noise would disrupt only passive visual tasks, such as the maintenance of a coloured stimulus in memory, whereas spatial tapping would affect more active spatial tasks, such as mental rotation. The

functional autonomy of the spatial and the visual components has been supported by experiments adopting a dual-task procedure (e.g., Logie & Marchetti 1991; Quinn & McConnell 1996). There is a body of evidence according to which the imitation of movements presented by the experimenter disrupts the maintenance of a sequence of spatial movements (i.e., passive task), which would be carried out by the inner scribe (Smith & Pendleton 1989). However, irrelevant visual stimuli which involve the visual cache interfere with the execution of visual imagery tasks (i.e., active tasks) (e.g., Quinn & McConnell 1996). This outcome seems to suggest that passive and active functions can be distinguished both in the visual and in the spatial WM. A variety of empirical evidence offers further support to this hypothesis. For example, Cornoldi and colleagues (Cornoldi, Rigoni, Venneri, & Vecchi 2000) found a double dissociation between passive and active visuo-spatial processes in children with poor non-verbal abilities but high verbal intelligence: a selective deficit in the capacity of storing visuo-spatial stimuli did not imply an impairment of the ability to process, manipulate or transform visuo-spatial material. Such results were interpreted in light of Cornoldi and Vecchi's WM model (Cornoldi & Vecchi 2000, 2003; Cornoldi 1995): briefly, Cornoldi and Vecchi propose a multi-componential organization of WM in which passive and active functions can be individuated both in the spatial and visual components.

The next section will offer a more detailed discussion of Cornoldi and Vecchi's WM account and of its relationship with the original construct proposed by Baddeley and Hitch (1974).

## The Working Memory Model proposed by Cornoldi and Vecchi

As mentioned earlier, Cornoldi and Vecchi (Cornoldi 1995; Cornoldi & Vecchi 2000, 2003) support the idea of a visuo-spatial WM whose internal organization resembles that of the PL. A part from the literature based on the application of the dual-task paradigm and the observation of brain-injured individuals, the assumption of distinct but analogous verbal and visuo-spatial WM components is also due to the fact that many of the effects related to the immediate order recall of verbal information, such as the phonological similarity effect (e.g., Conrad 1964; Hulme, Maughan, & Brown 1991), the concurrent articulatory suppression (Murray 1968) and the irrelevant speech effects (see Baddeley 1986) can also be found (with due adaptations) in the retrieval of serial visuo-spatial stimuli (e.g., Hitch, Halliday, Schaafstal, & Schraagen 1988, for the visual similarity effect).

Cornoldi and Vecchi (2000, 2003) argue that WM is a system with limited resources employed differently depending on the nature of the information to be maintained (i.e., verbal, visual, spatial, or haptic) and on the requests of the task to be carried out (i.e., passive versus active). Embracing a "continuous" view of the system, WM is represented as a conical structure organised along a horizontal and a vertical dimension. The horizontal continuum distinguishes WM processes in terms of the na-

ture of the material to be recalled (thus, verbal, visual and spatial WM correspond to different areas of the horizontal continuum); conversely, the vertical continuum defines the amount of cognitive resources required in order to maintain information (i.e., the level of control necessary to carry out the task). Specifically, completely separate peripheral processes deputed to the temporary storage of information that require a limited level of control are located on the lower end of the vertical plain, hence it is likely that a simultaneous task can be carried out. Whereas the high-level active tasks, consisting of a transformation of the perceptual input (or material from long-term memory) in order to process an output (e.g., mental images) occupy the highest positions of this continuum, because they need a larger amount of cognitive resources. Hence, considering the vertical dimension from bottom to top, the distance between two different processes represents the difference in the amount of active processing required: the higher a task is placed along the vertical continuum, the more its specificity is reduced and the less likely it is that a simultaneous activity can be carried out. It follows that each WM process is defined in terms of its position along both the two continua. Furthermore, the conical structure of WM indicates that the distance between two tasks in the horizontal continuum diminishes the higher they are placed along the vertical continuum, that is to say they loose in modality-specificity with an increase in the level of the control required. Such an assumption also implies that processes which are differentiated along a dimension can be similarly located on the other continuum: for example, verbal and spatial tasks that occupy distant positions on the horizontal dimension may nonetheless share the same level of control, expressed by a similar position on the vertical continuum. Thus, a forward verbal recall task, such as the Digit Span Test, and the maintenance of spatial positions on a matrix, such as the Visual Pattern Test (Della Sala, Gray, Baddeley, & Wilson 1997), although occupying different positions on the horizontal continuum (being distinct modality-specific processes), are similarly located at the very low extremity of the vertical continuum, since they both require a similar limited degree of control. Conversely, two tasks might share the same modality but require a different amount of control: for example, the Digit Span Test and the Listening Span Test (Daneman & Carpenter 1980) both rely on the verbal domain but the amount of cognitive resources they use is pretty different. In fact, while (as mentioned above) the Digit Span Test is located in the lower portion of the vertical dimension, the Listening Span Test, requiring active manipulation of verbal stimuli and inhibition of irrelevant information, is a more demanding active task placed in a high point along the vertical continuum.

Hence, with regards to the original WM model by Baddeley and Hitch (1974), the theoretical account by Cornoldi and Vecchi generates at least four important implications: first, it supports the assumption of a multiple-component WM in which the substructures are distinguished in terms of the nature of the material (e.g., verbal, visual, spatial and haptic) and the task's requirements (passive storage vs. active manipulation). Second, the assumption of a continuous perspective along the horizontal dimension implies that different components (e.g., spatial and visual) can be distinguished but be closer than others (e.g. spatial and verbal). The latter, due to their

greater distance, can be involved simultaneously in a cognitive activity depending on the modality of the information to be processed. Third, WM is not hierarchically organised, hence the idea of a superior control component (i.e., the Central Executive) that supervises the slave systems is substituted by a distinction in terms of the level of control required to carry out the task (i.e. passive and active WM functions). Finally, the differentiation between passive and active processes is assumed to be present in all domains (i.e., verbal, visual, spatial, haptic).

A fruitful approach to the study of WM is research on individual differences: in particular, research on gender differences has supported the functional distinction between verbal and visuo-spatial processes in WM (e.g., Oltman 1968; Hyde 1981; Richardson 1994; Vecchi & Girelli 1998; Vecchi 2001). Experimental data show that males tend to perform better in visuo-spatial tasks, whereas verbal abilities are particularly developed in females (e.g., Harshman, Hampson, & Berenbaum 1983; Maccoby & Jacklin 1974; Metzler & Shepard 1974). Specifically, females seem to outperform males in carrying out verbal fluency, word production and verbal memory tasks (e.g., Cohen, Schaie, & Gribbin 1977; Hyde 1981; Kimura 1999). In contrast, males obtain higher scores in active VSWM tasks, such as spatial path-finding (Oltman 1968), mental rotation and transformation (e.g. Harshman, et al. 1983; Vecchi & Girelli 1998; see also Voyer, Voyer, & Bryden 1995) and artificial movement recognition tasks (Price & Goodale 1988). In a similar vein, further investigations showed that while males outperform females in dynamic mental rotation tasks (e.g., Paivio & Harshman 1983; Linn & Petersen 1985), females are more efficient than males in static recognition tasks and in judging stimuli size (e.g., Harshman et al. 1983; Paivio & Clark 1991).

While the distinction in WM between the visuo-spatial and the verbal components has been well-demonstrated (also by the reported studies on gender differences), the distinction between the WM's visual and spatial components is more controversial, since both the subsystems can be involved simultaneously in the execution of the same task. For instance, in children with nonverbal disabilities it is hard to test the efficiency of the visual and of the spatial components separately, because instruments usually considered as "pure" visual or spatial WM measures – such as the Corsi Block Task – actually simultaneously involve both these components (Vandierendonck, Kemps, Fastame, & Szmalec 2004; Cavallini, Fastame, Palladino, Rossi, & Vecchi 2003–2004). However, both studies on congenitally and totally blind people (e.g., Vecchi 1998, 2001) and research on brain-damaged patients (Farah, Hammond, Levine, & Calvanio 1988; Luzzatti, Vecchi, Agazzi, Cesa-Bianchi, & Vergani 1998) show that visual and spatial WM can be (partially) independent (such research will be discussed in more detail when dealing with the relationship between imagery, perception and VSWM; see later on in this chapter). Furthermore, the cognitive profiles of some individuals with genetic syndromes offer a significant contribution in corroborating the (at least partial) functional independence between the visual and the spatial WM substructures: for instance, although nonverbal abilities are inadequate in Williams syndrome's individuals, their visual WM's component is relatively more efficient than the spatial one (Udwin & Yule 1991; Vicari, Bellucci, & Carlesimo 2003). These results are also

supported by developmental studies that demonstrate that the visual span increases more rapidly than the capacity to recall a pattern of positions on a matrix (e.g., Logie & Pearson 1997; Vicari et al. 2003).

Finally, a variety of neuropsychological studies on specific learning disabilities support the distinction between passive and active processes both in the verbal, visual and spatial WM. Children with normal intellective functioning and a specific reading disability (i.e., dyslexia) perform very poorly in passive verbal WM tasks, whereas they can easily carry out active verbal tests (e.g., Banai & Ahissar 2004). The opposite pattern is observed in children with high nonverbal intelligence and a specific difficulty in text comprehension: these individuals perform inadequately in tasks requiring the manipulation of verbal material (e.g., Listening Span Test), whereas the passive maintenance of verbal stimuli is preserved (e.g., De Beni, Palladino, Pazzaglia, & Cornoldi 1998). Similarly, a double dissociation between the passive and active functions has been found also in the visuo-spatial domain: as mentioned earlier, Cornoldi et al. (2000) found that a selective impairment of the active functions does not imply the disruption of the capacity for retaining visuo-spatial material (see also Rourke 1989). Further support for the separation between the passive and active processes is also offered by studies on elderly people manifesting a selective decline in the capacity to manipulate stimuli associated with a more preserved ability to store information (e.g., Schaie 1983; Salthouse 1994, 1996; Vecchi, Richardson, & Cavallini 2005). Gender studies also provide some support for this view, by suggesting that women show a selective disadvantage in visuo-spatial tasks requiring active elaboration of the material (Vecchi & Girelli 1998).

In conclusion, we believe that the model developed by Cornoldi and Vecchi provides a more exhaustive specification of WM compared to the original model proposed by Baddeley and Hitch (1974), of which it should be considered an integration rather than a completely alternative view point.

When describing the different subcomponents of the WM system, we have anticipated that one of the functions of the VSWM system is to manipulate information also in the absence of a corresponding perceptual experience. In other words, in our view, VSWM is responsible for mental imagery. The capacity to generate and manipulate mental images has catalysed the attention of philosophers and psychologists for years. In the next section we will examine how imagery can be related to the activity of the VSWM system, also briefly summarising the history of mental images in psychological research. A controversial issue is the nature of the generated images compared to the images that result from the act of perceiving: consistent experimental evidence will be provided that suggests how visuo-spatial WM and perception, although sharing some functional properties, should be regarded as independent systems.

## VSWM, imagery and perception

Mental imagery is a vital part of human cognition. Generally, visual mental imagery is regarded as the capacity of envisaging objects and scenes in their absence (e.g., Cornoldi, et al. 1991). As it will be discussed in the following paragraphs, mental imagery could be regarded as a critical function of visuo-spatial working memory. Furthermore, when describing Cornoldi and Vecchi's model, we have seen how the areas at the basis of the WM continuum are close to the perceptual system, through which the information stored and (eventually) actively manipulated in WM is acquired: in the next paragraphs we will see that VSWM and perceptual mechanisms share – at least in part – common functional properties, though remaining independent systems (see Cornoldi & Vecchi 2003).

## A brief history of imagery

Important anticipations on mental imagery go back to philosophical thinking (important sources can be found in Herrnstein & Boring 1973). Whether based on impressions stamped on a wax block by perceptions and thoughts (Plato, Theatatus 191c, d) or pictures painted in the soul by an inner artist (Plato, Philebus 39c), the ancient philosophers agreed that "the soul never thinks without a mental image" (Aristotle, De anima 431a 15–20).

Interest in mental imagery declined during Behaviourism but was then revived by the cognitive revolution of the 1960s and 70s. Of critical importance was Paivio's research on the facilitating effects of imagery on memory performance (Paivio 1971, 1986, 1991) and Bower's research on imagery mnemonics (Bower 1972). Well-known experiments on mental rotation (Shepard & Metzler 1971; Shepard & Cooper 1982) and mental scanning (Kosslyn 1973, 1980) developed a view of mental imagery as a "quasi-pictorial" form or representation, analogous to the perceptual experience. In particular, Shepard and Meztler (1971) measured the reaction times in answering whether pairs of figures presented to subjects were the same or not. The two figures varied in the degrees of rotation they differed by: results indicated that reaction time of the "same" pairs correlated with the angle of rotation for which the two objects differed. These results were explained by assuming that people imagine the pictures and mentally rotate them.

In Kosslyn's (1973) experiments on mental scanning, participants had to memorise particular maps or figures and were subsequently asked to mentally scan the pathway from one location to another of the map, pressing a button once the indicated destination point was reached (for a review, see Denis & Kosslyn 1999). The results demonstrated that shifting attention between different parts of the image required an amount of time directly proportional to the distance between the two indicated points, as if the participants were really scanning a physical map with their own eyes (Kosslyn, Ball &, Rieser 1978). On the basis of such findings, images in the mind were

considered to be functionally equivalent to inner pictures, a sort of copy of previous sensory impressions. Such theoretical position was strongly criticised by Pylyshyn (1981), who suggested an alternative explanation for the mental scanning results on the basis of the "demand effects": in his view, participants took longer to scan across larger distances not because they experienced a mental picture-like representation of the scene but because, on the basis of their knowledge, they were aware that it requires more time to scan larger than shorter distances (see also Currie 1995). Pylyshyn proposed a propositional or "description" theory of imagery (1973, 1981, 1994): in his view, mental images consist of propositions or structural descriptions encoded in "mentalese" (Fodor 1975), a language-like representational format that underlies other non-imaginative cognitive processes. Thus, reasoning with mental images activates – in Pylyshyn' view – the same processes and kinds of representation as reasoning in general. Moreover, in Pylyshyn' s idea there is nothing specifically perceptual in the mental images' format: of course, mental images are real since they could be experienced as perceptual-like pictures, but they are an epiphenomenon since they are not essential to a representation of a specific object or scene and they do not serve any useful function. The controversy regarding the analogical versus the propositional status of the mental images has become famous as the "imagery debate" (for a review, see Tye 1991). However, already more than two decades ago, Anderson (1978) observed that such a debate cannot be solved on the basis of empirical evidence alone, since a depictive theory can always be reformulated as a propositional one and vice versa. In fact, any depictive theory that, on the basis of the processes that operate on a mental representation, assumes that such a representation has a picture-like nature can be mimicked by an alternative theory that claims a different nature of the same representation (e.g., a sequence of symbols) generated on the basis of a different set of processes.

In more recent years, research on mental images has focused on more specific issues, partially abandoning the debate on the analogical vs. propositional format of mental representations.

## The study of mental imagery and its relationship withVSWM

Mental imagery has been defined as "the mental invention or recreation of an experience that at least in some respects resembles the experience of actually perceiving an object or event, either in conjunction with, or in absence of, direct sensory simulation" (Finke 1989: 2), or, more recently, as "a cognitive process that makes the figural aspects of previously seen objects, or scenes when these are no longer accessible to perception, temporarily available to the mind [. . .]. Imagery reinstates quasi-pictorial internal experiences that reconstruct the figural appearance of objects (including their color, shape, internal structure, etc.)" (Rinck & Denis 2004: 1211).

From a wider perspective, mental images are not just visual: in fact, it is possible to experience also auditory, motor, gustatory and olfactory mental images. Paivio (1971), reviewing studies on imagery, wrote: "The term image and imagery will generally be

used to refer to concrete imagery, that is nonverbal memory representations of concrete objects and events, or nonverbal modes of thought (e.g., imagination) in which such representations are actively generated and manipulated by the individual. This will usually be taken to mean visual imagery, although it is clear that other modalities (e.g., auditory) could be involved [...]. Imagery, so defined, will be distinguished from verbal symbolic processes, which will be assumed to involve implicit activity in an auditory-motor speech system" (Paivio 1971:12). Similarly, since our discussion concerns the relationship between imagery and visuo-spatial working memory, we will use the term "imagery" referring specifically to visuo-spatial imagery. By maintaining some of the properties of the corresponding perceptive visuo-spatial representations, the format of the representations obtained through imagery is assumed to be, at least in part, "analogical" resulting in the feeling of "seeing a picture in one's head".

A different but related issue regards the sources of the visuo-spatial mental imagery: a visual image is not necessarily generated on the basis of visual perception, but it could be activated by auditory or haptic perception too. In a recent research with both sighted and blind subjects, Pietrini and colleagues (Pietrini, et al. 2004) found that both tactile exploration and visual perception of artificial objects (e.g., shoes and bottles) activate the posterior inferior temporal region of the visual extrastriate cortex indicating that the objects are represented in the ventral visual pathway not simply as visual images but in terms of more abstract features of the object form. Moreover, while an immediate memory visual trace depends upon a very recent visual experience and it is thus very close to perceptual processes, a mental image results from a constructive process involving also long term memory: that is to say, mental images are not just a derivate of perception but "could be fed into working memory through either perception or long-term memory"(Baddeley & Andrade 2000:128). Although analogical, mental images are the result of a complex process, similar but not identical to perception and in which long term memory also plays a critical role (e.g., Cornoldi, De Beni, Giusberti, & Massironi 1998). The importance of verbal and semantic processes in visuo-spatial imagery abilities has already been well-demonstrated (Intons-Peterson 1996).

Kosslyn (1980, 1994) elaborated a sophisticated architecture of mental imagery in which imagery mechanisms are assumed to overlap substantially with perceptual ones but are not completely reducible to them. In fact, Kosslyn claims an involvement of long-term knowledge in mental imagery: the images that can be generated are stored in long term memory as "deep representations", structural descriptions not directly accessible to awareness, that are utilised to generate the actual depictive-analogical images in the "visual buffer". The mechanism for generating a mental image could be exemplified by thinking about what happens in a computer graphics program: data are saved in particular files (similar to the "deep representations" stored in LTM) on the basis of which pictures can be generated on the computer screen. In the human cognitive system, the generation of such images takes place in the "visual buffer" which is also involved in perceptual information processing: in the visual buffer information becomes available to consciousness and can be analysed by the "mind's eye" function.

The visual buffer is thus the medium that supports depictive representations and is assumed to be composed of several retinopic maps of the brain's occipital cortex (Kosslyn 1994; Kosslyn, et al. 1999; Kosslyn, Thompson, Kim, & Alpert 1995). From the visual buffer signals are sent to areas that store visual memories with whom the transmitted input is matched in order to be interpreted. Thus the "mind's eye" should be considered as a metaphor of this mechanism and not as a "homunculus" looking at images in the mind (for a more extensive discussion of Kosslyn's model, see Cornoldi & Vecchi 2003). Finally, just as "unicorn pictures are not similar to unicorns, because there is nothing they could be similar to" (Goodman & Elgin 1993:150) so mental images do not derive uniquely from perception or from long term memory, but can be originated by combining in quite new and original ways different elements that are or have been available from our experience. It has been demonstrated that, for example, novel images can be constructed on the basis of a text describing spatial configurations and that participants behave similarly in scanning such newly constructed configuration as they did in scanning images derived from visual experience (e.g., Denis & Cocude 1997; Denis & Zimmer 1992). Again, a conspicuous literature on the role of imagery in creativity has demonstrated that people are able to visualize novel shapes that they have never seen before (e.g., Finke, Ward & Smith 1992).

Since the very first attempts to investigate the nature of mental representations, a recurrent issue has been the distinction between such representations and the medium in which they occur. In our view, this medium is the visuo-spatial working memory system: "[...] the visuospatial sketchpad is assumed to maintain and manipulate visual information and to be involved in visual imagery, whereas the phonological loop performs a similar function for auditory and verbal material" (Baddeley & Andrade 2000:127). Furthermore, several findings have indicated that the generation, maintenance and manipulation of mental images are functions that could be partially ascribed to the central executive too (Duff & Logie 2001; Pearson, De Beni & Cornoldi 2001). Such data could appear incongruent with the assumption of the amodal nature of the central executive (Baddeley 1986), given that on the contrary mental images have a specific modal format. However, such incongruence disappears by assuming with Cornoldi and Vecchi that the VSWM system is a "continuum" differentiated on the basis of both the inputs' modality (i.e., visual, spatial, auditory, haptic) and the active elaboration required by a particular task: from this perspective, mental imagery is located higher along the continuum compared to other visuo-spatial (passive) tasks that require only the maintanance of information without manipulating it.

Imagery could be considered as a peculiar function of the VSWM system: the critical role of mental images in improving memory for different types of material has been paradigmatically demonstrated by Paivio (1971). According to Paivio's dual-code theory, information can be processed either verbally or visually: picture memory is overall superior because whenever we see a picture we tend to also represent that picture verbally, while a word does not necessarily activate a corresponding mental image. Associating two different codes – verbal and visual – to the to-be-remembered stimulus results in a stronger memory trace and this explains the pictures' advantage

usually reported in literature. Also, these encoding operations could be referred to the Working Memory activity, respectively to its verbal and visuospatial components.

Several studies have focused on the relationship between imagery and creative problem-solving, indicating that visualization facilitates innovative solutions and can clearly lead to novel and inventive discoveries (e.g., Einstein's use of combinatory play; Kekule's insight into the structure of benzene) (e.g., Antonietti 1991; Denis, Logie, Cornoldi, de Vega, & Engelkamp 2001; Knauff & Johnson-Laird 2002; Knauff, Fangmeier, Ruff, & Johnson-Laird 2003). The relationship between these tasks and VSWM has also been systematically studied (Pearson et al. 2001, for a review).

## Perception and VSWM

Experimental studies on visual mental imagery, neuropsychological findings and research on congenitally blind people support the assumption that VSWM and perception present some common functional properties, though remaining quite independent systems.

A main difference between a visual percept and a visual image is that the former appears to be the end product of (mainly) bottom-up mechanisms (but see the "active vision" approach, Findlay & Gilchrist 2003), since the visual stimulus has to be transferred from the retina through the thalamus to cortical areas, whereas the latter – involving also semantic knowledge – results from top-down processes. As underlined by Pylyshyn (1981), many low-level visual phenomena are not present in imagery: for instance, imagery is unable to anticipate the results of novel mixtures of colours or could not mimic the effects of motor tracking. However, as stressed by Kosslyn and colleagues (Kosslyn, Thompson, & Ganis 2002), such processes are all stimulus-driven (for example, colour mixing begins to occur at the retina), so it shouldn't be expected that such bottom-up processes could be mimicked by imagery. Several studies add evidence against a reduction of mental imagery to perception by showing that visuo-spatial mental images do not necessarily derive from a visual acquisition of the stimulus (see Cornoldi, et al. 1998): in fact, visual images may be activated by stimuli acquired in different sensorial modalities – for example, auditory or tactile – or by information stored in long-term memory. Such information is processed by the VSWM system resulting in a mental representation whose format can be different from the acquired perceptual (or conceptual) one. Accordingly, evidence has been reported in favour of similarities between representations activated by vision or haptic exploration (e.g., Easton, Srinivas, & Greene 1997; Pietrini, et al. 2004). In addition, in favour of an independence of the VSWM' s imagery processes from the perceptual ones, it has been found that perceptive and representative abilities develop and decay differently with age (Cornoldi et al. 1998; Hartman & Potter 1998).

However, the border between perceptual and imagery processes in VSWM is very thin as suggested by studies on the integration of visual images and visual percepts (e.g., Brockmole, Irwin, & Wang 2003) or by the conspicuous evidence indicating that

imagery and perceptual tasks involving the same modality usually interfere with each other (Brooks 1967, 1968; Segal 1971; Craver-Lemley & Reeves 1992). Several studies have also demonstrated that visual illusions, such as the Müller-Lyer illusion (Berbaum & Chung 1981), the Ponzo, Wundt and Hering illusions (Wallace 1984) or, more recently, the "oblique effect" (i.e., the fact that oblique line gratings are resolved less than vertical or horizontal ones) (Kosslyn, Sukel & Bly 1999) can be induced through imagery (for a review, see Finke 1989), but these results have been questioned by another study finding an absence of the visual illusions in the imagery field, at least in the case of the Ponzo and Ebbinghaus illusions (Giusberti, Cornoldi, De Beni, & Massironi 1998). Again, people seem to have the capacity of "breaking up" the elementary shapes organized by early vision in order to visualise new patterns (e.g., Rouw, Kosslyn, & Hamel 1997, 1998). Although quite persuasive in indicating common mechanisms underlying imagery and perceptual experience, the previous results are controversial. In fact, other studies reported that some effects well established at the perceptual level, such as pop-out, illusions (e.g., Massironi, Rocchi, & Cornoldi 2001) and similarities (Cornoldi, Rigoni, Tressoldi, & Vio 1999) do not find a correspondence at the VSWM imaginative (or representative) level. For example, Chambers and Reisberg (1985) required participants to mentally visualise the alternative interpretation of a reversible figure of which they had previously memorised only one potential view. People were unable to imagine the alternative figure, although some of them could see the other interpretation when required to draw the figure (see also Reisberg & Chambers 1991; Slezak 1995). However, it has been suggested that under certain circumstances mental images can be reinterpreted too (for a review, see Cornoldi, Logie, Brandimonte, Kaufmann, & Reisberg 1996). Other studies have demonstrated that people can often fail to reach novel insights on the basis of imagery alone, although such insights become obvious when the same material is visualised and not imagined. For instance, Reed & Johnsen (1975) showed that participants performed very poorly in discovering hidden figures within imagined patterns, compared to when the same patterns were made visually available as drawings.

The relationship between VSWM and perception has been largely investigated in the neuropsychological domain. Several neuroimaging studies have attested that mental imagery and perception share common processing systems: in particular, an event-related fMRI was used to monitor cortical activation during either imagery or visual perception tasks and reported a similar pattern of activation in Area 17 of the visual cortex (e.g., Kosslyn, Ganis, & Thompson 2001; Formisano, et al. 2002; Ganis, Thompson, & Kosslyn 2004). An overlap between perceptual and imagery mechanisms was assessed by studies using transcranial magnetic stimulation (TMS): for example, by impairing activity in the medial occipital cortex Kosslyn and colleagues (Kosslyn et al. 1999) showed that this manipulation disrupted both imagery and perception to the same extent. Similarly, Sparing and others (Sparing, et al. 2002) showed that visual mental imagery activated the medial occipital cortex (usually active during visual perception) while a control auditory task did not. Other studies have demonstrated that an impaired capacity in elaborating colours, spatial features, visual stimuli and a

spatial unilateral neglect may affect the perceptive level as much as the representative one (Nichelli 1999). Such evidence suggests that early visual cortex is strongly involved in visual imagery.

Furthermore, abundant neuropsychological evidence reports a strong parallelism between the organisation of the visual (perceptive) and the visuo-spatial memory systems. Two different cortical pathways have been individuated in the human visual cortex (e.g. Clark, et al. 1996; Haxby, et al. 1991; but see, Rao, Rainer, & Miller 1997): the occipitotemporal pathway (ventral or "what" stream) specialised in object recognition and the occipitoparietal pathway (dorsal or "where" stream) devoted to processing spatial features and important in motion coding related to the control of action (Milner & Goodale 1995). Interestingly, the same domain specificity organisation was found in human prefrontal cortex, the area of the brain usually associated with working memory: in fact, a dissociation was demonstrated between processing visual features like colour, shape, brightness, texture (inferior prefrontal cortex) and spatial features (superior prefrontal cortex) (e.g., Courtney, Ungerleider, Keil, & Haxby 1996; Landau & Jackendoff 1993; Luzzatti, et al. 1998; Smith & Jonides 1996; Smith, et al. 1995). A similar neural dissociation between encoding of location and of visual features like colour has been reported in studies specifically attesting visuo-spatial working memory abilities (e.g., Carlesimo, Perri, Turriziani, Tomaiolo, & Caltagirone 2001; Hecker & Mapperson 1997) and in spatial imagery, for example in studies on schizophrenia (e.g., Aleman, de Haan, & Kahn 2005).

Incidentally, it might be worth mentioning that in some cases tasks assessing different domains have been found to activate similar cerebral areas thus recommending caution in assigning specific cognitive functions to single cortical areas: in fact, it is likely that cognitive processes could emerge from highly distributed and interactive neural networks (e.g., D'Esposito, et al. 1998; D'Esposito, Postle, Ballard, Lease 1999; Ishai, Ungerleider, Martin, Schouten, & Haxby 1999; Reichle, Carpenter, & Just 2000). Coming back to the spatial and visual dissociation in the human cortex, schizophrenic patients manifesting different deficits in object versus spatial perceptual tasks (Tek, Gold, Blaxton, Wilk, McMahon, & Buchanan 2002) showed a similar dissociation at the imagery level too, with a specific impairment of object imagery compared to spatial imagery (Aleman et al. 2005). A similar pattern was reported in a study on the effects of schizophrenia on spatial and object working memory (Coleman, et al. 2002).

However, evidence exists against a complete overlapping of imagery and the perceptual neural circuits (Roland & Gulyás 1994; Mellet, et al. 1996). For example, patients suffering of cortical blindness could manifest relatively normal imagery abilities (Chatterjee & Southwood 1995); other patients with localized damage in the retinotopically mapped areas were found to experience vivid visual hallucinations precisely in the "blindsighted" part of their visual field (Ramachandran & Hirstein 1997). More generally, many neuropsychological studies attested a dissociation between visual agnosia and a mental imagery deficit (e.g., Behrmann, Moscovitch, & Winocur 1994). Similarly, schizophrenic patients with VSWM deficits were found to have preserved basic perceptive abilities (Fleming, Goldberg, Binks, & Randolph 1997). These findings

suggest that perception and imagery processes in VSWM, although partially sharing common neural processes, should be regarded as complementary but independent mechanisms.

Research on congenitally blind people is a further and quite fruitful tool to investigate to what extent visual perception is involved in the generation and manipulation of visuo-spatial images. By comparing blind and sighted people in different visuo-spatial tasks (such as mental scanning, mental rotation, memory for paths, etc. . .), it emerges that although blind people can only experience the to-be-imagined objects in a haptic or auditory way (e.g., Arditi, Holtzman, & Kosslyn 1988), they are nonetheless able to create and manipulate visuo-spatial images (e.g., Vecchi 1998, 2001; Cornoldi, Cortesi, & Preti 1991; Marmor & Zaback 1976; Kerr 1983; Carreiras & Codina 1992; Klatzky, Golledge, Loomis, Cicinelli, & Pellegrino 1995; Aleman, van Lee, Mantione, Verkoijen, & de Haan 2001) and, according to Marmor (1978), they could even experience mental representations of colours. For instance, Marmor and Zaback (1976) found that the time taken by blind people to judge whether two figures (acquired by tactile exploration) differently oriented in the third dimension were identical or not depended upon their rotation angle, suggesting that blind participants were "visualising" the figures in their mind in order to rotate them. Such a pattern of results completely resembles that usually reported with sighted participants in the traditional mental rotation task (Shepard & Metzler 1971), although blind participants needed a longer time to perform the task (Marmor & Zaback 1976). It has been suggested that the longer time taken by blind pople occurred because of their scare familiarity with the material used: in fact, in a successive task assessing the ability to recognise sequences of letters written in Braille (familiar to blind subjects) but presented in a right/left inverted format, blind participants outperformed sighted ones (Heller, Calcaterra, Green, & Lima 1999).

However, blindness results in selective deficits, such as particular difficulties in mentally manipulating three-dimensional material (e.g., Cornoldi, et al. 1991; Cornoldi, Bertuccelli, Rocchi, & Sbrana 1993). Cornoldi et al. (1991) tested blind subjects in a task requiring the generation and processing of a sequence of positions within a matrix: blind participants were able to perform the task as accurately as the sighted when matrices used were two-dimensional, but their performance significantly decreased with 3D matrices. Again, blind participants show particular difficulties in mentally representing the rules of perspective (Arditi, et al. 1988), in foreshortening drawings (Heller, Calcaterra, Tyler, & Burson 1996) and in particularly complex or time-pressured tasks (e.g., Cornoldi et al. 1993). More generally, blind participants encounter serious difficulties whenever the task requires active processing abilities, as for instance when more than one image has to be generated, maintained and manipulated at the same time (a problem that seems to be exaggerated when using 3D materials) (Vecchi 1998; Vecchi, Monticelli, & Cornoldi 1995; Vecchi et al. 2006; Vecchi, Tinti & Cornoldi 2004).

Overall, research on congenitally blind people suggests that, although important, visual perception is not indispensable for mental imagery processes in VSWM.

## Alternative approaches to (Visuo-Spatial) Working Memory

The importance of the WM visuo-spatial component has been highlighted, starting from Baddeley's (1986) original idea of a visuo-spatial sketchpad for encoding and maintaining visuo-spatial information and continuing with Logie's (1995) assumption of a distinction between a visual cache and an inner scribe and with Cornoldi and Vecchi's (2000) "continuous" approach to the WM visuo-spatial component as a complex and articulated Visuo-Spatial WM system. Other models of WM (Engle & Kane 2004; Cowan 1988; Ericsson & Kintsch 1995) place more attention to the relationship between the WM and the long-term memory system and less to the peculiarity of the visuo-spatial component. Although in such models the VSWM is less defined and articulated than in Baddeley (1986), Logie (1995) and Cornoldi and Vecchi (2003) studies, a brief introduction to such views will be offered, in order to provide the reader with a much richer "panorama" of the VSWM notion.

In recent years, Engle and colleagues (Kane, et al. 2004; Engle & Kane 2004; Engle, Kane, & Tuholski 1999a) developed a "controlled" attention model of working memory: "WM is a system consisting of those long-term memory traces active above threshold, the procedures and skills necessary to achieve and maintain that activation, and limited-capacity, controlled attention" (Engle et al. 1999a: 102). The WM capacity would be jointly determined by the capacity of short-term memory and by the efficiency of an a-modal centre of "controlled" attention and would be organised as a "hierarchical structure with a general domain-free factor overarching several subordinate domain-specific factors" (Engle et al. 1999a: 125). Such conceptualisation is not too far from Baddeley' s tripartite model of WM (Baddeley 1986), in which the WM capacity is determined by the capacities of the slave systems plus the central executive's one. Domain-specific skills, strategies, and storage abilities specifically pertain to short-term memory (Kane et al. 2004), with the often reported separation between visuo-spatial and verbal domains primarily reflecting the specificity of the storage and rehearsal processes and only marginally the contribution of the central executive. Conversely, an a-modal general ability factor would be involved in operative processes of WM, as suggested by the high correlation between the verbal and visuo-spatial working memory span tasks reported by Kane et al. (2004) and by many other latent-variable studies (e.g., Ackerman, Beier, & Boyle 2002; Oberauer, Süß, Wilhelm, & Wittmann 2003; Süß, Oberauer, Wittman, Wilhelm, & Schulze 2002; Park, et al. 2002) (for neuropsychological evidence, see also Kane & Engle 2002)

In Engle and Kane's (2004) model, the visuo-spatial component of WM is thus involved both at the level of the LTM traces active above threshold, that could have a visuo-spatial nature, and at the level of the encoding strategies and procedures for maintaining activation that could be specifically visual or spatial (but also phonological, motor, auditory, etc. . . .). Furthermore, it is possible to interpret the differentiation proposed by Engle (Engle et al. 1999a) between a domain-general factor underlying WM abilities and domain-specific processes emerging in STM tasks, as the difference proposed by Cornoldi and Vecchi (2003) between modality-specific processes at the

basis of the WM continuum and more general processes, less domain-specific, placed at the top of the continuum. However, in Cornoldi and Vecchi's model control is associated, but not identified with attention: in fact, complex passive tasks may require more attention than simple active tasks and the WM control is never "amodal" but varies along a continuum maintaining modality-specific features (although in a more limited manner). This should clarify why Engle and Kane's (2004) and Cornoldi and Vecchi's model (2003) should not be conisdered as being too similar. Interestingly, Engle and colleagues (Engle, Tuholski, Laughlin, & Conway 1999b) found that not only spatial reasoning, but also general fluid reasoning was predictable on the basis of performance in spatial storage-rehearsal tasks and that the domain-general attention factor was strongly correlated with general fluid reasoning (e.g., Conway, Kane, & Engle 2003). These last findings deserve particular attention since they could help in clarifying how the VSWM continuous dimensions in Cornoldi and Vecchi's (2003) model are organised and interrelated with one another.

Another interesting approach to WM is Cowan's (1995, 1999, 2001) "embedded processes" model, in which WM is regarded as the activated portion of LTM. Working memory is the result of contributions from three different components: active memory, the focus of attention and long term memory. The organisation is "embedded", since the focus of attention is a subset of active memory – also defined as a short term memory store – that is itself a subset of long-term memory (Cowan 1988, 1995). Information can be (consciously) attended to only if it has been activated in the focus of attention: this activation might follow an attention's automatic transfer caused, for example, by relevant changes in the physical properties of the stimuli, or could result by voluntary shifts of attention. In Cowan's view (1999), the VSWM becomes a particular type of memory activation, and visualization is one of the processes that can be adopted to reactivate this memory. For instance, the visuo-spatial component is involved in the elaborative rehearsal of information: as the author explains (Cowan 2001), two items (e.g., "fish" and "brick") presented consecutively may be memorised as a single chunk of information by generating a mental image in which they are combined (e.g., a dead fish on a brick). The focus-of-attention has a limited capacity of 3–5 unrelated items (to be intended as integrated objects) common to both the processing and storage mechanisms: while carrying out processing tasks in the focus of attention, the information could be outside such subsystem but still in the activated area, to which attention is shifted whenever the memory load has to be recalled. The assumption of a common capacity between storage and processing mechanisms is not dissimilar to Cornoldi and Vecchi's (2003) WM continuous view, in which the cognitive load associated to a specific task is determined both by the interested modality (visual, auditory, etc...) and by the active elaboration required. However, Cowan diverges from Cornoldi and Vecchi when he claims a potentially unlimited capacity of the activated area of memory, of which the VSWM system is a modality. Whilst Cornoldi and Vecchi assign specific limits to the VSWM system, due to the amount of active control required and to the reciprocal interference of tasks relying on a similar modality, Cowan (2001) assumes that the VSWM, to be intended in his model as a

type of activated memory in which not-consciously attended information is nonetheless available for retrieval, is just time-limited: activation declines within about 10 to 20 seconds unless it is reactivated and it is sensitive to interference from subsequent stimuli (especially if they are in the same modality or requiring a similar process).

Conversely, Cowan (1999) is closer to Cornoldi and Vecchi's (2003) idea of active processes occurring in VSWM when he assumes that the information in the focus of attention, and potentially the activated information, can be integrated with other simultaneously attended elements or with successively acquired material and such integrated information is transferred to LTM. Interestingly, an information could be considered to be in working memory also if it is not even activated but whenever "there are cues in working memory that point to the item and raise the likelihood that it could be retrieved if necessary" (Cowan 1999:66): the WM system is thus enlarged to embrace also LTM. Similarly to Cornoldi and Vecchi's "continuous" approach to VSWM, for Cowan (1988, 1995) activation of information is not an all-or-none process, but LTM information could be activated to different degrees so that in each situation a specific information could be more or less available. In this respect, Cowan's model is not so dissimilar from Cornoldi and Vecchi's view, which in fact assumes a less rigid fractionation of the WM system compared to Baddeley's original model (1986) but it significantly diverges in positing a strong dependence of VSWM on LTM, without clarifying – for example – how material could be manipulated in VSWM without being transferred into the LTM.

Ericsson & Kintsch (1995) have approached the study of WM by investigating expert-performance, under the assumption that an exceptional functioning of the WM system should clarify also the general mechanisms of WM in other skilled everyday activities. "The phenomenon of working memory includes all those mechanisms that maintain selective access to the information and the procedures that are necessary for a subject to complete one or more specific concurrent tasks" (Ericsson & Delaney 1999:260). Since much of the authors's experimental evidence comes from observations of expert chess players and since the game of chess specifically involves visuo-spatial abilities, the assumption of Ericsson and collaborators is that the WM system may be considered as referring to the VSWM system too. In particular, it could be said that the VSWM system is considered by Ericsson and collaborators in terms of a particular task "environment", with its specific methods for encoding and retrieving visuo-spatial information. Ericsson and Kintsch (1995) measured the effect of different interruptions or interferences on the ongoing tasks assessing experts in their domain of expertise: they found that such interruptions marginally impacted performance, suggesting that information required to carry out those tasks is not stored primarily in temporary storage (at least for skilled performance) but in LTM. Experts are able to rapidly encode information in LTM with numerous and elaborated cues related to prior knowledge: such "indexed" information can be later accessed very efficiently with retrieval cues. Encoding could occur by means of retrieval structures – that is "a set of retrieval cues [that] are organized in a stable structure" (Ericsson & Kintsch 1995:216) – and/or by connecting items to other items in LTM through knowledge-

based associations resulting in an integrated representation of information in LTM. It is argued that the retrieval structures assessed in expert performance could be extended to a wide variety of tasks (e.g., text comprehension, problem solving) beyond the expert's domain. In summary, from this perspective VSWM should be considered as a long-term VSWM: "cognitive processes are viewed as a sequence of stable states representing end products of processing" and "acquired memory skills allow these end products to be stored in long-term memory and kept directly accessible by means of retrieval cues in short-term memory [...]" (Ericsson & Kintsch 1995:211). By stressing the importance of LTM in WM tasks, the model conflicts with more traditional accounts of WM that conversely insist on the transitory storage capacity of the system and it diverges from Cornoldi and Vecchi (2003) in underestimating the operative capacity of a temporary memory system as the WM could be, by assigning the principal role to the LTM.

Although Baddeley (1986) reports that one of the functions of WM is to be used in learning, it is not clear in his original model which mechanisms allow stimuli temporarily stored in WM to be learned and to become long-term representations, neither is it clear how long-term memory (LTM) influences WM processes. However, as could be inferred by the discussion of their models, Baddeley and Logie (1999) seem to refuse the assumption that WM is an activated part of the LTM: in their view, LTM and WM are related but represent functionally distinct systems. The assumption of a distinct WM and LTM is supported by a series of neuropsychological studies on the dissociation between the two memory systems. For instance, Beschin, Cocchini, Della Sala & Logie (1997) reported the case of a patient showing an evident impairment in the capacity to create and manipulate visual images, whereas the ability in encoding information in LTM was preserved. In recent years Baddeley (2000) reviewed his WM model, adding a further subcomponent, the episodic buffer, which is a limited capacity store responsible for the temporal retention and integration of information coming both from the episodic long-term memory and from the slave systems. Furthermore, Logie (1995) considers the contribution of LTM as fundamental in processing information coming from the environment. Specifically, long-term knowledge would support the visual peripheral subsystems in the detection of the stimuli, contributing to the visual recognition of the to–be-processed objects.

We have already examined in the previous section the theoretical position of Cornoldi and Vecchi (2003) as regards the relationship between LTM and WM. Briefly, although the authors postulate a clear separation between LTM and WM, they agree with the assumption that information can be transferred from one memory's structure to the other. In particular, Cornoldi and Vecchi argue that long-term knowledge could be involved in the execution of active tasks that require the integration of information coming from different sources (e.g., verbal, visual, haptic sensory systems and semantic memory). However, if WM were included within LTM, it would be unclear how memory traces stored in WM could rapidly decay, how it would be possible to manipulate visuo-spatial abstract stimuli (such as mentally rotating an imagined

three-dimensional configuration) and operate on new information detected in the external world without a contribution from LTM.

## VSWM and consciousness

The concept of consciousness (or awareness) has always been critical in philosophical and psychological studies. According to Chalmers (1996), "awareness" is a functional state in which some information that we are aware of can be used to influence behaviour and can be verbally reported, whereas "consciousness" (or "experience") indicates an intrinsically non-functional qualitative state that is not related to behaviour. However, for the purpose of our discussion, we will consider the terms "consciousness" and "awareness" as interchangeable.

Research on consciousness has been carried out from many different perspectives: for instance, an interesting approach could be found in a quite recent review on the peculiarity of "Self" in experimental psychology and cognitive neuroscience (Gillihan & Farah 2005) which highlights how the concept of conscious awareness is strongly related to the concept of "Self". Interestingly, it has been suggested that imagery might be involved in self-awareness. People can frequently examine themselves by using imagery: for example, highly self-conscious people often use imagery as a means of introspection (Turner, Scheier, Carver, & Ickes 1978; Barrios & Singer 1981–82). Also, (moderate) correlations have been reported between frequency of daydreaming (a form of imagery) and self-consciousness (Gold & Henderson 1981). Again, Suler (1990:199) suggests that "Images serve as internal reference points for the sense of continuity of one's experience of self and objects across time." Furthermore, in Kitamura's view, "imagery is perhaps a product of our desire or need to pick up certain information about our total situation and ourselves from the viewpoint of the other person" (Kitamura 1985:92). Cartright (1980) believes that identity is a construct consisting in a set of self-images referring to either common activities, past experiences, future actions and experiences, feelings, moods, and so forth. Morin argues that humans possess "self-representational processes" for mentally reproducing social mechanisms responsible for self-awareness (Morin 1993; Morin & DeBlois 1989): mental images allow people to see themselves behaving as others would see them. Morin also specifies that imagery is more adequate in making a person aware of the more public aspects of the self (i.e., an individual's observable behaviours and visible physical characteristics) compared to the more private ones (e.g., moods, motives, mental processes, desires, etc. . . .).

The issue of conscious awareness has been largely explored in the perceptual domain (see Adams 1957). Much of the literature has focused on subliminal messages, i.e. inputs that cannot be consciously perceived because their intensity is insufficient to reach the human's awareness threshold. For instance, Underwood (1994) investigated the effects of a subliminal unreportable smiling face on the perception of a subsequent consciously perceived neutral face: he found that people that saw the subliminal happy

face tended to attribute a sad expression to the neutral face significantly more often than people that did not see the face (an effect known as "negative contrast effect").

Two different approaches have been adopted in perceptual research to measure awareness, using either an objective or a subjective criterion (for a review, see Tunney & Shanks 2003). Both criteria measure the relationship between a performance and the level of awareness for the information that influences that performance. The subjective criterion requires participants "to respond according to their own internal state of awareness" (Tunney & Shanks 2003: 1061). Accordingly participants have to either provide a verbal report about what they are aware of, or say how confident they are in the correctness of a discrimination made, or estimate the overall level of their accuracy. Another type of subjective measure is the "guessing criterion" for which a piece of information is unconscious whenever participants believe that they are guessing it (e.g., Dienes, Altmann, Kwan, & Goode 1995). On the other side, the objective approach defines awareness in terms of performance in tasks assessing perceptual discriminations (see Reingold 2004): participants have to make a discriminative choice without necessarily giving a verbal report about its discriminability. Both the criteria have some limits: the subjective threshold has the limit of leaving to the perceiver the choice of what is "awareness", so that one individual may be more conservative and another more liberal in his reports; the objective criterion sometimes gives a rather too strict awareness threshold so that it is often impossible to demonstrate unconscious processing following this method.

As reported by Underwood and Bright (1996), many studies have shown that some stimuli can be recognised even without attention (or awareness). For instance, several neuropsychological studies with "blindsighted" patients (i.e., individuals with a lesion in the visual cortex that determines blindness in a specific region of the visual field) reveal that although these patients report that they cannot see in the blind region corresponding to their scotoma, when asked to guess among different alternatives about what appeared in the blind region, they answered correctly well above chance level (e.g., Weiskrantz 1986; Pöppel, Held, & Frost 1973). This suggests that such individuals could see, although they were unaware of what they were seeing. Again, dichotic shadowing experiments have demonstrated that unattended words – although not available for verbal report (and thus below the awareness threshold) – might still influence ongoing behaviour (e.g., Lewis 1970; Underwood 1977).

The term "awareness" has often been interpreted in terms of the opposition between implicit and explicit cognitive processes (see Underwood & Bright 1996). The distinction implicit/explicit may be referred both to learning and memory processes. Implicit learning is observed when material explicitly unavailable is observed to influence performances (e.g., Nelson 1978; Kunst-Wilson & Zajonc 1980): that is to say, performances in a particular task increase (i.e., a previously learnt task is subsequently re-learnt faster) but without a corresponding increase in the verbal knowledge about how to carry out the task (see the seminal research of Reber on the implicit learning of artificial grammars 1967). However, other authors are skeptical about the possibility of

implicit learning (e.g., Carlson & Dulaney 1985; for a more recent review, see Shanks & St. John 1994).

Implicit memory (for a review, see Schacter, Chiu, & Ochsner 1993) refers to situations in which although a particular information (consciously acquired, see Berry & Dienes 1991) cannot be retrieved in a subsequent free-recall paradigm, it can nonetheless influence subsequent (more indirect) memory measures. For instance, implicit memory phenomena have been observed in direct priming experiments, in which exposure to a word or object on a study list facilitates its subsequent identification when degraded perceptual cues are provided (e.g., Tulving & Schacter 1990).

Conscious processes have also been interpreted in terms of automatic processes versus effortful processes, according to Hasher and Zacks's theory (1979). Hasher and Zacks (1979) assumed that automatic processes operate continually, independently of awareness or intention, while effortful processes are intentional, conscious, planned and controlled. However, although automatic processes may be carried out without the necessity of conscious control, this does not imply that the knowledge acquired through automatic processes cannot be accessed by consciousness (Hasher & Zacks 1979). Other more recent views tend to conceive of automaticity (or consciousness) in terms of a "continuum" with new, unskilled activities placed at the conscious control end and familiar, highly practiced processes at the other extreme (e.g., Kahneman & Chajzyck 1983; Cohen, Dunbar, & McClelland 1990).

Such studies raise a critical theoretical issue, i.e. whether consciousness is an all-or-none state or a more continuous and gradual phenomenon. In a recent research Sergent and Dehaene (2004) tested the all-or-none character of conscious perception by adopting an "attentional blink" paradigm (see Raymond, Shapiro, & Arnell 1992). The attentional blink occurs when two target-stimuli are embedded in a rapid sequence of distractors: the second target most of the time cannot be explicitly reported if it is presented within an interval of 200–500 ms from the first target. The goal of the authors was to clarify whether participants were really unconscious of the second target, that is to say whether the attentional blink was determined by an all-or-none loss of conscious access or by a continuous degradation of the information about the second target. The findings indicated that the attentional blink phenomenon yielded to an all-or-none response pattern, leading the authors to conclude for an all-or-none nature of (perceptual) consciousness. According to these findings, the "global neuronal workspace" model developed by Dehaene and colleagues (Dehaene, Kerszberg, & Changeux 1998; Dehane & Naccache 2001) offers a non-continuous view of consciousness. In particular, the theory assumes that a stimulus is first automatically encoded by a number of cerebral areas activated sequentially in a bottom-up fashion. Successively, in order to be consciously perceived, other top-down processes occur that reinforce the previous bottom-up codes by means of long-distance connections among different regions of the brain. Such recurrent interactions between distant cortical areas are thus regarded as necessary in order to experience conscious perception (e.g. Dehaene et al. 1998; Di Lollo, Enns, & Rensink 2000; Lamme 2003). In this way the stimulus accesses a sort of "global neural workspace" (Dehaene et al. 1998) that allows both the

maintenance of the stimulus and the execution of controlled processes such as verbal report, voluntary manipulation, voluntary action and long-term memorisation of information. Whenever a stimulus only enhances bottom-up processes, without the subsequent top-down amplification, such stimulus remains unavailable to controlled processes and cannot be consciously perceived.

Conversely, other studies suggest a continuous view of consciousness (e.g., Bar, et al. 2001; Kanwisher 2001): for example, in their "sensorimotor contingency" theory, O'Regan and Noë (2001) argue that visual awareness is not a yes-or-no phenomenon, but it is a "matter of degree". They assume that when we perceive a scene we are aware only of some of the scene's attributes that influence our actual behaviour. Furthermore, the authors distinguish between two kinds of visual consciousness: a "transitive visual consciousness" or "consciousness of" and a visual consciousness "in general". The first type of consciousness (transitive visual consciousness) consists in being conscious of an aspect of a scene (for example, the shape of an object or its colour) and implies that such information can be integrated in the viewer's planning, reasoning, decision-making and linguistic activities. Different features of the same scene could become "transitively conscious" by shifting the attention to them. The second type of consciousness (visual consciousness in general) is a higher-order capacity, that consists of the ability to become aware of different features of a scene, condition that, in the authors' view, is not available to blind people or while sleeping. Visual perception consists of a skilful exploratory activity carried out on the basis of practical knowledge: visual awareness depends on the integration of these patterns of skilful exercise into ongoing planning, reasoning, and so forth.

To come closer to the WM models, several recent studies seem to support the view that WM and conscious awareness are intimately related (Andrade 2001; Baars 2002; Baddeley 1993). In a recent review of his model of working memory, Baddeley (2003) suggests that conscious awareness might be related to the "episodic buffer", the fourth component recently added to the original WM model (Baddeley 2000). As already mentioned, the episodic buffer "is assumed to be a limited capacity store that binds together information to form integrated episodes. It is assumed to be attentionally controlled by the executive and to be accessible to conscious awareness. Its multi-dimensional coding allows different systems to be integrated, and conscious awareness provides a convenient binding and retrieval process" (Baddeley 2003: 836). Also other working memory models, presented in the preceding sections, seem to have important implications for the concept of consciousness, as the conscious content of the mind could be associated with the content of working memory which is under the attentional focus.

Baars and Franklin (2003) proposed a "Global Workspace" theory, according to which "consciousness is associated with a global work-space in the brain – a fleeting memory capacity whose focal contents are widely distributed ('broadcast') to many unconscious specialized networks" (Baars & Franklin 2003: 166). The classical view of WM proposed by Baddeley (1986), with the distinction among a visuo-spatial sketchpad, a phonological loop and central executive functions, is maintained in the "Global

Workspace" theory (Baars & Franklin 2003), but here the role of conscious elements is specified in greater detail. In particular, the authors argue that some unconscious networks (e.g., unconscious verbal or visuo-spatial automatisms, and unconscious executive functions), that they defined as "contexts", work together to determine the conscious contents, that is to say "conscious contents recruit widespread unconscious functions, via a broadcast of the contents" (Baars & Franklin 2003:170).

From a neuropsychological perspective, it has been demonstrated that the activation of specialised areas in the ventral visual pathways interacting with other specific areas of the prefrontal and parietal cortex is associated with visual awareness (Crick & Koch 1995; for a review, see Rees, Kreiman, & Koch 2002). Interestingly, spatial working memory seems to be similarly mediated by a network of predominantly right-hemisphere regions that include areas in the posterior parietal, occipital, and frontal cortex (Smith & Jonides 1996).

In summary, experimental studies and neuropsychological evidence suggest a strong link between awareness and Working Memory, and in particular VSWM: an intriguing possibility would be to identify a further transversal "continuum" in Cornoldi and Vecchi (2003) VSWM model responsible for the level of consciousness associated with each specific task, independently of the tasks content (i.e., its location along the horizontal continuum) and the level of control it requires (i.e., its location along the vertical continuum). In fact, the continuity approach inspiring Cornoldi and Vecchi's model could be also used for considering consciousness as a continuous feature of working memory associated with its degree of activation.

## Conclusions

The aim of the present chapter was to illustrate the architecture and functioning of the Visuo-Spatial Working Memory system as conceptualized by Cornoldi and Vecchi's (2003) model: throughout the chapter, we specifically examined all the important functions ascribed to VSWM and we contrasted the model with other WM alternative approaches to better outline its peculiarities.

The VSWM is a system devoted to the retention and the active manipulation of visuo-spatial material that plays a critical role in many cognitive activities, such as mentally generating and maintaining those dynamic spatial representations that allow us to move and interact with our environment. In his original model of WM, Baddeley (1986; Baddeley & Hitch 1974) outlined a system for the maintenance of visuo-spatial information, the so-called Visuo-Spatial Sketchpad (VSSP), but such a system was defined primarily as a storage component without the active connotation conversely implicit in the term "VSWM". Logie (1995) partially reformulated the traditional WM model, by distinguishing between a visual-passive component (the "visual cache") and an active spatial component ("the inner scribe") within the VSSP.

Partially diverging from the previous formulations of the WM system, Cornoldi and Vecchi have proposed an alternative "continuous" model of WM, organised along

a horizontal and a vertical dimension. The horizontal continuum expresses the task's content (e.g., visuo-spatial, verbal, tactile) while the vertical dimension indicates the amount of cognitive active control required for it to be carried out.

In Cornoldi and Vecchi's model, mental imagery is a critical function of the VSWM system: in fact, imagery is a WM process that yields an internal visuo-spatial representation, that could be temporarily retained and processed within a limited memory store.

According to the "continuous" conical model of the VSWM (Cornoldi & Vecchi 2003), the areas at the basis of the conical structure acquire information from either LTM or through the perceptual system. It is thus of critical interest to establish how VSWM is related to perception and to LTM. Many experiments conducted on congenitally blind people have showed that the lack of visual experience does not prevent the generation and manipulation of mental images, although specific deficits may occur associated with a particular task demand. Such findings, consistently supported by other experimental and neuropsychological evidence, suggest that perception and VSWM, although sharing functionally common properties, should be regarded as independent systems.

Other research has focused on the relationship between WM and LTM: some theories argue that WM is an activated portion of LTM (e.g., Ericsson & Kintsch 1995; Cowan 1988), others consider WM and LTM as related but functionally distinct systems. Cornoldi and Vecchi (2003) disagree with the assumption of a WM included within the LTM: in fact, if a WM task always implies the activation of long-term knowledge, it is unclear how our cognitive system can process and manipulate new stimuli detected in the environment or how mental representations stored in WM can rapidly decay.

Finally, a critical issue is the relationship between the WM system, the VSWM in particular, and conscious awareness. Studies on implicit cognition have demonstrated that many cognitive processes carried out by the VSWM system operate below the level of consciousness; it still remains unclear why certain material and/or mental processes are accessible to consciousness whilst others are not.

Many questions regarding the structure and functioning of the WM system remain open. Although not considered in the present chapter, new answers may also come from the development of connectionist models. For instance, some researchers have proposed connectionist models for information ordering (e.g., Burgess & Hitch 1999; Henson 1998; Page & Norris 1998), but such models are only partially consistent with human data (e.g., Cumming, Page, & Norris 2003; Hitch, Fastame, & Flude 2005).

In summary, although at present general agreement on the organization and functioning of the WM structure is still lacking, conspicuous neuropsychological and experimental evidence supports many assumptions of the VSWM model proposed by Cornoldi and Vecchi (2003).

## References


Ackerman, P. L., Beier, M. E., & Boyle, M. O. (2002). Individual differences in working memory within a nomological network of cognitive and perceptual speed abilities. *Journal of Experimental Psychology: General, 131,* 567–589.

Adams, J. K. (1957). Laboratory studies of behaviour without awareness. *Psychological Bulletin, 54*, 383–405

Aleman, A., de Haan, E. H. F., & Kahn, R. S. (2005). Object versus spatial visual mental imagery in patients with schizophrenia. *Journal of Psychiatry and Neuroscience, 30* (1), 53–56.

Aleman, A., van Lee, L., Mantione, M. H. M., Verkoijen, I. G., & de Haan, E. H. F. (2001). Visual imagery without visual experience: Evidence from congenitally blind people. *Neuroreport, 12*, 2601–2604.

Anderson, J. R. (1978). Arguments concerning representations for mental imagery. *Psychological Review, 85*, 249–277.

Anderson, J. R., Reder, L. M., & Lebiere, C. (1996). Working memory: Activation limitations on retrieval. *Cognitive Psychology, 30*, 221–256.

Andrade, J. (Ed.) (2001). *Working memory in perspective.* Philadelphia, PA: Psychology Press.

Antonietti, A. (1991). Why does mental visualisation facilitate problem solving? In R. H. Logie & M. Denis (Eds.), *Mental images in human cognition*. Amsterdam: North Holland.

Arditi, A., Holtzman, J. D., & Kosslyn, S. M. (1988). Mental imagery and sensory experience in congenital blindness. *Neuropsychologia, 26*, 1–12.

Baars, B. J. (2002). The conscious access hypothesis: Origins and recent evidence. *Trends in Cognitive Sciences, 6*, 47–52.

Baars, B. J., & Franklin, S. (2003). How conscious experience and working memory interact. *Trends in Cognitive Sciences, 7*, 166–172.

Baddeley, A. D. (1986). *Working memory*. Oxford: Oxford University Press.

Baddeley, A. D. (1993). Short-term phonological memory and long-term learning: A single case study. *European Journal of Cognitive Psychology, 5*, 129–148.

Baddeley, A. D. (1996). Exploring the central executive. *Quarterly Journal of Experimental Psychology, 49A*, 5–28.

Baddeley, A. D. (2000). The episodic buffer: A new component of working memory? *Trends in Cognitive Sciences, 4*, 417–423.

Baddeley, A. D., & Andrade, J. (2000). Working memory and the vividness of imagery. *Journal of Experimental Psychology: General, 129*, 126–145.

Baddeley, A. D., & Hitch, G. (1974). Working memory. In G. H. Bower (Ed.), The psychology of learning and motivation: *Advances in research and theory, Vol. 8* (pp. 47–89). New York: Academic Press.

Baddeley, A. D., & Logie, R. H. (1999). Working memory: The Multiple-component Model. In A. Myake & P. Shah (Eds.), *Models of working memory: Mechanisms of active maintenance and executive control* (pp. 28–61). Cambridge: University Press.

Baddeley, A. D., Papagno, C., & Vallar, G. (1988). When long-term memory learning depends on short-term storage. *Journal of Memory and Language, 27*, 586–595.

Banai, K., & Ahissar, M. (2004). Poor Frequency Discrimination Probes Dyslexics with Particularly Impaired Working Memory. *Audiology and Neuro-Otology, 9* (6), 328–340.

Bar, M., Tootell, R. B., Schacter, D. L., Greve, D. N., Fischl, B., Mendola, J. D., Rosen, B. R., & Dale, A. M. (2001). Cortical mechanisms specific to explicit visual object recognition. *Neuron, 29*, 529–535.

Barrios, M. V., & Singer, J. L. (1981–82). The treatment of creative blocks: A comparison of waking imagery, hypnotic dream, and rational discussion techniques. *Imagination, Cognition and Personality, 1* (1), 89–109.

Behrmann, M., Moscovitch, M., & Winocur, G. (1994). Intact visual imagery and impaired visual perception in a patient with visual agnosia. *Journal of Experimental Psychology: Human Perception and Performance, 20*, 1068–1087.

Berbaum, K., & Chung, C. S. (1981). Müller-Lyer illusion induced by imagination. *Journal of Mental Imagery, 5*, 125–128.

Berry, D. C. & Dienes, Z. (1991). The relationship between implicit memory and implicit learning. *British Journal of Psychology*, 82, 359–73.

Beschin, N., Cocchini, G., Della Sala, G., & Logie, R. H. (1997). What the eyes perceive, the brain ignores: A case of pure unilateral representational neglect. *Cortex, 33*, 3–26.

Bower, G. H. (1972). Mental imagery and associative learning. In L. W. Gregg (Ed.), *Cognition in Learning and Memory*. Wiley, New York.

Brockmole, J. R., Irwin, D. E., & Wang, R. F. (2003). The locus of spatial attention during the temporal integration of visual memories and percepts. *Psychonomic Bulletin and Review, 10*, 510–515.

Brooks, L. R. (1967). The suppression of visualisation by reading. *Quarterly Journal Experimental Psychology, 19*, 289–299.

Brooks, L. R. (1968). Spatial and verbal components in the act of recall. *Canadian Journal of Psychology, 22*, 349–368.

Burgess, N., & Hitch, G. (1999). Memory for serial order: A network model of the phonological loop and its timing. *Psychological Review, 106*, 551–581.

Carlesimo, G. A., Perri, R., Turriziani, P., Tomaiuolo, F., & Caltagirone, C. (2001). Remembering what but not where: Independence of spatial and visual working memory in the human brain. *Cortex, 37*, 519–537.

Carlson, R. A., & Dulaney, D. E. (1985). Conscious attention and abstraction in concept learning. *Journal of Experimental Psychology: Learning, Memory and Cognition, 11* (1), 45–58.

Carreiras, M., & Codina, M. (1992). Spatial cognition of the blind and sighted: Visual and amodal hypotheses. *Cahiers de Psychologie Cognitive, 12*, 51–78.

Cartright, D. S. (1980). Exploratory analyses of verbally stimulated imagery of the self. *Journal of Mental Imagery, 4*, 1–21.

Cavallini, E., Fastame, M. C., Palladino P., Rossi, S. & Vecchi T. (2003–2004). Visuo-spatial span and cognitive functions: A theoretical analysis of the "Corsi" task. *Imagination, Cognition and Personality, 23* (2–3), 217–224.

Chalmers, D. J. (1996) *The conscious mind: In search of a fundamental theory*. New York, NY, USA: Oxford University Press.

Chambers, D., & Reisberg, D. (1985). Can mental images be ambiguous? *Journal of Experimental Psychology: Human Perception and Performance, 11*, 317–328.

Chatterjee, A., & Southwood, M. H. (1995). Cortical blindness and visual imagery. *Neurology, 45*, 2189–2195.

Clark, V. P., Keil, K., Maisog, J. M., Courtney, S., Ungerleider, L.G., & Haxby, J. V. (1996). Functional magnetic resonance imaging (fMRI) of human visual cortex during face matching: A comparison with positron emission tomography (PET). *Neuroimage, 4*, 1–15.

Cohen, J. D., Schaie, K. W., & Gribbin, K. (1977). The organisation of spatial abilities in older men and women. *Journal of Gerontology, 32*, 578–585.

Cohen, J. D., Dunbar, K., & McClelland, J. L. (1990). On the control of automatic processes: A parallel distributed processing account of the Stroop effect. *Psychological Review, 97*, 332–61.

Coleman, M. J., Cook, S., Matthysse, S., Barnard, J., Lo, Y., Levy, D. L., Rubin, D. B., & Holzman, P. S. (2002). Spatial and object working memory impairments in schizophrenia patients. *Journal of Abnormal Psychology, 111*, 425–35.

Conrad, R. (1964). Acoustic confusions in immediate memory. *British Journal of Psychology, 55*, 75–84.

Conway, A. R. A., Kane, M. J., & Engle, R. W. (2003). Working memory capacity and its relation to general intelligence. *Trends in Cognitive Sciences, 7*, 547–552.

Cornoldi, C. (1995). La memoria di lavoro visuo-spaziale. In F. S. Marucci (Ed.), *Le immagini mentali* (pp. 145–181). Roma: Nuova Italia Scientifica.

Cornoldi, C., Bertuccelli, B., Rocchi, P., & Sbrana, B. (1993). Processing capacity limitations in pictorial and spatial representations in the totally congenitally blind. *Cortex, 29*, 675–689.

Cornoldi, C., Cortesi, A., & Preti, D. (1991). Individual differences in the capacity limitations of visuospatial short-term memory: Research on sighted and totally congenitally blind people. *Memory and Cognition, 19*, 459–468.

Cornoldi, C., De Beni, R., Giusberti, F., Marucci, F. S., Massironi, M., & Mazzoni, G. (1991). The study of vividness of images. In R. H. Logie & M. Denis (Eds.), *Mental images in human cognition* (pp. 305–312). Amsterdam: North-Holland, Elsevier.

Cornoldi, C., De Beni, R., Giusberti, F., & Massironi, M. (1998). Memory and imagery: A visual trace is not a mental image. In M. A. Conway, S. E. Gathercole, & C. Cornoldi (Eds.), *Theories of memory*, Vol. II. Hove, UK: Psychology Press.

Cornoldi, C., Logie, R. H., Brandimonte, M. A., Kaufmann, G., & Reisberg, D. (1996). *Stretching the imagination: Representation and transformation in mental imagery*. New York: Oxford University Press.

Cornoldi, C., Rigoni, F., Tressoldi, P. E., & Vio, C. (1999). Imagery deficits in non verbal learning disabilities. *Journal of Learning Disabilities, 32*, 48–57.

Cornoldi, C., Rigoni, F., Venneri, A., & Vecchi, T. (2000). Passive and active processes in visuo-spatial memory: Double dissociation in developmental learning disabilities. *Brain and Cognition, 43*, 17–20.

Cornoldi, C., & Vecchi, T. (2000). Mental imagery in blind people: The role of passive and active visuo-spatial processes. In M. Heller (Ed.), *Touch, representation, and blindness* (pp. 143–181). Oxford: Oxford University Press.

Cornoldi, C., & Vecchi, T. (2003). *Visuo-spatial working memory and individual differences.* Hove: Psychology Press.

Courtney, S. M., Ungerleider, L. G., Keil, K., & Haxby, J. V. (1996). Object and spatial working memory activate separate neural systems in human cortex. *Cerebral Cortex, 6*, 39–49.

Cowan, N. (1988). Evolving conceptions of memory storage, selective attention, and their mutual constraints within the human information processing system. *Psychological Bulletin, 104*, 163–191.

Cowan, N. (1995). *Attention and memory: An integrated framework*. New York: Oxford University Press.

Cowan, N. (1999). An Embedded-Processes Model of Working Memory. In A. Myake & P. Shah (Eds.), *Models of working memory: Mechanisms of active maintenance and executive control* (pp 62–101). Cambridge: University Press.

Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences, 24* (1), 87–114.

Craver-Lemley, C., & Reeves, A. (1992). How visual imagery interferes with vision. *Psychological Review, 99*, 633–649.

Crick, F., & Koch, C. (1995). Are we aware of neural activity in primary visual cortex? *Nature, 375*, 121–123.

Cumming, N., Page, M. & Norris, D. (2003). Testing a positional model of the Hebb Effect. *Memory, 11*, 43–63.

Currie, G. (1995). Visual imagery as the simulation of vision. *Mind and Language, 10*, 25–44.

D'Esposito, M., Aguirre, G. K., Zarahn, E., Ballard, D., Shin, R. K., Lease, J. (1998). Functional MRI studies of spatial and nonspatial working memory. *Cognitive Brain Research, 7*, 1–13.

D'Esposito, M., Postle, B. R., Ballard, D., Lease, J. (1999). Maintenance versus manipulation of information held in working memory: An event-related fMRI study. *Brain and Cognition, 41*, 66–86.

Daneman, M., & Carpenter, P. A. (1980). Individual differences in working memory and reading. *Journal of Verbal Learning and Verbal Behaviour, 19*, 450–466.

De Beni, R., Palladino, P., Pazzaglia, F., & Cornoldi, C. (1998). Increases in intrusion errors and working memory deficit of poor comprehenders. *Quartely Journal of Experimental Psychology, 51A*, 305–320.

Dehaene, S., Kerszberg, M., & Changeux, J. P. (1998). A neuronal model of a global workspace in effortful cognitive tasks. *Proceedings of the National Academy of Sciences, USA, 95*, 14529–14534.

Dehane, S., & Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: Basic evidence and a workspace framework. *Cognition, 79* (1–2), 1–37.

Della Sala, S., Gray, C., Baddeley, A. D., & Wilson, L. (1997). *Visual Pattern Test*. Bury St. Edmunds: Thames Valley Test Company.

Denis, M., & Cocude, M. (1997). On the metric properties of visual images generated from verbal descriptions: Evidence for the robustness of the mental scanning effect. *European Journal of Cognitive Psychology, 9*, 353–379.

Denis, M., & Kosslyn, S. M. (1999). Scanning visual mental images: A window on the mind. *Cahiers de Psychologie Cognitive, 18*, 409–465.

Denis, M., Logie, R. H., Cornoldi, C., De Vega, M., & Engelkamp, J. (Eds.). (2001). *Imagery, Language and Visuo-spatial thinking*. Hove, UK: Psychology Press.

Denis, M., & Zimmer, H. D. (1992). Analog properties of cognitive maps constructed from verbal descriptions. *Psychological Research, 54*, 286–298.

Dienes, Z., Altmann, G. T. M., Kwan, L., & Goode, A. (1995). Unconscious knowledge of artificial grammars is applied strategically. *Journal of Experimental Psychology: Learning, Memory and Cognition, 21*, 1322–1338.

Di Lollo, V., Enns, J. T., & Rensink, R. A. (2000). Competition for consciousness among visual events: The psychophysics of reentrant visual processes. *Journal of Experimental Psychology: General, 129*, 481–507.

Duff, S. C., & Logie, R. H. (2001). Processing and storage in working memory span. *Quarterly Journal of Experimental Psychology, 54A*, 31–48.

Easton, R. D., Srinivas, K., & Greene, A. J. (1997). Do vision and haptics share common representations – Implicit and explicit memory within and between modalities. *Journal of Experimental Psychology: Learning, Memory and Cognition, 23*, 153–163.

Engle, R. W., Cantor, J., & Carullo, J. J. (1992). Individual differences in working memory and comprehension: A test of four hypotheses. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 18*, 972–992.

Engle, R. W. & Kane, M. J. (2004). Executive attention, working memory capacity, and a two-factor theory of cognitive control. In B. Ross (Ed.), *The psychology of learning and motivation* (pp. 145–199). New York: Academic Press.

Engle, R. W., Kane, M. J., & Tuholski, S. W. (1999a). Individual differences in working memory capacity and what they tell us about controlled attention, general fluid intelligence, and functions of the prefrontal cortex. In A. Miyake & P. Shah (Eds.), *Models of working memory* (pp. 102–134). Cambridge: Cambridge University Press.

Engle, R. W., Tuholski, S. W., Laughlin, J. E., & Conway, A. R. A. (1999b). Working memory, short-term memory, and general fluid intelligence: A latent-variable approach. *Journal of Experimental Psychology: General, 128*, 309–331.

Ericsson, K. A., & Delaney, P. F. (1999). Long-term working memory as an alternative to capacity models of working memory in everyday skilled performances. In A. Miyake & P. Shah (Eds.), *Models of working memory* (pp. 257–298). Cambridge: Cambridge University Press.

Ericsson, K. A., & Kintsch, W. (1995). Long-term working memory. *Psychological Review, 102*, 211–245.

Farah, M. J., Hammond, K. M., Levine, D. N., & Calvanio, R. (1988). Visual and spatial mental imagery: Dissociable systems of representation. *Cognitive Psychology, 20*, 439–462.

Findlay, G. M., & Gilchrist, I. D. (2003). *Active vision: The psychology of looking and seeing*. Oxford: University Press

Finke, R. A. (1989). *Principles of mental imagery*. Cambridge, MA: MIT Press.

Finke, R. A., Ward, T. B., & Smith, S. M. (1992). *Creative cognition: Theory, research, and applications*. Cambridge, MA: MIT Press.

Fleming, K., Goldberg, T. E., Binks, S., & Randolph, C. (1997). Visuospatial working memory in patients with schizophrenia. *Biological Psychiatry, 41*, 43–49.

Fodor, J. A. (1975). *The language of thought*. New York: Thomas Crowell.

Formisano, E., Linden, D. E. J., Di Salle, F., Trojano, L., Esposito, F., Sack, A. T., Grossi, D., Zanella, F. E., & Goebel, R. (2002). Tracking the mind's image in the brain I: Time-resolved fMRI during visuospatila mental imagery. *Neuron, 35* (1), 185–194

Ganis, G., Thompson, W., & Kosslyn, S. M. (2004). Brain areas underlying visual mental imagery and visual perception: An fMRI study. *Cognitive Brain Research, 20* (2), 226–241.

Gillihan, S. J., & Farah, M. J. (2005). Is self special? A critical review of evidence from experimental psychology and cognitive neuroscience. *Psychological Bulletin, 131*, 76–97.

Giusberti, F., Cornoldi, C., De Beni, R., & Massironi, M. (1998). Perceptual illusions in imagery. *European Psychologist, 3*, 281–288.

Gold, S. R., & Henderson, B. B. (1981). Daydreaming, self-consciousness, and memory monitoring. *Journal of Mental Imagery, 5*, 101–106.

Goodman, N., & Elgin, C. Z. (1993). *Revisionen – Philosophie und andere Künste und Wissenschaften*. Frankfurt/M.: Suhrkamp.

Hanley, J. R., Young, A. W., & Pearson, N. A. (1991). Impairment of the visuo-spatial sketch pad. *Quarterly Journal of Experimental Psychology, 43A*, 101–125.

Harshman, R. A., Hampson, E., & Berembaum, S. A. (1983). Individual differences in cognitive abilities and brain organization, Part 1: Sex and handedness differences in ability. *Canadian Journal of Psychology, 37*, 144–192.

Hartman, M., & Potter, G. (1998). Sources of age differences on the Rey-Osterrieth Complex Figure Test. *Clinical Neuropsychologist, 12,* 513–524.

Hasher, L., & Zacks, R. T. (1979). Automatic and effortful processes in memory. *Journal of Experimental Psychology: General, 108*, 356–388.

Haxby, J. V., Grady, C. L., Horwitz, B., Ungerleider, L. G., Mishkin, M., Carson, R. E., Herscovitch, P., Shapiro, M. B., & Rapaport, S. I. (1991). Dissociation of object and spatial vision processing pathways in human extrastriate cortex. *Neurobiology, 88*, 1621–1625.

Hecker, R., & Mapperson, B. (1997). Dissociation of visual and spatial processing in working memory. *Neuropsychologia, 35*, 599–603.

Heller, M. A., Calcaterra, J. A., Green, S., & Lima, F. (1999). The effect of orientation on braille recognition in persons who are sighted and blind. *Journal of Visual Impairment and Blindness, 93*, 416–419.

Heller, M. A., Calcaterra, J. A., Tyler, L. A., & Burson, L. L. (1996). Production and interpretation of perspective drawings by blind and sighted people. *Perception, 25*, 321–334.

Henson, R. N. A. (1998). Short-term memory for serial order: The start-end model. *Cognitive Psychology, 36*, 73–137.

Herrnstein, R. J., & Boring, E. G. (Eds.). (1973). *A Source Book in the History of Psychology*. Cambridge, MA: Harvard University Press.

Hitch, G. J., Fastame, M. C., & Flude, B. (2005). How is the serial order of a verbal sequence coded? Some comparisons between models. *Memory, 13*, 247–258.

Hitch, G. J., Halliday, M. S., Schaafstal, A. M., & Schraagen, J. M. C. (1988). Visual working memory in young children. *Memory and Cognition, 16*, 120–132.

Hodapp, R. M., Evans, D. & Grey, F. L. (1999). Intellectual development in children with Down syndrome. In T. A. Rondal, J. Perera & L. Nadel (Eds.), *Down's sindrome: A review of current knowledge* (pp. 124–132). London: Whurr Publishers.

Hulme, C., Maughan, S., & Brown, G. D. A. (1991). Memory for familiar and unfamiliar words: Evidence for a long-term memory contribution to short-term memory span. *Journal of Memory and Language, 30*, 685–701.

Hyde, J. S. (1981). How large are cognitive gender differences? *Developmental Psychology, 20*, 722–736.

Intons-Peterson, M. J. (1996). Integrating the components of imagery. In M. de Vega, M. J. Intons-Peterson, P. N. Johnson-Laird, M. Denis, & M. Marschark (Eds.), *Models of visuospatial cognition* (pp. 20–89). New York: Oxford University Press.

Ishai, A. L., Ungerleider, L. G., Martin, A., Schouten, J. L., & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences, USA, 96*, 9379–9384.

Jarrold, C., & Baddeley, A. D. (1997). Short-term memory for verbal and visuo-spatial information in Down's syndrome. *Cognitive Neuropsychiatry, 2*, 101–122.

Jarrold, C., Baddeley, A. D., & Hewes, A. K. (1998). Verbal and nonverbal abilities in the Williams syndrome phenotype: Evidence for diverging developmental trajectories. *Journal of Child Psychology and Psychiatry, 39*, 511–523.

Jarrold, C., Baddeley, A. D., & Hewes, A. K. (1999). Genetically dissociated components of working memory: Evidence from Down's and Williams syndrome. *Neuropsychologia, 37*, 637–651.

Kahneman, D., & Chajzyck, D. (1983). Tests of the automaticity of reading: Dilution of Stroop efffects by color-irrelevant stimuli. *Journal of Experimental Psychology: Human Perception and Performance, 9*, 497–509.

Kane, M. J., & Engle, R. W. (2002). The role of prefrontal cortex in working memory capacity, executive attention, and general fluid intelligence: An individual-differences perspective. *Psychonomic Bulletin & Review, 9*, 637–671.

Kane, M. J., Hambrick, D. Z., Tuholski, S. W., Wilhelm, O., Payne, T. W., & Engle, R. W. (2004). The generality of working memory capacity: A latent-variable approach to verbal and visuo-spatial memory span and reasoning. *Journal of Experimental Psychology: General, 133*, 189–217.

Kanwisher, N. (2001). Neural events and perceptual awareness. *Cognition, 79* (1–2), 89–113.

Kerr, N. H. (1983). The role of vision in visual imagery experiments: Evidence from the congenitally blind. *Journal of Experimental Psychology: General, 112*, 265–277.

Kitamura, S. (1985). Similarities and differences between perception and mental imagery. *Journal of Mental Imagery, 9* (2), 83–92.

Kimura, D. (1999). *Sex and cognition*. Cambridge, MA: MIT Press.

Klatzky, R. L., Golledge, R. G., Loomis, J. M., Cicinelli, J. G., & Pellegrino, J. W. (1995). Performance of blind and sighted persons on spatial tasks. *Journal of Visual Impairment and Blindness, 91*, 70–82.

Knauff, M., Fangmeier, T., Ruff, C. C., & Johnson-Laird, P. (2003). Reasoning, models, and images: Behavioral measures and cortical activity. *Journal of Cognitive Neuroscience, 4*, 559–573.

Knauff, M., & Johnson Laird, P. (2002). Visual imagery can impede reasoning. *Memory and Cognition, 30*, 363–371.

Kosslyn, S. M. (1973). Scanning visual images: Some structural implications. *Perception and Psychophysics, 14*, 90–94.

Kosslyn, S. M. (1980). *Image and Mind*. Cambridge, MA: Harvard University Press.

Kosslyn, S. M. (1994). *Image and Brain*. Cambridge, MA: MIT Press.

Kosslyn, S. M., Ball, T. M., & Rieser, B. J. (1978). Visual images preserve metric spatial information: Evidence from studies of image scanning. *Journal of Experimental Psychology: Human Perception and Performance, 4*, 47–60.

Kosslyn, S. M., Ganis, G., & Thompson, W. L. (2001). Neural foundations of imagery. *Nature Reviews Neuroscience, 2*, 635–642.

Kosslyn, S. M., Pascual-Leone, A., Felician O., Camposano, S., Keenan, J. P., Thompson, W. L., Ganis, G., Sukel, K. E., & Alpert, N. M. (1999). The role of area 17 in visual imagery: Convergent evidence from PET and rTMS. *Science, 284,* 167–170.

Kosslyn, S. M., Sukel, K. E., & Bly, B. M. (1999). Squinting with the mind's eye: Effects of stimulus resolution on imaginal and perceptual comparisons. *Memory and Cognition, 19*, 276–282.

Kosslyn, S. M., Thompson, W. L., & Ganis, G. (2002). Mental imagery doesn't work like that. *Behavioral and Brain Sciences, 25* (2), 198–200.

Kosslyn, S. M., Thompson, W. L., Kim, I. J., & Alpert, N. M. (1995). Topographical representation of mental images in primary visual cortex. *Nature, 378*, 496–498.

Kunst-Wilson, W. R., & Zajonc, R. B. (1980). Affective discrimination of stimuli that cannot be recognized. *Science, 207*, 557–8.

Lamme, V. A. (2003). Why visual attention and awareness are different. *Trends in Cognitive Sciences, 7*, 12–18.

Landau, B., & Jackendoff, R. (1993). "What" and "where" in spatial language and spatial cognition. *Behavioral and Brain Sciences, 16*, 217–265.

Lanfranchi, S., Cornoldi, C. & Vianello, R. (2004). Verbal and Visuospatial Working Memory Deficits in Children with Down Syndrome. *American Journal on Mental Retardation, 109* (6), 456–466.

Lewis, J. L. (1970). Semantic processing of unattended messages using dichotic listening. *Journal of Experimental Psychology, 85*, 225–8.

Linn, M. C., & Petersen, A. C. (1985). Emergence and characterization of sex differences in spatial ability: A meta-analysis. *Child Development, 56*, 1479–1498.

Logie, R. H. (1986). Visuo-spatial processing in working memory. *Quarterly Journal of Experimental Psychology, 38A*, 229–247.

Logie, R. H. (1995). *Visuo-spatial working memory*. Hove, UK: Lawrence Erlbaum Associates.

Logie, R., & Baddeley, A. D. (1990). Imagery and Working Memory. In P. J. Hampson, D. F. Marks, J. T. E. Richardson (Eds.), *Imagery: Current Developments*. London: Routledge.

Logie, R. H., & Marchetti, C. (1991). Visuo-spatial working memory: Visual, spatial or central executive. In R. H. Logie & M. Denis (Eds.), *Mental images in human cognition* (pp. 105–115). Amsterdam: North-Holland, Elsevier.

Logie, R. H., & Pearson, D. (1997). The inner eye and the inner scribe of visuo-spatial working memory: Evidence from developmental fractioning. *European Journal of Cognitive Psychology, 9*, 241–257.

Logie, R. H., Zucco, G. M., & Baddeley, A. D. (1990). Interference with visual short-term memory. *Acta Psychologica, 75*, 55–74.

Luzzatti, C., Vecchi, T., Agazzi, D., Cesa-Bianchi, M., & Vergani, C. (1998). A neurological dissociation between preserved visual and impaired spatial processing in mental imagery. *Cortex, 34*, 461–469.

Maccoby, E. E., & Jacklin, C. N. (1974). *The psychology of sex differences*. Stanford, CA: Stanford University Press.

Marmor, G. S. (1978). Age at onset of blindness and the developmental of the semantics of colour names. *Journal of Experimental Child Psychology, 25*, 267–278.

Marmor, G. S., & Zaback, L. A. (1976). Mental rotation by the blind: Does mental rotation depends on visual imagery? *Journal of Experimental Psychology: Human Perception and Performance, 2*, 515–521.

Massironi, M., Rocchi, P., & Cornoldi, C. (2001). Does regularity affect the construction and memory of a mental image in the same way it affects a visual trace. *Psicologica, 22*, 115–142.

Mellet, E., Tzourio, N., Crivello, F., Joliot, M., Denis, M., & Mazoyer, B. (1996). Functional anatomy of spatial mental imagery generated from verbal instructions. *Journal of Neuroscience, 16*, 6504–6512.

Metzler, J., & Shepard, R. N. (1974). Transformational studies of the internal representation of three-dimensional objects. In R. L. Solso (Ed.), *Theories in cognitive psychology*. Potomac, MD: Lawrence Erlbaum Associates.

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.

Morin, A. (1993). Self- talk and self-awareness: On the nature of the relation. *The Journal of Mind and Behavior, 14* (3), 223–234.

Morin, A., & DeBlois, S. (1989). Gallup's mirrors: More than an operationalization of self-awareness in primates? *Psychological Reports, 65*, 287–291.

Murray, D. J. (1968). Articulation and acoustic confusability in short-term memory. *Journal of Experimental Psychology, 78* (4), 679–684.

Nelson, T. O. (1978). Detecting small amounts of information in memory: Savings for nonrecognized items. *Journal of Experimental Psychology: Human Learning, Memory and Cognition, 4*, 453–68.

Nichelli, P. (1999). Visuospatial and imagery disorders. In G. Denes & L. Pizzamiglio (Eds.), *Handbook of clinical and experimental neuropsychology* (pp. 453–477). Hove, UK: Psychology Press.

Oberauer, K., Süß, H.-M., Wilhelm, O., & Wittmann, W. W. (2003). The multiple faces of working memory: Storage, processing, supervision, and coordination. *Intelligence, 31*, 167–193.

Oltman, P. K. (1968). A portable rod and frame test apparatus. *Perceptual and Motor Skills, 26*, 503–506.

O'Regan, J. K. & Noë, A. (2001). A sensorimotor account of vision and visual consciousness. *Behavioral and Brain Sciences, 24* (5), 939–1031.

Page, M. P. A., & Norris, D. G. (1998). The primacy model: A new model of immediate serial order recall. *Psychological Review, 105*, 761–781.

Paivio, A. (1971). *Imagery and Verbal processes*. New York: Holt, Reinhart & Winston.

Paivio, A. (1986). *Mental representations: A dual coding approach*. New York: Oxford University Press.

Paivio, A. (1991). Dual coding theory: Retrospect and current status. *Canadian Journal of Psychology, 45*, 255–287.

Paivio, A., & Clark, J. M. (1991). Static versus dynamic imagery. In C. Cornoldi & M. A. McDaniel (Eds.), *Imagery and cognition* (pp. 221–245). New York: Springer-Verlag.

Paivio, A., & Harshman, R. A. (1983). Factor analysis of a questionnaire on imagery and verbal habits and skills. *Canadian Journal of Psychology*, *37*, 461–483.

Park, D. C., Lautenschlager, G., Hedden, T., Davidson, N., Smith, A. D., & Smith, P. K. (2002). Models of visuospatial and verbal memory across the adult life span. *Psychology and Aging, 17*, 299–320.

Pearson, D., De Beni, R., & Cornoldi, C. (2001). The generation, maintenance, and transformation of visuo-spatial mental images. In M. Denis, R. H. Logie, C. Cornoldi, M. de Vega & J. Engelkamp (Eds.), *Imagery, language and visuo-spatial thinking* (pp. 1–27). Hove, UK: Psychology Press.

Pietrini, P., Furey, M. L., Ricciardi, E., Gobbini, M. I., Wu, W. H. C., Cohen, L., Guazzelli, M., & Haxby, J. V. (2004). Beyond sensory images: Object-based representation in the human ventral pathway. *Proceedings of the National Academy of Sciences, USA, 101* (15), 5658–5663.

Pöppel, E., Held, R., & Frost, D. (1973). Residual visual function after brain wounds involving the central visual pathways in man. *Nature, 243* (405), 295–296.

Price, B. M., & Goodale, M. A. (1988). *Asymmetries in the perception of biological motion*. Unpublished manuscript, University of Western Ontario, London, Canada.

Pylyshyn, Z. W. (1973). What the mind's eye tells the mind's brain: A critique of mental imagery. *Psychological Bulletin, 80*, 1–24.

Pylyshyn, Z. W. (1981). The imagery debate: Analogue media versus tacit knowledge. *Psychological Review, 88*, 16–45.

Pylyshyn, Z. W. (1994). Mental images on the brain. *Nature, 372*, 289–290.

Quinn, J. G., & McConnell, J. (1996). Irrelevant pictures in visual working memory. *Quarterly Journal of Experimental Psychology, 49A*, 200–21.

Ramachandran, V. S., & Hirstein, W. (1997). Three laws of qualia: What neurology tells us about the biological functions of consciousness. *Journal of Consciousness Studies, 4*, 429–457.

Rao, C., Rainer, G., Miller, E. K. (1997). Integration of what and where in the primate prefrontal cortex. *Science, 276*, 821–824.

Raymond, J. E., Shapiro, K. L., & Arnell, K. M. (1992). Temporary suppression of visual processing in a RSVP task: An attentional blink? *Journal of Experimental Psychology: Human perception and Performance, 18*, 849–860.

Reber, A. S. (1967). Implicit learning of artificial grammars. *Journal of Verbal Learning and Verbal Behaviour, 6*, 855–863.

Reed, S., K., & Johnsen, J., A. (1975). Detenction of parts in patterns and images. *Memory and Cognition, 3*, 569–575.

Rees, G., Kreiman, G., & Koch, C. (2002). Neural correlates of consciousness in humans. *Nature Reviews Neuroscience, 3*, 261–270.

Reichle, E. D., Carpenter, P. A., & Just, M. A. (2000). The neural bases of strategy and skill in sentence-picture verification. *Cognitive Psychology, 40*, 261–295.

Reingold, E. M. (2004). Unconscious perception: Assumptions and interpretative difficulties. *Consciousness and Cognition, 13*, 117–122.

Reisberg, D., & Chambers, D. (1991). Neither pictures nor propositions: What can we learn from a mental image? *Canadian Journal of Psychology, 45*, 336–352.

Richardson, J. T. E. (1994). Gender differences in mental rotation. *Perceptual and Motor Skills, 78*, 435–448.

Rinck, M., & Denis, M. (2004). The Metrics of Spatial Distance Traversed During Mental Imagery. *Journal of Experimental Psychology: Learning, Memory and Cognition, 30* (6), 1211–1218.

Roland, P. E., & Gulyás, B. (1994). Visual imagery and visual representation. *Trends in Neuroscience, 17*, 281–286.

Rourke, B. P. (1989). *Nonverbal disabilities, the syndrome and the model.* New York, Guilford.

Rouw, R., Kosslyn, S. M., & Hamel, R. (1997). Detecting high-level and low-level properties in percepts and mental images. *Cognition, 63*, 209–226.

Rouw, R., Kosslyn, S. M., & Hamel, R. (1998). Aspects of mental images: Is it possible to get the picture? *Cognition, 66*, 103–107.

Salthouse, T. A. (1994). The nature of the influence of speed on adult age differences in cognition. *Developmental Psychology, 30*, 240–259.

Salthouse, T. A. (1996). General and specific speed mediation of adult age differences in memory. *Journal of Gerontology: Psychological Sciences, 51B*, 30–42.

Schacter, D. L., Chiu, C. Y., & Ochsner, K. N. (1993). Implicit memory: A selective review. *Annual Review Neuroscience, 16*, 159–182.

Schaie, K. W. (1983). The Seattle Longitudinal Study: A twenty-one year exploration of psychometric intelligence in adulthood. In K. W. Schaie (Ed.), *Longitudinal studies of adult psychological development*. New York: Guilford Press.

Segal, S. J. (1971). Processing of the stimulus in imagery and perception. In S. J. Segal (Ed.), *Imagery: Current cognitive approaches* (pp. 73–100). New York: Academy Press.

Sergent, C., & Dehaene, S. (2004). Is consciousness a gradual phenomenon? *Psychological Science, 15* (11), 720–728.

Seung, H. K. & Chapman, R. (2004). Sentence memory for individuals with Down's syndrome and typically developing children. *Journal of Intellectual Disability Research, 48* (2), 160–171.

Shah, P., & Miyake, A. (1996). The separability of working memory resources for spatial thinking and language processing: An individual differences approach. *Journal of Experimental Psychology: General, 125*, 4–27.

Shanks, D. & St. John, M. (1994). Characteristics of dissociable learning systems. *Behavioral and Brain Sciences, 17*, 367–447.

Shepard, R. N., & Cooper, L. A. (1982). *Mental images and their transformations*. Cambridge, MA: MIT Press.

Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science, 171*, 701–703.

Slezak, P. (1995). The "philosophical" case against visual imagery. In P. Slezak, T. Caelli, & E. R. Clark (Eds.), *Perspectives on cognitive science: theories, experiments and foundations* (pp. 69–98). Stamford, CT: Ablex.

Smith, E. E., & Jonides, J. (1996). Working memory in humans: Neuropsychological evidence. In M. Gazzaniga (Ed.), *The Cognitive Neurosciences* (pp. 1009–1020). Cambridge, MA: MIT Press.

Smith, E. E., Jonides, J., Koeppe, R. A., Awh, E., Schuhmacher, E. H., & Minoshima, S. (1995). Spatial versus object working memory: PET investigations. *Journal of Cognitive Neuroscience, 7*, 337–356.

Smith, M. M., & Pendleton, L. R. (1989). Working memory for movements. *Quarterly Journal of Experimental Psychology, 41A*, 235–250.

Sparing, R., Mottaghy F. M., Ganis G., Thompson W. L., Töpper R., Kosslyn, S. M., & Pascual-Leone A. (2002).Visual cortex excitability increases during visual imagery – A TMS study in healthy human subjects. *Brain Research, 938*, 92–97.

Süß, H.-M., Oberauer, K., Wittman, W. W., Wilhelm, O., & Schulze, R. (2002). Working memory capacity explains reasoning ability – And a little bit more. *Intelligence, 30*, 261–288.

Suler, J. (1990). Images of the self in Zen meditation. *Journal of Mental Imagery, 14* (3/4), 197–203.

Tek, C., Gold, J., Blaxton, T., Wilk, C., McMahon, R. P., & Buchanan, R. W. (2002). Visual perceptual and working memory impairments in schizophrenia. *Archives of General Psychiatry*

Tulving, E., & Schacter, D. L. (1990). Priming and human memory systems. *Science, 247*, 301–306.

Tunney, R. J., & Shanks, D. R. (2003). Subjective measures of awareness and implicit cognition. *Memory and Cognition, 31* (7), 1060–1071.

Turner, R. G., Scheier, M. S., Carver, C. S., & Ickes, W. (1978). Correlates of self-consciousness. *Journal of Personality Assessment, 42*, 285–289.

Tye, M. (1991). *The imagery debate*. Cambridge, MA: MIT Press.

Udwin, O., & Yule, W. (1991). A cognitive and behavioural phenotype in Williams syndrome. *Journal of Clinical and Experimental Neuropsychology, 13*, 232–244.

Underwood, G. (1977). Contextual facilitation from attended and unattended messages. *Journal of Verbal Learning and Verbal Behaviour, 16*, 99–106.

Underwood, G. (1994). Subliminal perception on TV. *Nature, 370*, 103.

Underwood, G., & Bright, J. E. H. (1996). Cognition with and without awareness. In G. Underwood (Ed.), *Implicit Cognition* (pp. 1–40). Oxford: Oxford University Press.

Vandierendonck, A., Kemps, E., Fastame, M. C., & Szmalec, A. (2004). Working memory components of the Corsi blocks Task. *British Journal of Psychology, 95*, 57–79.

Vecchi, T. (1998). Visuo-spatial limitations in congenitally totally blind people. *Memory, 6*, 91–102.

Vecchi, T. (2001). Visuo-spatial processing in congenitally blind people: Is there a gender-related preference? *Personality and Individual Differences, 29*, 1361–1370.

Vecchi, T., Cattaneo, Z., Monegato, M., Pece, A., Cornoldi, C., & Pietrini, P. (2006). Why cyclops could not compete with ulysses: Monocular vision and mental images. *Neuroreport, 17*, 723–726.

Vecchi, T., & Girelli, L. (1998). Gender differences in visuo-spatial processing: The importance of distinguishing between passive storage and active manipulation. *Acta Psychologica, 99*, 1–16.

Vecchi, T., Monticelli, M. L., & Cornoldi, C. (1995). Visuo-spatial working memory: Structures and variables affecting a capacity measure. *Neuropsychologia, 33*, 1549–1564.

Vecchi, T., Richardson, J. T. E., & Cavallini, E. (2005). Passive storage versus active processing in working memory: Evidence from age-related variations in performance. *European Journal of Cognitive Psychology, 17*, 521–539.

Vecchi, T., Tinti, C., & Cornoldi, C. (2004). Spatial memory and integration processes in congenital blindness. *Neuroreport, 15* (18), 2787–2790.

Vicari, S., Bellucci, S., & Carlesimo, G. A. (2003). Visual and spatial working memory dissociation: Evidence from a genetic syndrome. *Developmental Medicine and Child Neurology, 45* (4), 269–273.

Voyer, D., Voyer, S., & Bryden, M. P. (1995). Magnitude of sex differences in spatial abilities: A meta-analysis and consideration of critical variables. *Psychological Bulletin, 117*, 250–270.

Wallace, B. (1984). Apparent equivalence between perception and imagery in the production of various visual illusions. *Memory and Cognition, 12*, 156–162.

Wang, P. P., & Bellugi, U. (1994). Evidence from two genetic syndromes for a dissociation between verbal and visuo-spatial short-term memory. *Journal of Clinical and Experimental Neuropsychology, 16*, 317–322.

Weiskrantz, L. (1986). *Blindsight: A case study and implications.* Oxford: Oxford University Press.

CHAPTER 2.3

# The episodic buffer

## Implications and connections with visuo-spatial research

David G. Pearson

### Introduction

Many cognitive models of working memory have been proposed over the years, but the multi-component approach first published in 1974 by Baddeley and Hitch has proved to be one of the most influential and enduring. One of the reasons for this success is that the model has been able to interpret a tremendous amount of empirical data within a relatively simple theoretical framework. This framework as originally stated comprised three separate, limited-capacity components: the phonological loop, the visuo-spatial sketchpad, and the central executive. Over the last thirty years all three components have been modified to some extent from their original conception. The phonological loop has been fractionated into two separate but inter-related components; the phonological store and the articulatory loop (Baddeley & Lewis 1981; Baddeley 1986). A similar distinction has been made within the visuo-spatial component between a passive visual store and an active spatial 'inner scribe' (Logie 1995). Finally, the concept of the central executive has undergone considerable development in recent years, with increased attempts to specify in more detail the extent and limitations of its functioning (Baddeley 1996; Logie, Cocchini, Della Sala, & Baddeley 2004). However, outside of these theoretical developments the basic tripartite structure of the model has remained remarkably stable. While alternative competing accounts of working memory have evolved into fairly complex theoretical frameworks (for example, ACT-R (Anderson & Lebiere 1998), or the Interacting Cognitive Subsystems framework (Barnard 1985; Barnard 1999)), the multi-component model first proposed by Baddeley and Hitch has largely resisted changes to specify additional components in the face of new empirical findings.

This status quo changed when Baddeley (2000) put forward a reformulation of the original theoretical framework that included a potential fourth component; the "episodic buffer". The purpose of this was to offer an account of a number of empirical findings that appeared difficult to interpret within the existing three-component

framework, as well as address a wider range of theoretical issues such as the role of consciousness in working memory, and how modality-specific information stored in the different subsystems becomes integrated together into a multimodal representation (the problem of temporary 'binding' in working memory).

A full consideration of the concept of an episodic buffer and an assessment of its implications is well beyond the scope of this chapter. Instead, the chapter will focus specifically on the relationship between the concept of an episodic buffer and current theories of visuo-spatial working memory and mental imagery. I will argue that the theoretical development of the episodic buffer has widespread connections with the literature on visuo-spatial cognition, and that it raises a number of conceptual issues regarding the links between episodic memory, working memory, and visuo-spatial ability.

## Serial recall in visual short-term memory

In laying out the case for a potential fourth component of working memory, Baddeley (2000) reviewed a number of problems faced by the previous version of the model. One of these is the presence of an apparent "back-up store" during the short-term recall of visually presented verbal material. When participants recall a series of digits that have been visually presented they still show evidence of a phonological similarity effect, indicating that the visual material has been converted into a phonological code via the operation of the articulatory loop (Baddeley 1986). This is further confirmed by the finding that the phonological similarity effect is abolished if visual presentation of the items is accompanied by concurrent articulation that blocks the operation of the loop (Murray 1968). However, even under these circumstances participants are still able to recall up to five out of seven presented items (Baddeley, Lewis, & Vallar 1984). These results imply the existence of a secondary memory store that can be used to retain the identity of the visually-presented items when rehearsal in verbal working memory is not possible.

One potential candidate for this back-up store would be the second slave system in the working memory framework; the visuo-spatial sketchpad. However, Baddeley (2000) does not regard this as viable alternative, claiming that while the sketchpad is good at storing a single complex pattern, it is not suited to the task demands of serial recall. This conclusion is based on studies carried out by Phillips and Christie (1977a, 1977b) that examined short-term memory for a series of novel visual patterns. They found that the serial position curves for novel visual patterns were markedly different from those previously reported for serial recall of verbal material. There was no evidence of a primacy effect for patterns presented towards the beginning of a list, but there was a pronounced recency effect that was confined to the very last item. This one-item recency effect was resistant to list length and visual masking, but could be abolished by requiring participants to perform mental arithmetic for three seconds prior to recall. Phillips and Christie attributed this one-item recency effect to the op-

eration of an extremely limited-capacity visual short-term store, with the pre-recency items reflecting more stable representations held in long-term memory (1977a).

A common interpretation of the flat serial position curves reported by Phillips and Christie is that they are modality-specific and demonstrate a highly limited capacity for serially-presented items in visual short-term memory. However, this interpretation has been challenged by a series of studies on short-term recall of novel patterns carried out by Avons (Avons 1998; Avons & Mason 1999; Avons, Ward & Melling 2004). The majority of studies that have examined verbal short-term memory adopt procedures that require explicit memory for serial order. In contrast, Phillips and Christie's procedure (1977a) used recognition tests for novel patterns that did not require participants to demonstrate explicit knowledge of each patterns' serial order position or time of presentation. In response to this Avons (1998) re-examined short-term memory for novel visual patterns by requiring participants to explicitly report serial order by selecting the presented patterns in their order of appearance. In contrast to the flat serial position curves reported by Phillips and Christie (1977a), this modified procedure produced bowed serial position curves that were more typical of those found for verbal material. Avons (1998) concluded that the flat serial position curves reported by Phillips and Christie (1997a) where due to the task demands of their item recognition procedure, and where not a product of modality-specific processes in visual short-term memory.

In a later study Avons and Mason (1999) examined visual similarity effects in the short-term recall of novel visual patterns. They found that visual similarity had a large disruptive effect on performance for the serial recall of both novel visual patterns and familiar patterns that had been previously learned. In contrast there was no evidence of a visual similarity effect for an item recognition task that required knowledge of the appearance of the patterns without any requirement to recall serial order. Avons and Mason (1999) concluded from these findings that the visual similarity effect in serial recall of novel patterns was analogous to the phonological similarity effect found with verbal serial recall. Overall these findings suggest that visual short-term memory may be much more similar to verbal short-term memory than has been previously thought. Certainly, the findings do not support the conclusion that visual short-term memory is especially ill suited to the task demands of serial recall.

### Imagery strategies in serial recall tasks

The one-item recency effect first shown by Phillips and Christie (1997a) has been attributed to a visualisation strategy; i.e., participants attempt to remember the identity of the final presented pattern in a list by forming a visual mental image of it. Evidence suggests that such imagery strategies are under the conscious voluntary control of participants and can influence the shape of associated serial position curves (Phillips 1983; Avons, Ward, & Melling 2004). I have previously argued for a functional distinction between a visual buffer that supports conscious mental imagery and a separate visual cache that holds visual representations in a non-conscious form (Pearson 2001). The

visual buffer component can be viewed as having a highly limited capacity in the sense that participants cannot consciously experience two mental images simultaneously, unless both become integrated in a single representation. For example, if presented with a picture of a dog followed by a picture of an elephant, a participant can generate a single image that represents both pictures side by side. In contrast, with the pattern span procedure used by Phillips and Christie the patterns to be remembered are abstract, complex, and unfamiliar. Under these conditions it may be extremely difficult for participants to incorporate multiple patterns within a single mental image, and they are therefore forced to adopt a strategy of only using visualisation for the final pattern. However, this need not be the case for the retention of visually presented digits and words. If a participant is presented with a sequence of digits they could create a mental image which represented all the digits as if written on a single sheet of paper; e.g., "57329". Such an image could maintain serial order provided that a participant applied a common heuristic during encoding; e.g., "sequential digits added to image left to right". The serial order of the digits could then be retrieved from the image just as a telephone number can be read from a notepad.

Such imagery strategies have been linked to performance in other forms of serial recall task. In the Brooks Matrix task participants are required to serially recall a sequence of verbally presented directions that refer to a 4×4 matrix (Brooks 1967). Although spatial resources are utilised during the encoding of the sequences, they are then subsequently retained in the form of a static visual image (Smyth & Pendleton 1989; Quinn 1991). Similar processes have been argued for performance of the Corsi Blocks task, in which participants serially recall a sequence of spatial locations (Corsi 1972; Milner 1971). Evidence suggests that participants encode the sequences as a "path" that can be represented as a single visuo-spatial representation (Smirni, Villardita, & Zappala 1983; Kemps 2001; Helstrup 1999). This may account for why spatial span in Corsi is less affected by a backwards span procedure than equivalent verbal span (Isaacs & Vargha-Khadem 1989; Berch & Foley 1998), because the backwards sequence can be "read off" from a static mental image of the encoded path (Berch, Krikorian, & Huha 1998). There is also evidence that participants may favour reliance on visuo-spatial representations for backwards span in verbal recall, because the computational load of reversing a phonologically encoded sequence is too high (Li & Lewandowsky 1995).

Many studies have demonstrated participants using verbal re-coding strategies in order to enhance performance during visuo-spatial imagery and working memory tasks (e.g., Brandimonte & Gerbino 1993; Brandimonte, Hitch, & Bishop 1992; Intons-Peterson 1996; Pearson, Logie, & Gilhooly 1999). However, few studies have addressed the converse; i.e., the extent to which participants employ visual re-coding in order to enhance performance of predominantly verbal tasks. Logie, Della Sala, Wynn, and Baddeley (2000) examined the impact of visual similarity on recall of visually presented words and digits. They found a robust visual similarity effect that resulted in poorer recall for both words and digits. In addition, the visual similarity effect occurred irrespective of whether articulatory suppression was present during encoding

or not, suggesting that participants were able to use a visual code in order to retain the items in conjunction with verbal storage within the phonological loop. These findings are consistent with earlier work by Logie, Della Sala, Laiacona, Chalmers, and Wynn (1996) that found that the word length and phonological similarity effects associated with the operation of the phonological loop failed to occur in up to 43% of a sample tested on immediate verbal serial recall with visual and auditory presentation. Furthermore, the test-retest reliability of finding both effects in the same individual was poor across different testing sessions. The implication of such data is that visual and phonological encoding in temporary memory, as well as the use of visualisation as a retention strategy, may be best regarded as cognitive strategies whose deployment is strongly influenced by individual differences and task demands, rather than cognitive components that are always tapped by specific experimental procedures.

I would not wish to claim that all phenomenon associated with "secondary memory" effects in working memory can be accounted for in terms of visual encoding of visually presented stimuli. However, it is clear that either visual encoding using a visual cache, or else a visualisation strategy that makes use of a mental images in a visual buffer, can be employed by participants to retain visually presented verbal information under circumstances in which storage using the phonological loop is blocked. The question that then arises is whether such encoding strategies can be accounted for using the traditional tripartite model of working memory, or whether they require the addition of a fourth component in the form of an episodic buffer.

## Is the episodic buffer a mental imagery system?

Baddeley (2000) outlines a number of principal features of the proposed episodic buffer component. It has a limited capacity, and provides temporary storage of representations using some form of multimodal code. It possesses the ability to bind information from the slave systems and long-term memory into a unitary episodic representation. The buffer is controlled by the central executive component, and representations are retrieved from it in the form of conscious awareness.

It is notable that many of these features are similar to those often attributed to a mental imagery system. Mental imagery is also limited in capacity, and images can represent a combination of multimodal information (Kosslyn 1980, 1994). Mental images can integrate information from short and long-term memory, and imagery has been linked to the formation of episodic autobiographical memories (Conway & Pleydell-Pearce 2000). Mental imagery has also been closely linked to the operation of the central executive component (Pearson, Logie, & Green 1996; Pearson 2001). Finally, images are experienced through conscious awareness in the form of quasi-perceptual mental experiences (Galton 1880; Marks 1973).

This raises a wide number of issues regarding the relationship between the episodic buffer and mental imagery. Activities associated with the episodic buffer often appear directly linked to the use of mental images. For example, Baddeley (2000)

describes the case of someone considering the idea of an "ice-hockey-playing elephant" (pg. 420). He points out that such an idea is unlikely to have been encountered frequently by an individual in the past, and would therefore likely require active maintenance and manipulation of relevant information in working memory. The episodic buffer is put forward as a medium for providing a back-up store for the creation and manipulation of such mental models. This example could be characterised as a form of mental synthesis, in which separate representations are manipulated and combined to form new and original configurations (Finke 1989; Cooper 1990). Mental synthesis has been closely linked to the use of mental imagery (Finke & Slayton 1988; Finke 1990). Although images utilise pre-existing visual representations stored in long-term memory, it is not difficult to use imagery to create representations of objects never previously experienced, such as an elephant playing ice-hockey. Imagery has been shown to be extremely effective at allowing the visualisation of ideas that would be hard or impossible to experience in reality (Shepard 1978, 1988; Miller 1984), and has also been strongly linked to the operation of creative thought (Finke 1990; Finke, Ward, & Smith 1992). Mental synthesis has also been associated with the operation of executive resources in working memory. Pearson, Logie, and Green (1996) found significantly greater interference with mental synthesis from concurrent random number generation than from articulatory suppression or spatial tapping, implying a crucial role for executive resources during performance. A subsequent study proposed a model of mental synthesis in which the conscious experience of imagery in a visual buffer was directly linked to the executive component of working memory (Pearson, Logie, & Gilhooly 1999).

Imagery is also increasingly linked in the literature to the formation of episodic and autobiographical memories. Conway and Pleydell-Pearce (2000) have proposed a model of autobiographical memory in which transitory mental representations are constructed within a self-memory system (SMS). Autobiographical memories are viewed as containing knowledge at different levels of specificity, including an interlinking of event-specific knowledge (ESK) and more general events and lifetime periods (Conway 1992, 1996). Conway and Pleydell-Pearce (2000) argue that ESK is the type of knowledge most strongly associated with mental imagery, and that it may induce or trigger autonoetic consciousness (the recollective experiencing of past events). More recently Conway, Meares, and Standart (2004) have proposed that a principle function of mental imagery in memory is to represent information pertaining to goals that can relate to either future events or those that have influenced the past. The role of imagery in establishing and maintaining goals has also been linked to behaviours associated with addiction and desire (Kavanagh, Andrade, & May 2005), as well as aspects of the psychopathology of memory (Hackmann & Holmes 2004).

Neuroimaging studies have shown that areas of visual cortex in the brain activated by mental imagery vary depending on the type of visual information being retrieved. Ishai, Ungerleider, and Haxby (2000) have used functional magnetic resonance imaging (fMRI) to examine the perception and imagery of horses, faces, and chairs. They found activation in a parietal and frontal network and claimed that this mediated the

"top-down" control of the retrieval of visual information from long-term memory and the construction and maintenance of mental images in consciousness. Their findings suggest that the retrieval of ESK may involve reactivation of brain regions that are preferentially associated with the type of information being retrieved. More recently Wheeler and Buckner (2004) have used fMRI to study the neural correlates of making "remember" and "know" judgements about past events. They found that "remember" judgements activated brain regions associated with the perception and/or judgement that the event had been experienced previously, as well as regions preferentially associated with visual content. In contrast, "know" judgements did not involve any activation of regions associated with visual content. Again, these results suggest that the retrieval of event-specific knowledge from autobiographical memory may depend significantly on mental imagery and the activation of sensory-perceptual information within the brain.

Due to the considerable overlap between the postulated functions of an episodic buffer and those attributable to mental imagery, any development of the concept of such a buffer in working memory must clearly take into account mental imagery and its potential role in the encoding and retrieval of episodic and autobiographical memory. What is not clear as yet is whether imagery should be viewed as a cognitive process linked to the operation of the buffer, or instead as an integral aspect of its functioning. This issue will be returned to later in the concluding section of the chapter.

## Current directions in episodic buffer research

Recently a growing number of studies in the literature have examined the concept of an episodic buffer and attempted to expand on its characteristics and functionality. Baddeley (2000) has suggested that the episodic buffer may be capacity-limited, but it is unclear whether the maintenance of information within the buffer is passive in nature or requires the active involvement of attentional resources. This issue has been addressed by Bunting and Cowan (2005), who attempt to link the concept of an episodic buffer to Cowan's previous work on the role of attention in working memory. Cowan (2001) has argued that the integration of information in working memory requires that attention be divided between several objects at once, and that this is constrained by a fundamental capacity limit of four objects or chunks of information on average. This capacity limit is consistent with observations of performance on participants' ability to keep track of multiple moving targets (Pylyshyn & Storm 1988), and also to integrate together separately presented events in visual working memory (Luck & Vogel 1997). More recently Cowan (2005) has argued that a participant's control of attention in working memory is flexible, and can either 'zoom in' on a specific task goal, or 'zoom out' to apprehend an average field of around four independent objects or chunks of information. Bunting and Cowan (2005) applied this theory to performance of a conceptual span task, in which participants were required to recall four consecutive words from a twelve-word list in response to semantic and colour-name

cues (i.e., a semantic category such as 'animals', or the colour in which the name was printed). They found that when the colour of the cue matched that of the cued items 75% of the time, recall performance was significantly impaired on the 25% of trials on which the cues were mismatched. However, when the colour of the cue matched the cued items only 25% of the time, the significant effect of cue mismatching was removed. Bunting and Cowan claim that these results are consistent with an active role for attention during the maintenance of episodic information, as the distraction of a mismatch between cues only interfered with memory when colour cues were frequently relevant to recall. These findings support the notion that executive resources may play a crucial role during the maintenance of information within the episodic buffer. However, a caveat to this conclusion is the extent to which Cowan's theory of the operation of attention in working memory can be directly linked to the operation of an episodic buffer. Cowan's work is very process-orientated and does not favour the fractionation of working memory into functionally separable components, which is integral to the addition of the episodic buffer to the existing tripartite model. The lack of specification in current descriptions of the episodic buffer also means that it may be open to interpretation in significantly different ways. Bunting and Cowan characterise the buffer as holding semantic and abstract types of information, but this need not necessarily be a feature of multimodal representations in working memory, particularly in the absence of a clear understanding of the nature of the representations stored in the visuo-spatial sketchpad (Pearson 2001; Pearson & Logie 2004).

Other studies on the episodic buffer have focused on features associated with the recall of prose. Recall of words that have been organised into a meaningful sentence is considerably greater than recall of a sequence of unrelated words, and span is far higher than the usual capacity of the phonological loop (Baddeley, Vallar, & Wilson 1987). Furthermore, some amnesic patients show preserved immediate recall of prose despite severe impairment on delayed prose recall (Wilson & Baddeley 1988). Baddeley and Wilson (2002) have predicted that a lack of impairment on immediate prose recall in amnesic patients would be associated with preserved executive function, which would be consistent with the immediate recall of prose being associated with an episodic buffer. Data from two densely amnesic patients studied by Baddeley and Wilson seemed to support this prediction, and also showed that the patients' immediate prose recall scores were positively correlated with measures of executive function and fluid intelligence, but not with measures of crystallised intelligence. However, another study of amnesic patients conducted by Gooding, Isaac, and Mayes (2005) has failed to replicate this finding, and found no significant positive correlations between immediate prose recall and measures of executive function or fluid intelligence. Gooding et al. point out that a more convincing demonstration of this hypothesis would be to find amnesic patients who displayed impaired immediate prose recall in conjunction with otherwise normal working memory functioning, which would suggest that the episodic buffer could be functionally separated from the operation of the other working memory systems. To date, however, no such patients have been reported in the literature.

Another class of patients related to this issue are those suffering from transient global amnesia (TGA), a neurological syndrome characterised by acute onset of temporary memory impairment in the absence of accompanying neurological deficits. Quinette et al. report a study of patients' working memory functioning during a TGA episode (Quinette, Guillery, Desgranges, de la Sayette, Viader, & Eustache 2003). They found no impairment of verbal or visuo-spatial subcomponents of working memory in the TGA patients. There was also normal performance on executive functions measured by backwards digit span and an N-Back updating procedure. However, the TGA patients were impaired on the Brown-Peterson's paradigm (Brown 1958; Peterson & Peterson 1959), and also made reduced numbers of "remember" versus "know" judgements on an episodic memory test conducted several days after the TGA episode. Quinette et al. concluded from this pattern of results that the episodic memory impairments displayed by the TGA patients were not linked to impairment in normal executive functioning. Again, as with the findings of Gooding et al., this is not consistent with the involvement of an episodic buffer that is intimately connected with the capacity-limited central executive system.

Further evidence on prose recall has been provided by Jefferies, Ralph, and Baddeley (2004). They examined the effect of an attentionally-demanding secondary task on the recall of stories, unrelated sentences, and unrelated words. The concurrent task disrupted recall of unrelated sentences to a greater extent than for unrelated words, which is consistent with a higher executive involvement in the recall of sentences. However, a similar large dual-task decrement was not found for the recall of naturalistic prose in the form of stories. This suggests that the episodic buffer (at least as characterised as being an attentionally-demanding system) does not play a substantial role in the binding of phonological information with linguistic information stored in long-term memory, which instead seems to occur via the operation of relatively automatic linguistic processes.

Studies of prose recall address the issue of binding in terms of the integration of information between long-term memory and the phonological loop. An alternative approach to studying binding is to look at the integration of information between modalities, particularly the verbal and visual domains. Zhang et al. (2004) have reported a fMRI study which examined the neural correlates of a cross-modal memory task in which participants were asked to recall sequences of auditory digits and visual locations either in cross-modality or within-modality conditions (Zhang, Zhang, Sun, Li, Wang, He, & Hu 2004). They found patterns of activation suggesting that the right pre-frontal cortex of the brain might play a key role during the integration of information across different modalities. A similar pattern of activation has been shown by an earlier study conducted by Prabhakaran, Narayanan, Zhao, and Gabrieli (2000), which required participants to recall letters and spatial locations in integrated and unintegrated conditions. They also found activation of right pre-frontal cortex during the integration condition, suggesting that this region of the brain may be linked to the binding operation of the episodic buffer.

Differential involvement of the episodic buffer may also occur between different types of visuo-spatial procedure. Zimmer, Speiser, and Seidler (2003) studied participants' short-term memory for objects' location in contrast to their performance of the Corsi Blocks procedure. While Corsi performance was significantly disrupted by concurrent spatial tapping, memory for objects' locations was unaffected by either concurrent tapping or dynamic visual noise. Zimmer et al. concluded that short-term memory for the configuration of objects could be based on information stored in the episodic buffer. However, these results could also be accounted for by participants employing mental imagery as a strategy to reconstruct the configuration of objects based on previous perceptual information. As discussed in the previous sections, the extent to which the employment of mental imagery as a retention strategy might involve the episodic buffer is currently uncertain.

## Conclusions

The proposal of an episodic buffer is a hugely important development in the modelling of working memory, and it has already provoked a wide range of studies addressing the cognitive processes involved during the encoding and retrieval of information across different modalities, and between short and long-term memory. It has also raised a number of issues connected to the study of visuo-spatial cognition, even if this was not a direct objective of the buffer being proposed in the first place.

It is clear that future developments regarding the episodic buffer must address its relationship with processes associated with mental imagery. There is strong evidence linking imagery not only to episodic and autobiographical memory, but also to the creation of multimodal representations that temporarily bind auditory and visual information together. Existing mental imagery models can already offer accounts of many of the cognitive processes that the episodic buffer is attempting to explain. If the episodic buffer stores integrated multimodal representations, and if these are accessed directly by the medium of consciousness, does this mean they are directly equivalent to mental images? And if so, does this mean that the episodic buffer is functionally equivalent to the visual buffer specified in Kosslyn's computational model of imagery (Kosslyn 1980, 1994)? There already exists a vast literature on mental imagery, including a growing body of knowledge addressing the neural correlates of imagery processes. Research on the episodic buffer will need to take this literature into account if it is to address some of the same conceptual issues. My own feeling on this is that the range of functions attributed to the episodic buffer is broader than that which can be accounted for by imagery alone. However, this then raises the issue of how valuable it is to attempt to assign such a diverse range of functions to a single cognitive mechanism.

Certainly, it is clear that the concept of an episodic buffer would benefit from a greater level of specification, particularly regarding its function of binding information together within working memory. In current research on the episodic buffer binding has been used to refer both to the 'chunking' of verbal information during prose recall,

and also to refer to the integration of modality-specific information held separately in verbal and visuo-spatial subcomponents. It need not necessarily follow, however, that the same cognitive system is responsible for both of these processes or that prose recall requires any form of multimodal representation to be established or maintained. In addition, the extent to which the episodic buffer is dependent on the operation of the central executive remains to be confirmed. Evidence so far is mixed, with some aspects of episodic memory formation and retrieval appearing not to be related to executive control. Evidence for executive involvement in mental imagery, on the other hand, is much stronger. As discussed above, however, the relationship of imagery to the episodic buffer is itself an issue that requires a greater level of theoretical specification.

A final comment is that the proposed addition of the episodic buffer to the original tripartite working memory architecture has thrown into stark relief the inadequacies of current modelling of the visuo-spatial sketchpad component. Baddeley's (2000) original proposal for an episodic buffer highlighted a number of areas of uncertainty in current understanding of the sketchpad, including issues such as how visuo-spatial material is rehearsed, and the ability of the sketchpad to store a sequence of presented items. The number of research studies that examine visuo-spatial working memory has increased substantially in recent years, and considerable progress has been made in understanding how visuo-spatial information is encoded and maintained within short-term memory. However, it remains the case that theoretical models of the visuo-spatial sketchpad lag considerably behind those which have been proposed for the phonological loop component, largely because the range of cognitive tasks attributable to the sketchpad is much more diverse, and has therefore proved harder to integrate within a single coherent framework (Pearson 2001). I would argue that any useful theoretical development of the concept of an episodic buffer will also require a greater delineation of the functioning and limitations of the existing subcomponents. For example, it will be extremely difficult to establish a model of how multimodal binding occurs within working memory without first clearly establishing the nature of the modality-specific representations that are being bound together in the first place. The visuo-spatial sketchpad has historically been one of the more overlooked aspects of working memory research. This will need to change for the concept of an episodic buffer to reach its full potential.

## References

Anderson, J. R., & Lebiere, C. (1998). *The atomic components of thought.* Mahwah, NJ, LEA.

Avons, S. E. (1998). Serial report and item recognition of novel visual patterns. *British Journal of Psychology, 89* (2), 285–308.

Avons, S. E., & Mason, A. (1999). Effects of visual similarity on serial report and item recognition. *Quarterly Journal of Experimental Psychology, 52A* (1), 217–240.

Avons, S. E., Ward, G., & Melling, L. (2004). Item and order memory for novel visual patterns assessed by two-choice recognition. *Quarterly Journal of Experimental Psychology-A, 57* (5), 865–891.

Baddeley, A. D. (1986). *Working memory*. Oxford: Oxford University Press.

Baddeley, A. D. (1996). Exploring the central executive. *Quarterly Journal of Experimental Psychology: Human Experimental Psychology, 49A,* 5–28.

Baddeley, A. D. (2000). The episodic buffer: A new component of working memory? *Trends in Cognitive Sciences, 4* (11), 417–423.

Baddeley, A. D., & Hitch, G. J. (1974). Working memory. In G. Bower (Ed.), *The psychology of learning and motivation, Vol. VIII* (pp. 47–90), New York: Academic Press.

Baddeley, A. D., & Lewis, V. J. (1981). Inner active processes in reading: The inner voice, the inner ear and the inner eye. In A. M. Lesgold & C. A. Perfetti (Eds.), *Interactive processes in reading* (pp. 107–129). Hillsdale, NJ: LEA.

Baddeley, A. D., Lewis, V. J., & Vallar, G. (1984). Exploring the articulatory loop. *Quarterly Journal of Experimental Psychology, 36*, 233–52.

Baddeley, A., Vallar, G., & Wilson, B. (1987). Sentence comprehension and phonological memory: Some neuropsychological evidence. *Attention and Performance, 12,* 509–529.

Baddeley, A. D., & Wilson, B. (2002). Prose recall and amnesia: Implications for the structure of working memory. *Neuropsychologia, 40,* 1737–1743.

Barnard, P. J. (1985). Interacting cognitive subsystems: A psycholinguistic approach to short-term memory. In A. Ellis (Ed.), *Progress in the psychology of language* (Vol. 2, pp. 197–258). London: LEA.

Barnard, P. J. (1999). Interacting cognitive subsystems: Modelling working memory phenomena within a multiprocessor architecture. In A. Miyake & P. Shah (Eds.), *Models of working memory: Mechanisms of active maintenance and executive control* (pp. 298–339). Cambridge: Cambridge University Press.

Berch, D. B., & Foley, E. J. (1998). Processing demands associated with relational complexity: Testing predictions with dual-task methodologies. *Behavioral and Brain Sciences, 21* (6), 832.

Berch, D. B., Krikorian, R., & Huha, E. M. (1998). The Corsi block-tapping task: Methodological and theoretical considerations. *Brain and Cognition, 38* (3), 317–338.

Brandimonte, M., & Gerbino, W. (1993). Mental image reversal and verbal recoding: When ducks become rabbits. *Memory and Cognition, 21,* 23–33.

Brandimonte, M., Hitch, G. J., & Bishop, D. (1992). Verbal recoding of visual stimuli impairs mental image transformations. *Memory and Cognition, 20,* 449–455.

Brooks, L. R. (1967). The suppression of visualisation by reading. *Quarterly Journal of Experimental Psychology, 19,* 289–299.

Brown, J. (1958). Some tests of the decay theory of immediate memory. *Quarterly Journal of Experimental Psychology A, 10,* 12–21.

Bunting, M. F., & Cowan, N. (2005). Working memory and flexibility in awareness and attention. *Psychological Research, 69,* 412–419.

Cowan, N. (2001). The magic number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences, 24,* 87–185.

Cowan, N. (2005). Working-memory capacity limits in a theoretical context. In C. Izawa & N. Ohta (Eds.), *Human learning and memory: Advances in theory and application.* Mahwah, NJ: Erlbaum.

Conway, M. A. (1992). A structural model of autobiographical memory. In M. A. Conway, D. C. Rubin, H. Spinnler, & E. W. A. Wagenaar (Eds.), *Theoretical perspectives on autobiographical memory* (pp. 167–194). Dordrecht, the Netherlands: Kluwer Academic.

Conway, M. A. (1996). Autobiographical memories and autobiographical knowledge. In D. C. Rubin (Ed.), *Remembering our past: Studies in autobiographical memory* (pp. 67–93). Cambridge, England: Cambridge University Press.

Conway, M. A., Meares, K., & Standart, S. (2004). Images and goals. *Memory, 12* (4), 525–531.

Conway, M. A., & Pleydell-Pearce, C. W. (2000). The construction of autobiographical memories in the self-memory system. *Psychological Review, 107* (2), 261–288.

Cooper, L. A. (1990). Mental representation of three-dimensional objects in visual problem solving and recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *16*, 1097–1106.

Corsi, P. M. (1972). *Human memory and the medial temporal region of the brain.* Doctoral dissertation, McGill University, Montreal.

Finke, R. (1989). *Principles of mental imagery*. Cambridge, MA: MIT Press.

Finke, R. (1990). *Creative imagery: Discoveries and inventions in visualization.* Hillsdale, NJ: Lawrence Erlbaum.

Finke, R., & Slayton, K. (1988). Explorations of creative visual synthesis in mental imagery. *Memory and Cognition, 16,* 252–257.

Finke, R., Ward, T. B., & Smith, S. M. (1992). *Creative cognition: Theory, research, and applications.* Cambridge, MA: M.I.T. Press.

Galton, F. (1880). Statistics of mental imagery. *Mind, 5,* 301–318.

Gooding, P. A., Isaac, C. L., & Mayes, A. R. (2005). Prose recall and amnesia: More implications for the episodic buffer. *Neuropsychologia, 43,* 583–587.

Hackmann A., & Holmes, E. (2004). Reflecting on imagery: A clinical perspective and overview of the special issue of Memory on mental imagery and memory in psychopathology. *Memory, 12* (4), 389–402.

Helstrup, T. (1999). Visuo-spatial encoding of movement patterns. *European Journal of Cognitive Psychology, 11* (3), 357–371.

Intons-Peterson, M. J. (1996). Linguistic effects in a visual manipulation task. *Psychologische Beitrage, 38* (3/4), 251–278.

Isaacs, E. B., & Vargha-Khadem, F. (1989). Differential course of development of spatial and verbal memory span: A normative study. *British Journal of Developmental Psychology, 7,* 377–380.

Ishai, A., Ungerleider, L. G., & Haxby, J. V. (2000). Distributed neural systems for the generation of visual images. *Neuron, 28* (3), 979–990.

Jefferies, E., Ralph, M. A. L., & Baddeley, A. D. (2004). Automatic and controlled processing in sentence recall: The role of long-term and working memory. *Journal of Memory and Language, 51* (4), 623–643.

Kavanagh, D. J., Andrade, J., & May, J. (2005). Imaginary relish and exquisite torture: The elaborated intrusion theory of desire. *Psychological Review, 112* (2), 446–467.

Kemps, E. (1999). Effects of complexity on Visuo-spatial Working Memory. *European Journal of Cognitive Psychology, 11* (3), 335–356.

Kosslyn, S. M. (1980). *Image and mind.* Cambridge, MA: Harvard University Press.

Kosslyn, S. M. (1994). *Image and brain: The resolution of the imagery debate.* Cambridge, MA: MIT Press.

Li, S. C., & Lewandowsky, S. (1995). Forward and backward recall: Different retrieval processes. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 21* (4), 837–847.

Logie, R. H. (1995). *Visuo-spatial working memory*. Hove: LEA.

Logie, R. H., Cocchini, G., Della Sala, S., & Baddeley, A. D. (2004). Is there a specific executive capacity for dual task coordination? Evidence from Alzheimer's disease. *Neuropsychology, 18* (3), 504–513.

Logie, R. H., Della Salla, S., Laiacona, M., & Chalmers, P, & Wynn, V. (1996). Group aggregates and individual reliability: The case of verbal short-term memory. *Memory and Cognition, 24,* 305–321.

Logie, R. H., Della Sala, S., Wynn, V., & Baddeley, A. D. (2000). Visual similarity effects in immediate verbal serial recall. *Quarterly Journal of Experimental PsychologyA, 53* (3), 626–646,

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature, 390* (6657), 279–281.

Marks, D. F. (1973). Visual imagery differences in the recall of pictures. *British Journal of Psychology, 64,* 407–412.

Miller, A. I. (1984). *Imagery in scientific thought: Creating 20th century physics.* Boston: Birkhauser.

Milner, B. (1971). Interhemispheric differences and psychological processes. *British Medical Bulletin, 27,* 272–277.

Murray, D. J. (1968). Articulation and acoustic confusability in short-term memory. *Journal of Experimental Psychology, 78*, 679–84.

Pearson, D. G. (2001). Imagery and the visuo-spatial sketchpad. In J. Andrade (Ed.), *Working Memory in Perspective*. Hove, UK: The Psychology Press.

Pearson, D. G., & Logie, R. H. (2004). Effects of stimulus modality and working memory load on mental synthesis performance. *Imagination, Cognition, and Personality, 23* (2/3), 183–191.

Pearson, D. G., Logie, R. H., & Gilhooly, K. (1999). Verbal representations and spatial manipulation during mental synthesis. *European Journal of Cognitive Psychology, 11* (3), 295–314.

Pearson, D. G., Logie, R. H., & Green, C. (1996). Mental manipulation, visual working memory, and executive processes. *Psychologische Beitrage, 38,* 324–342.

Peterson, L. R., & Peterson, M. J. (1959). Short-term retention of individual verbal items. *Journal of Experimental Psychology, 58,* 193–198.

Phillips, W. A. (1983). Short-term visual memory. *Philosophical Transactions of the Royal Society B, 302*, 295–309.

Phillips, W. A., & Christie, D. F. M. (1977a). Components of visual memory. *Quarterly Journal of Experimental Psychology, 29,* 117–133.

Phillips, W. A., & Christie, D. F. M. (1977b). Interference with visualization. *Quarterly Journal of Experimental Psychology, 29,* 637–650.

Prabhakaran, V., Narayanan, K., Zhao, Z., & Gabrieli, J. D. (2000). Integration of diverse information in working memory within the frontal lobe. *Nature Neuroscience, 4,* 317–323.

Pylyshyn, Z. W., & Storm, R. W. (1988). Tracking multiple independent targets: Evidence for a parallel tracking mechanism. *Spatial Vision, 3* (3), 179–197.

Quinette, P., Guillery, B., Desgranges, B., de la Sayette, V., Viader, F., & Eustache, F. (2003). Working memory and executive functions in transient global amnesia. *Brain, 126,* 1917–1934.

Quinn, J. G. (1991). Towards a clarification of spatial processing. *Quarterly Journal of Experimental Psychology, 47A,* 465–480.

Shepard, R. N. (1978). Externalization of mental images and the act of creation. In B. S. Randhawa & W. E. Coffman (Eds.), *Visual learning, thinking, and communication.* New York: Academic Press.

Shepard, R. N. (1988). The imagination of the scientist. In K. Egan & D. Nadaner (Eds.), *Imagination and education* (pp. 153–185). New York: Teachers College Press.

Smirni, P., Villardita, C., & Zappala, G. (1983). Influence of different paths on spatial memory performance in the block-tapping test. *Journal of Clinical Neuropsychology, 5,* 355–359.

Smyth, M. M., & Pendleton, L. R. (1989). Working memory for movements. *Quarterly Journal of Experimental Psychology, 41* (A), 235–250.

Wheeler, M. E., & Buckner, R. L. (2004). Functional-anatomic correlates of remembering and knowing. *Neuroimage, 21* (4), 1337–1349.

Wilson, B. A., & Baddeley, A. D. (1988). Semantic, episodic and autobiographical memory in a post-meningitic amnesic patient. *Brain and Cognition, 8,* 31–46.

Zhang, D., Zhang, X., Sun, X., Li, Z., Wang, Z., He, S., & Hu, X. (2004). Cross-modal temporal order memory for auditory digits and visual locations: An fMRI study. *Human Brain Mapping, 22,* 280–289.

Zimmer. H. D., Speiser, H. R., & Seidler, B. (2003). Spatio-temporal working-memory and short-term object-location tasks use different memory mechanisms. *Acta Psychologica, 114,* 41–65.

CHAPTER 2.4

# Visuo-spatial components of numerical representation

Maria-Dolores de Hevia, Giuseppe Vallar, and Luisa Girelli

## Introduction

In recent years, a growing amount of experimental evidence strongly suggests that processing of numbers interacts with space. In fact, recent models of numerical cognition assume the existence of a spatially organized representation of numerical magnitude as the core of the number meaning. The close relationship between the spatial and the numerical domains is apparent not only when spatial effects automatically emerge from the performance in numerical tasks, but also when the processing of irrelevant numerical information clearly modulates the representation of visuo-spatial information. Further support for this interaction comes from neuropsychological data and neuroimaging studies that provide evidence for common neural substrates, partially overlapping in the parietal lobes, devoted to the processing of numbers and space.

## Numbers and imagery: Insight from introspective reports

The intuition that number representation may be spatially organized dates back to Galton's inquiries about the use of mental imagery. In 1880, Galton first described the way in which people consciously visualize numerical information. Among a series of pictorial metaphors, the image of a horizontal left-to-right oriented line appeared to be the most common mental depiction (Galton 1880). In this study Galton stated that these representations, so-called 'number forms', automatically become manifest into the subjects' mind whenever they think about numbers or perform arithmetic operations. Moreover, the author suggested that these visual forms are always precisely positioned in the subjects' visual field in relation to the direction in which they are looking at; they always have the same structure, with each number occupying the same position.

This preliminary evidence collected from individual, non-structured reports was further developed by Seron and collaborators a century later (Seron, Pesenti, Noël,

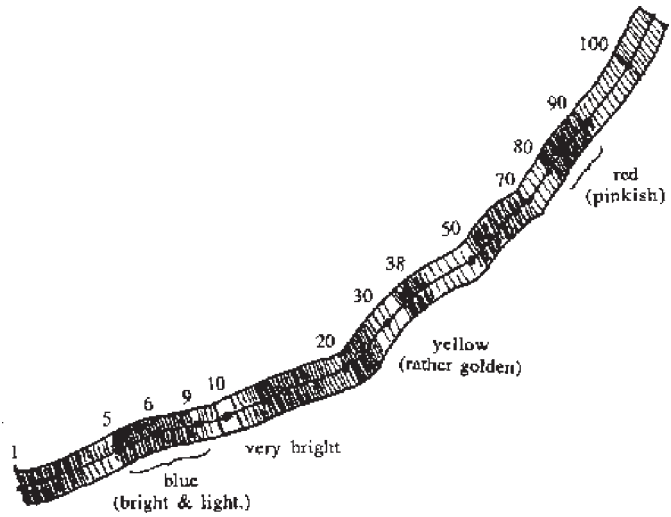



**Figure 1.** A 'number form'. Illustration of the mental image used by a subject when visualizing numbers; numbers are spatially organized in a left-to-right orientation and are associated to specific changes of colour and brightness. (Extracted from Galton 1880).

Deloche, & Cornet 1992). These authors explored the role that the visualization of numbers plays in numerical processing, by investigating its main properties, such as the structure, the functional aspects, and its role on everyday numerical tasks and calculation processes. To this aim participants were, first, informally required to describe the way in which they 'see' numbers in their mind and, then, those subjects who were aware of a spontaneous generation of images were asked to depict and describe them. Besides a few exceptions, the principal structures in which numbers were spatially organized were described as lines, scales or matrix, together with a series of colour codes associated to numbers. The authors claimed that the 'number forms' represent an interesting phenomena for the study of numerical processing, since they mirror properties of the numerical system. In fact, the features of the 'number forms' described in Seron's et al. study are similar to those reported by Galton: for instance, the spontaneous emergence during infancy; the constancy of the structure over time; the fragmentation into more and less precise portions – the visualized number appears well defined –; and the automatic activation.

## The mental number line hypothesis

The appealing concept of an imaginary line in which numbers are organized received once more the attention of psychologists from about the 60's. Restle (1970) renewed the 'mental number line' notion by exploiting Moyer and Landauer (1967) suggestion that numbers – when they are conveying magnitude information – are converted into

analogue magnitudes. This assumption was grounded on the *distance effect*, according to which the more distant two numbers are, the faster we can compare them. Along these lines, Restle (1970) postulated that numbers evoke an analogical system where magnitudes are represented by portions of activation inside a mental number line.

The hypothesis of the 'mental number line' acquired its highest relevance when formally included in the 'Triple Code Model' (Dehaene 1992) as one of the three codes in which numbers can be mentally represented. Besides the visual-Arabic code – in which numbers are represented as digit strings (e.g., '3456') – and the verbal code – in which numbers are represented as sequences of words syntactically organized (e.g., 'one thousand and three') –, this model postulates an analogue code that represents numbers as variable distributions of local activation along a mental number line. It has been postulated that the mental number line is spatially oriented from left to right, with small-magnitude numbers represented on the left-hand side, whereas large-magnitude numbers on the right-hand side (Dehaene, Dupoux, & Mehler 1990). The analogue numerical representation is meant to convey numerical semantic information and is conceived as approximate, with fuzziness increasing with the numerical size according to the Weber-Fechner law (Dehaene, Dehaene-Lambertz, & Cohen 1998; Dehaene, Piazza, Pinel, & Cohen 2003).

Although an analogue representation of numerical magnitude is postulated by other models (Gallistel & Gelman 1992), spatial features have been only considered by the 'Triple Code Model' (Dehaene 1992). The experimental evidence that supports the analogue and spatially-organised mental number line comes from systematic effects observed in numerical tasks: the distance and the size effects, and the SNARC effect.

*Evidence for an analogue magnitude representation: The distance and the size effects*
Moyer and Landauer (1967) first described that, in a numerical comparison task, the time to decide the larger of two numbers is a logarithmic function of the distance between them. The farther apart two numbers are the easier it is to compare them, for instance, <5> and <2> can be compared faster than <5> and <4>. This effect was originally interpreted as evidence for the conversion of numbers into analogue magnitudes, similarly to the processes mediating comparison of other physical dimensions, e.g., brightness, loudness (Moyer & Landauer 1967). The distance effect is a consistent phenomenon that emerges also with two-digit numbers (Dehaene et al. 1990) and its presence is widely accepted as an index of semantic processing (Dehaene & Akhavein 1995).

Moreover, it is well established that the time required to compare two pairs of equally distant numbers increases with their magnitude (Moyer & Landauer 1967). For example, it is easier to compare <1> and <5> than <4> and <8>, even though the numerical distance within each pair of numbers is identical. This effect suggests that the distance between numbers is defined according to their *ratio*: that is, keeping the numerical distance equal, two large numbers (e.g., <21> and <22>) are represented closer than two smaller numbers (e.g., <1> and <2>). However, it has been suggested

that additional factors may contribute to this effect, such as the higher frequency of smaller numbers compared to larger ones (Dehaene & Mehler 1992).

This effect suggests that the analogue continuum is organized obeying the Weber-Fechner law, according to which the lineal increments in magnitude are proportional to the logarithm of the stimulus size. However, some authors have proposed an alternative linear representation, supported by performance of young infants and animals in comparative tasks (Gallistel & Gelman 1992), consisting of a non-verbal counting process in which approximation linearly grows with the magnitude to be represented. Even if both hypotheses – the linear accumulator (Gallistel & Gelman 1992, 2000) and the logarithmically compressed numerical line (Dehaene 2003; Dehaene et al. 2003) – successfully describe the distance and the size effects, it seems that the logarithmic function is more in accordance with data from single-cell recording in monkeys during coding of numerical quantities (Dehaene, Dehaene-Lambertz, & Cohen 1998; Dehaene et al. 2003; Nieder 2003). An integrative view in which both representations coexist and are activated on context-demands has been recently proposed. According to this suggestion a logarithmic organization corresponds to an intuitive representation used mainly by young children, whereas a lineal representation emerges from the increasing familiarity with numbers and quantities and is exploited by adults' in estimation performance (Siegler & Opfer 2003).

Thus, the distance and the size effects reflect a fundamental feature of the discrimination process, that is, the *ratio* between the magnitudes to be compared. Critically, these effects emerge even in comparisons of non-symbolic quantities (e.g., arrays of dots, sequences of tones) by infants and non-human animals. For example, six-month-old infants are able to discriminate between quantities as large as 16 vs. 32 (Xu, Spelke, & Goddard 2005), provided that the ratio difference meets the 1:2 relationship, e.g., infants can discriminate between arrays of 8 vs. 16 dots, but not 8 vs. 12, (Xu & Spelke 2000). Similarly, non-human animals can discriminate between different numerosities across a range of modalities showing both the distance and the size effects (Gallistel & Gelman 1992).

Overall, the presence of these effects when adults, infants, and non-human animals are representing numerical information is taken as evidence of a biologically determined, analogue magnitude representation of number (Dehaene, Dehaene-Lambertz et al. 1998).

*Evidence for a spatial representation: The SNARC effect*

The SNARC effect – Spatial Numerical Association of Response Codes – (Dehaene, Bossini, & Giraux 1993) constitutes the primary explicit index of an association between the numerical and the spatial domains. According to this effect, relatively small numbers are responded to faster with the left hand, whereas relatively large numbers are responded to faster with the right hand. In other words, small numbers spontaneously elicit a preferential left-oriented response, and large numbers spontaneously elicit a preferential right-oriented response. In fact the SNARC effect, by analogy with the Simon effect (Simon 1969; but see Mapelli, Rusconi, & Umiltà 2003 for the sug-

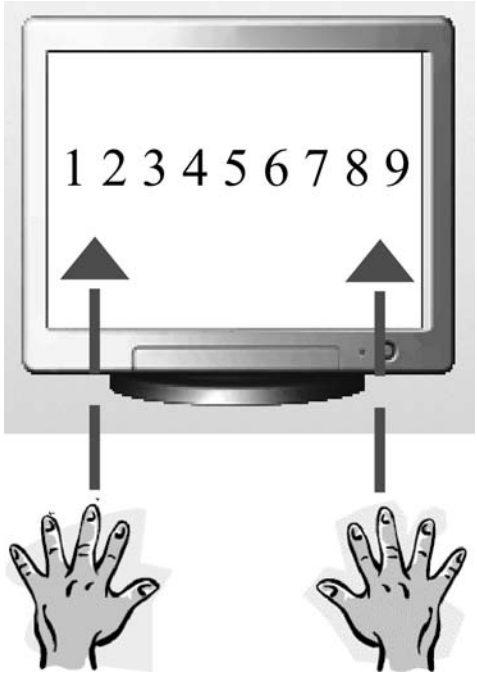



**Figure 2.** Schematic representation of the SNARC effect (Spatial-Numerical Association of Response Codes, Dehaene et al. 1993). In classification tasks, small magnitude numbers elicit faster left-sided responses and large magnitude numbers elicit faster right-sided responses.

gestion that these effects rest on distinct neural mechanisms), has been interpreted as a congruency between the lateralized response – the left and the right sides of the egocentric space – and the relative position of the number in an analogue numerical line – the left and the right sides of the representational space – (Dehaene et al. 1993).

The association between number and space was firstly observed in a numerical comparison task with two-digit Arabic numbers, where subjects were requested to decide whether a visually presented number was larger or smaller than an internally represented fixed standard (Dehaene et al. 1990). The SNARC effect was then systematically explored by disclosing its numerical and spatial properties by means of a parity judgment paradigm (Dehaene et al. 1993). The possibility that the SNARC effect might be associated to the absolute properties of the numbers – as, for instance, their physical appearance or their frequency –, was investigated by presenting subjects with two different intervals [0–5] and [4–9]. The results showed that the numbers <4> and <5> were responded to faster with the right hand in the numerical interval [0–5], whereas they were responded to faster with the left hand in the numerical interval [4–9],[1] suggesting that the association of a number with a side of the space depends on the numerical interval considered. This phenomenon was then explored with non-

numerical material, to test whether the SNARC effect is associated to the activation of ordinal information rather than to the activation of numerical magnitude. The absence of a preferential response effect in a classification of letters induced the authors to conclude that the automatic spatial association is specific to the numerical domain.

The SNARC effect was more robust with one-digit numbers and tended to disappear with numbers larger than 10, suggesting that simple digits have a privileged access to the mental number line (Dehaene et al. 1993). Moreover, the effect also emerged with verbal notation (Dehaene et al. 1993; Fias 2001). The SNARC effect emerged similarly in left-handed subjects as well as in crossed-handed performance, suggesting that it does not depend upon neither the manual laterality nor upon hemispheric asymmetry. However, the SNARC effect was modulated by the writing direction as reflected by the reversed SNARC effect in Iranian subjects (Dehaene et al. 1993), suggesting that orientation of the mental number line may depend on the spatial scanning habit (Zebian 2005).

The fact that the SNARC effect was originally observed in a parity judgment task suggested that the spatial representation was automatically activated (Dehaene et al. 1993). However, since parity and magnitude are both semantic dimensions of numbers, and considering this latter the most salient attribute, it is not surprising that magnitude information is processed even when parity is the attended dimension. More critical to the hypothesis of an automatic activation of the mental number line is the observation of the SNARC effect in a phoneme-monitoring task, where subjects are required to decide if a specific phoneme appeared in the name of an Arabic number (Fias et al. 1996).

Some studies aimed at establishing whether the mental number line differently represents units and decades. Reynvoet and Brysbaert (Reynvoet & Brysbaert 1999) showed that the masked presentation of an Arabic number similarly facilitates the processing of a one- and of a two-digit number (e.g., the presentation of '9' equally primes the numbers '7' and '11'), suggesting the existence of a continuous mental number line. On the other hand, Nuerk and collaborators (Nuerk, Weger, & Willmes 2001) reported, in a number comparison task, an additive compatibility effect for decades and units (e.g., despite equal numerical distance, it is easier to compare '52' and '67' than '47' and '62' since in the former pair, both decades and units yields similar comparative judgement) difficult to account invoking a single representational continuum.

Finally, the attempt to disclose the emergence of the SNARC effect in school-aged children indicates that the congruency between number and side of response is not a consistent and robust phenomenon. In fact, across 7- to 13- year-old children, the SNARC effect emerged intermittently or not significantly (Berch, Foley, Hill, & Ryan 1999), suggesting, among others, secondary factors (higher response times, weakness of the parity knowledge) and the non-automatic and unsteady activation of a spatially ordered numerical representation in development.

## Numerical influence in visuo-spatial tasks

Recently the hypothesis of a spatially organized numerical representation has been explored by testing the influence that numerical information may exert on visuo-spatial tasks. In particular, the association between numbers and space has been investigated by means of the bisection paradigm, a task that evaluates visuo-spatial attentional processes. The bisection task consists of determining the subjective centre of a stimulus, typically presented in a visual format in the form of a horizontal line. Performance from normal subjects in this task is characterized by a slightly leftward error, a phenomenon known as 'pseudoneglect' (Jewell & McCourt 2000).

In order to explore the hypothesis of a numerical representation with spatial properties, Fischer presented subjects with strings of identical digits representing a small magnitude (e.g., 1111111111111111) or a large magnitude (e.g., 88888888888888888) to-be-bisected (Fischer 2001). Data from bisection performance showed the presence of leftward biases in strings made of small magnitude digits ('1' and '2'), and rightward biases in strings made of large magnitude digits ('8' and '9'). These results were interpreted as the consequence of an automatic activation of a spatial response code, by analogy with the SNARC effect (Fischer 2001:825): the strings made of numbers '1' or '2' automatically activate a left-sided response code, and the strings made of number '8' or '9' automatically activate a right-sided response code, inducing the observed spatial biases. Moreover, bisection of lines flanked by different digits (e.g., 1–2; 9–8) showed the presence of spatial biases in the direction of the larger digit. These results were interpreted according to the 'mental number line' hypothesis, suggesting that the perception of two numbers automatically evokes a corresponding segment within this representation.

Following Fischer (2001), the hypothesis that the presentation of a numerical interval activates a corresponding spatial portion of the mental number line representation has been tested. The results showed that errors towards the position of the larger digit were systematically observed in the bisection of lines and of unfilled spaces flanked by different numbers (de Hevia, Girelli, & Vallar 2006); however, the size of the bisection bias was not modulated by the numerical distances (e.g., 1–2 vs. 1–7 yielded similar biases), undermining an account in terms of activation of a portion of the mental number line. The alternative suggestion was made that the numerical influence in visuo-spatial tasks may be considered as a sort of 'cognitive illusion', according to which processing of magnitude information results on an illusory compression (with small-magnitude numbers) or expansion (with large-magnitude numbers) of the perceptual space, that may be responsible for the spatial biases in the bisection tasks (de Hevia et al., 2006).

In order to further test the 'cognitive illusion' hypothesis, a length reproduction task with Arabic digits was adopted (de Hevia, Girelli, Bricolo, & Vallar, submitted). With the aim of verifying spatial mis-estimations induced by numbers, subjects were required to reproduce the length of a spatial extension delimited by two digits. Spaces were delimited by either similar or different numbers that varied in the numerical

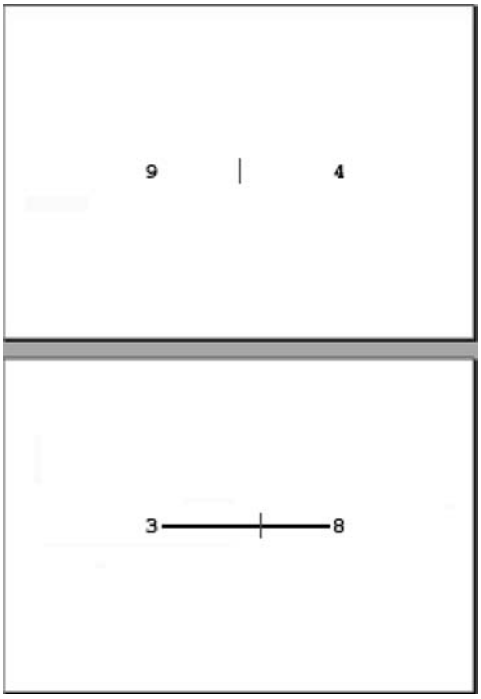



**Figure 3.** Illustration of the bisection paradigm with numerical material (de Hevia et al. 2006). In the top, an unfilled space is delimited on the left by the digit '9' and on the right by the digit '4'; in the bottom, a line is flanked on the left by the digit '3' and on the right by the digit '8'. In both cases, subjects tend to place the subjective midpoint towards the larger digit.

magnitude and in the numerical distance, respectively. The results showed the underestimation of spaces delimited by small-magnitude numbers ('1 1' or '2 2'), and the overestimation of spaces delimited by large-magnitude numbers ('8 8' or '9 9'). However, different numerical intervals (e.g. '1 2' vs. '1 7') did not yield significant effects. Taken together, these results confirm the predictions of the 'cognitive illusion' hypothesis, showing that higher-order cognitive information can modulate the representation of space; in particular, numerical processing may induce illusory expansion (with large-magnitude numbers) or compression (with small-magnitude numbers) of the perceptual space.

Further evidence for a numerical influence on visuo-spatial attention comes from a study showing that the mere perception of a digit draws the subjects' attention towards the left or right hemifields, depending upon the number magnitude -small/left, large/right- (Fischer, Castel, Dodd, & Pratt 2003). In a visual detection task, participants detected faster left-sided targets when preceded by presentation of centred small numbers and detected faster right-sided targets when preceded by presentation of centred large numbers. In particular, although numbers did not predict the position of the

circle, nor were they relevant to the task, the analyses of reaction times showed that for some intervals (400 and 500 ms), a black circle in the left-sided square was detected faster when it was preceded by the numbers '1' or '2', than when it was preceded by the numbers '8' or '9'; *vice versa*, a black circle in the right-sided square was detected faster when it was preceded by the numbers '8' or '9', than when it was preceded by the numbers '1' or '2'. Furthermore, numbers were showed to influence also saccadic eye movements, since subjects exhibit faster gaze responses towards the left visual-field when they categorize small magnitude numbers and towards the right visual-field when they categorize large magnitude numbers (Fischer, Warlop, Hill, & Fias 2004).

Recently, the interaction between numerical processing and visuo-motor control was explored using a pointing parity judgement task. Subjects were asked to move their arm, from a central position, towards either the left or the right depending on the parity of a centrally presented number (Fischer 2003). The results showed that when subjects classified small-magnitude numbers, leftward movements were initialised faster than rightwards movements; however, the effect did not emerge for large-magnitude numbers. On the other hand, leftward movements were finalised faster with the presentation of small-magnitude numbers, whereas rightward movements were finalised faster with the presentation of large-magnitude numbers. This study adds to the existing evidence related to the SNARC effect (Dehaene et al. 1993; Fias 2001; Fias et al. 1996), showing that response biases also extend to the stages of response selection as well as movement execution.

The fact that numerical effects emerge in visuo-spatial tasks may suggest that the two continuos dimensions (the numerical magnitude and the perceptual space) interact at a representational level. This is also the case when subjects make judgements about the size – either physical or numerical – of two numbers (e.g., 2 8), resulting on common interfering effects ('8' is numerically bigger and physically smaller, whereas '2' is numerically smaller and physically bigger) (Girelli, Lucangeli, & Butterworth 2000; Henik & Tzelgov 1982). Recently, an effect of the numerical magnitude has been described in grasping movements (Andres, Davare, Pesenti, Olivier, & Seron 2004). In particular, subjects were requested to perform grip closure or grip opening actions depending on the parity status of visually presented digits. Electromyographic recordings revealed that grip closure was initiated faster with small magnitude digits, whereas grip opening was initiated faster with large magnitude digits. The observed interaction between number and action has been interpreted in terms of a generalized system for processing of magnitude (Walsh 2003), where the information of time, space and quantity, being all processed in the inferior parietal cortex, are jointly used for the scope of sensorimotor transformations.

## Numerical magnitude and space: Evidence from anatomical and neuropsychological data

Even though the anatomical-functional model of Dehaene (Dehaene & Cohen 1995) already postulated the bilateral-parietal role on the representation of numerical magnitude, the neural localization of the mental number line representation was very recently the focus of several investigations.

Göbel and colleagues (Göbel, Walsh, & Rushworth 2001) employed the rTMS technique (repetitive Transcranial Magnetic Stimulation) in a numerical comparison task using numbers between 31 and 99 with 65 as a fixed standard. The authors observed that the bilateral stimulation of the angular gyrus – sited at the parietal lobe – disrupted the subjects' performance, while bilateral stimulation at the supramarginal gyrus did not (Göbel, Rushworth, & Walsh 2001). Assuming that number comparison is mediated by the activation of the mental number line, it was suggested that the angular gyrus – in both hemispheres – may be the cerebral substrate for this representation.

Fias and colleagues (Fias, Lauwereyns, & Lammertyn 2001) aimed at identifying the neuroanatomical correlates that underlie the interaction between the cognitive representation of numbers and the representation of space. Their experimental task consisted of responding to the orientation, colour, or shape of visually presented stimuli combined with task-irrelevant digits. The colour and shape features are non-spatial visual dimensions that may involve the ventral visual stream, whereas orientation is a spatial visual dimension that may involve the dorsal visual stream. Detection of the SNARC effect was interpreted as resulting from the common activation of numerical and spatial representations. Interestingly, irrelevant – digits presentation induced the SNARC effect when orientation was the dimension to be attended to; however, this was not the case when colour and shape had to be classified. The authors attributed the influence of numbers on the processing of spatial visual dimensions to the partially shared neural structures converging in the parietal cortex involved in both the attended (i.e., orientation) and the irrelevant (i.e., numerical magnitude) dimensions.

Several neuroimaging studies suggested that the anatomical locus of the conversion of numbers into abstract magnitude representation is the parietal cortex, more specifically, the intraparietal sulci (Fias, Lammertyn, Reynvoet, Dupont, & Orban 2003; Pesenti, Thioux, Seron, & De Volder 2000; Pinel, Dehaene, Rivière, & LeBihan 2001). Conventionally, the numerical distance effect has been used as the marker for localizing the cerebral correlates of the magnitude representation (Pinel et al. 2001; Pinel, Piazza, Le Bihan, & Dehaene 2004). Since the distance effect characterized comparison judgements of different continua, such as the length of a line or the size of named objects, animals or countries (Moyer 1973), studies have recently investigated if a common cerebral substrate underlies representation of these dimensions (Pinel et al. 2004). In a fMRI study, subjects had to perform comparative judgements of numerical size, physical size and luminance. Although performance on all three comparison tasks leads to activation in the bilateral occipito-temporal, parietal, and precentral ar-

eas, significant overlap was observed in the bilateral intraparietal sulci; however, at a behavioural level interference effects between physical and numerical sizes, and between physical size and luminance were present, but not between numerical size and luminance. Although a distributed and overlapping coding for the different dimensions along the intraparietal sulcus was proposed, differences in the processing of the three dimensions undermine the hypothesis of a single comparison system (Pinel et al. 2004).

Overall, the several attempts to localize the neural substrates of magnitude representation point to the key role of the bilateral parietal areas that are also involved in processing of spatial dimensions. The overlap at the neuroanatomical level is consistent with the functional interaction between numerical and spatial domains, with the mental number line representation as the theoretical construct (Dehaene 2003).

*Exploiting the syndrome of unilateral spatial neglect to explore the mental number line hypothesis*

The anatomical proximity of brain areas representing numbers and space together with the hypothesis of a spatial representation of numbers in the form of a left-to-right oriented number line, receive additional support from the investigation of unilateral spatial neglect (USN). This syndrome refers to a deficit in spatial processing mainly resulting by a right hemisphere damage. It consists of an inability to explore the controlesional side of space (Vallar 1998). Since the USN may compromise not only the physical but also the representational space (Bisiach & Luzzatti 1978), this syndrome offers the opportunity to verify the spatial nature of the mental number line. Accordingly, Zorzi and colleagues (2002) presented neglect patients with a mental bisection task requiring subjects to indicate the number that corresponded to the middle of an auditory presented numerical interval. Not only neglect patients produced more errors than healthy and neurologically impaired controls, but their performance was characterised by the presence of spatial biases towards the right side of the interval, similarly to their performance in physical line bisection: for example, when presented with the interval 11–19, the number 17 was indicated as the central number (Zorzi, Priftis, & Umiltà 2002). In line with this evidence, it has been observed that the beneficial effects that sensorimotor manipulations partially exert in many aspects of neglect (Rossetti et al. 1998), also apply to numerical tasks, in particular, to the numerical bisection task (Rossetti et al. 2004).

Additional evidence for a spatially oriented medium in number processing comes from the difficulties that spatial neglect patients present in the processing of the left-sided numbers within a numerical interval. When required to perform a numerical comparison task, neglect patients take longer to respond to numbers located to the left of a variable referent point despite normal access to magnitude information, (Vuilleumier, Ortigue, & Brugger 2004), as indexed by a normal SNARC effect (Priftis, Zorzi, Meneghello, Marenzi Umiltà, in press). These results suggest that abstract knowledge of numerical quantities and proximity relation between numbers are functionally

dissociated. Moreover, they are consistent with a spatially-organized number representation that is automatically accessed even though irrelevant to the task.

## Critical aspects on the spatial-numerical association: Order vs. magnitude

While the hypothesis of a spatially organized numerical representation is well supported by a series of studies in which the spatial aspect of number emerges, some authors have questioned the invariable properties of its spatial nature (Bachtold, Baumuller, & Brugger 1998), as well as its association with the activation of the numerical magnitude information (Gevers, Reynvoet, & Fias 2003; Gevers, Reynvoet, & Fias 2004).

The hypothesis of the mental number line predicts that numbers are canonically oriented from left to right depending on their magnitude (Dehaene 1992; Restle 1970). However, it has been demonstrated that this spatial-numerical association can be inverted: Bachtold and collaborators (1998) showed that it is possible to obtain a reversed SNARC effect by simply asking subjects to conceive numbers as arranged on a clock-face (see Figure 4). Participants were required to decide if a centrally presented number corresponded to an hour earlier or later than six o'clock: in these conditions, there was an advantage in responding to small numbers with the right hand and to large numbers with the left hand. Interestingly, the same participants showed the typical SNARC effect – small magnitude/left and large magnitude/right – when conceiving numbers displayed on a ruler. The authors concluded that the association of a number with a side of the space does not strictly depends on the magnitude of the number, but possibly on which side of the representational space a number is associated with (Bachtold et al. 1998). Similarly, a recent study provided evidence for a vertical organization of numbers, where small numbers were responded to faster with a bottom key, and large numbers with a top key, suggesting a mental organization of numbers within a 'representational map' instead of along a single line (Ito & Hatta 2004). The vertical bottom-to-top association has been observed also with saccadic movements – eye movements to a lower (upper) response location start earlier with smaller (larger) numbers –, indicating the independence of the number-space association from the manual responses and supporting the view of a space-related central magnitude representation (Schwarz & Keus 2004). Although spatial-numerical congruence seems to be preferentially associated with a left-to-right organization, these studies point to the complexity of the spatial arrangements into which numbers can be automatically organized in the representational space (Dehaene 1997).

The SNARC effect has long been taken as evidence for access to the numerical magnitude representation. In their seminal study, Dehaene and collaborators (1993) ruled out the possibility that the spatial-numerical association could simply reflect access to ordinal information. However, recent studies reported a spatial congruency effect with non-numerical ordinal series, such as the letters of the alphabet, the months of the year (Gevers et al. 2003), and the days of the week (Gevers et al. 2004) (see

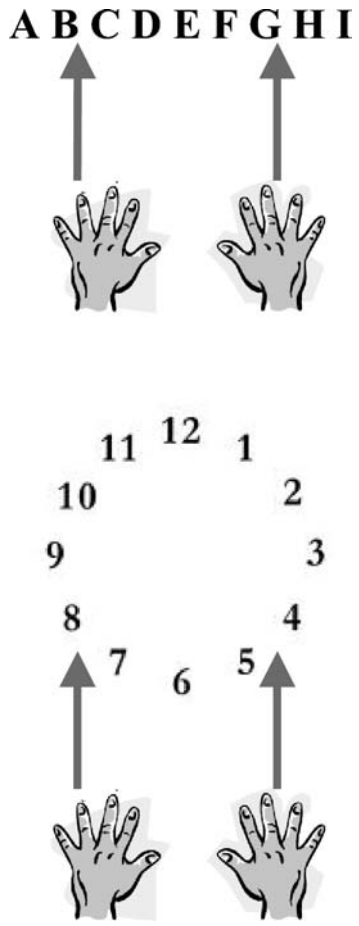



**Figure 4.** Schematic representation of the Spatial Association of Response Codes with non-numerical series, and with the image of a clock-face. In classification tasks, left-sided letters elicit left-sided responses and right-sided letters elicit right-sided responses (Gevers et al. 2003); in a clock-face, hours earlier than '6' elicit right-sided responses and later than '6' left-sided responses (Bachtold et al. 1999).

Figure 4). In these studies participants were required to perform 'before / after' classifications of ordinal series: in these conditions, 'before' judgements were faster with the left than with the right hand, whereas 'after' responses were faster with the right than with the left hand. More strikingly, this effect was maintained even with a phonological detection task – i.e., deciding whether a particular phoneme was present in the word of the stimuli –, highlighting the automatic access to the spatial representation of any ordered series.

Another critical point concerning the standard interpretation of the SNARC effect consists in the fact that it has been mainly observed when *no* explicit access to magni-

tude information was required, as in parity judgement tasks (Dehaene et al. 1993) and in phoneme detection tasks (Fias 2001; Fias et al. 1996). Surprisingly, in numerical comparison tasks, where the magnitude information is the attended dimension, the SNARC effect does not emerge (see Experiment 3 in Ito & Hatta 2004), questioning an interpretation based merely on access to magnitude representation.

Although perceptually simple visual stimuli, Arabic numbers have a special status since they specify complex semantic information. Numbers may convey, among other meanings (e.g., sequence, labelling), magnitude and order information (Fuson 1988). Ordinal information appears to be internally represented along spatial dimensions, as indexed by the spatial congruency effect described with numbers (SNARC effect), and with other non-numerical series (Gevers et al. 2003; Gevers et al. 2004). On the other hand, a growing amount of experimental evidence suggests that continuous dimensions interact at a representational level, as indexed by the numerical influence on spatial representation (de Hevia et al., submitted; de Hevia et al., 2006), and by the interference effects between numerical and physical size (Girelli et al. 2000; Pinel et al. 2004), between loudness and physical size (Gallace & Spence, in press), and between physical size and luminance (Pinel et al. 2004). In our view, this pattern of data suggest a theoretical distinction between a *discrete ordered space* in which discrete pieces of information (e.g., days of the week, sequence of numbers) may be ordered in a representational space; and an *analogue continuous space* in which estimation of magnitude of perceptual dimension (e.g., numerosity, weight, pain) exploits visuospatial resources. It remains untested, however, if comparison of continuous dimensions may evoke spatially organized representation or whether processing ordinal information may modulate visuospatial representations.

Overall, evidence so far, although somewhat controversial, extends Galton's original insight of a natural interaction between numbers and space beyond the representational level reaching our perceptual experience and brain circuits.

## Note

1. These results are further supported by Fias and colleagues' study in which the same stimuli and the same task were used (Fias, Brysbaert, Geypens, & d'Ydewalle 1996).

## References

Andres, M., Davare, M., Pesenti, M., Olivier, E., & Seron, X. (2004). Number magnitude and grip aperture interaction. *Neuroreport, 15*, 2773–2777.

Bachtold, D., Baumuller, M., & Brugger, P. (1998). Stimulus-response compatibility in representational space. *Neuropsychologia, 36*, 731–735.

Berch, D. B., Foley, E. J., Hill, R. J., & Ryan, P. M. (1999). Extracting parity and magnitude from Arabic numerals: Developmental changes in number processing and mental representation. *Journal of Experimental Child Psychology, 74*, 286–308.

Bisiach, E., & Luzzatti, C. (1978). Unilateral neglect of representational space. *Cortex, 14*, 129–133.

de Hevia, M. D., Girelli, L., Bricolo, E., & Vallar, G. (submitted). The representational space of numerical magnitude: Illusions of length.

de Hevia, M. D., Girelli, L., & Vallar, G. (2006). Numbers and space: A cognitive illusion? *Experimental Brain Research, 168*, 254–264.

Dehaene, S. (1992). Varieties of numerical abilities. *Cognition, 44*, 1–42.

Dehaene, S. (2003). The neural basis of the Weber-Fechner law: A logarithmic mental number line. *Trends in Cognitive Sciences, 7*, 145–147.

Dehaene, S. (Ed.). (1997). *The Number Sense*. Nueva York: Oxford University Press.

Dehaene, S., & Akhavein, R. (1995). Attention, automaticity, and levels of representation in number processing. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 21*, 314–326.

Dehaene, S., Bossini, S., & Giraux, P. (1993). The mental representation of parity and number magnitude. *Journal of Experimental Psychology: General, 122*, 371–396.

Dehaene, S., & Cohen, L. (1995). Towards an Anatomical and Functional Model of Number Processing. *Mathematical Cognition, 1*, 83–120.

Dehaene, S., Dehaene-Lambertz, G., & Cohen, L. (1998). Abstract representations of numbers in the animal and human brain. *Trends in Neurosciences, 21*, 355–361.

Dehaene, S., Dehaene-Lambertz, G., & Cohen, L. (1998). Abstract representations of numbers in the animal and human brain. *Trends in Neurosciences, 21*, 355–361.

Dehaene, S., Dupoux, E., & Mehler, J. (1990). Is numerical comparison digital? Analogical and symbolic effects in two-digit number comparison. *Journal of Experimental Psychology: Human Perception and Performance, 16*, 626–641.

Dehaene, S., & Mehler, J. (1992). Cross-linguistic regularities in the frequency of number words. *Cognition, 43*, 1–29.

Dehaene, S., Piazza, M., Pinel, P., & Cohen, L. (2003). Three parietal circuits of number processing. *Cognitive Neuropsychology, 20*, 487–506.

Fias, W. (2001). Two routes for the processing of verbal numbers: Evidence from the SNARC effect. *Psychological Research, 65*, 250–259.

Fias, W., Brysbaert, M., Geypens, F., & d'Ydewalle, G. (1996). The Importance of Magnitude Information in Numerical Processing: Evidence from the SNARC Effect. *Mathematical Cognition, 2*, 95–110.

Fias, W., Lammertyn, J., Reynvoet, B., Dupont, P., & Orban, G. A. (2003). Parietal representation of symbolic and nonsymbolic magnitude. *Journal of Cognitive Neuroscience, 15*, 47–56.

Fias, W., Lauwereyns, J., & Lammertyn, J. (2001). Irrelevant digits affect feature-based attention depending on the overlap of neural circuits. *Brain Research. Cognitive Brain Research, 12*, 415–423.

Fischer, M. H. (2001). Number processing induces spatial performance biases. *Neurology, 57*, 822–826.

Fischer, M. H. (2003). Spatial representations in number processing: Evidence from a pointing task. *Visual cognition, 10*, 493–508.

Fischer, M. H., Castel, A. D., Dodd, M. D., & Pratt, J. (2003). Perceiving numbers causes spatial shifts of attention. *Nature Neuroscience, 6*, 555–556.

Fischer, M. H., Warlop, N., Hill, R., & Fias, W. (2004). Oculomotor bias induced by number perception. *Experimental Psychology, 51*, 91–97.

Fuson, K. C. (1988). *Children's counting and concepts of number.* New York: Springer.

Gallace, A., & Spence, C. (in press). Multisensory synaesthetic interactions in the speeded classification of visual size. Perception and Psychophyscs.

Gallistel, C. R., & Gelman, R. (1992). Preverbal and verbal counting and computation. *Cognition, 1–2*, 43–74.

Gallistel, C. R., & Gelman, R. (2000). Non-verbal numerical cognition: From reals to integers. *Trends in Cognitive Sciences, 4*, 59–65.

Galton, F. (1880). Visualised numerals. *Nature, 21*, 252–256.

Gevers, W., Reynvoet, B., & Fias, W. (2003). The mental representation of ordinal sequences is spatially organized. *Cognition, 87*, B87–B95.

Gevers, W., Reynvoet, B., & Fias, W. (2004). The mental representation of ordinal sequences is spatially organized: Evidence from days of the week. *Cortex, 40*, 171–172.

Girelli, L., Lucangeli, D., & Butterworth, B. (2000). The Development of Automaticity in Accesing Number Magnitude. *Journal of Experimental Child Psychology, 76*, 104–122.

Göbel, S., Rushworth, M., & Walsh, V. (2001). rTMS disrupts the representation of small numbers in supramarginal gyrus. *Neuroimage, 13*.

Göbel, S., Walsh, V., & Rushworth, M. F. (2001). The mental number line and the human angular gyrus. *Neuroimage, 14*, 1278–1289.

Henik, A., & Tzelgov, J. (1982). Is three greater than five: The relation between physical and semantic size in comparison tasks. *Memory and Cognition, 10*, 389–395.

Ito, Y., & Hatta, T. (2004). Spatial structure of quantitative representation of numbers: Evidence from the SNARC effect. *Memory and Cognition, 32*, 662–673.

Jewell, G., & McCourt, M. E. (2000). Pseudoneglect: A review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia, 38*, 93–110.

Mapelli, D., Rusconi, E., & Umiltà, C. (2003). The SNARC effect: An instance of the Simon effect? *Cognition, 88*, B1–10.

Moyer, R. S. (1973). Comparing objects in memory – evidence suggesting an internal psychophysics. *Perceptual Psychophysics, 13*, 180–184.

Moyer, R. S., & Landauer, T. K. (1967). The time required for judgements of numerical inequality. *Nature, 215*, 1519–1520.

Nieder, A., & Miller, E. K. (2003). Coding of cognitive magnitude: Compressed scaling of numerical information in the primate prefrontal cortex. *Neuron, 37*, 149–157.

Nuerk, H. C., Weger, U., & Willmes, K. (2001). Decade breaks in the mental number line? Putting the tens and units back in different bins. *Cognition, 82*, B25–33.

Pesenti, M., Thioux, M., Seron, X., & De Volder, A. (2000). Neuroanatomical substrates of arabic number processing, numerical comparison and simple addition: A PET study. *Journal of Cognitive Neuroscience, 12*, 461–479.

Pinel, P., Dehaene, S., Rivière, D., & LeBihan, D. (2001). Modulation of Parietal Activation by Semantic Distance in a Number Comparison Task. *Neuroimage, 14*, 1013–1026.

Pinel, P., Piazza, M., Le Bihan, D., & Dehaene, S. (2004). Distributed and Overlapping Cerebral Representations of Number, Size, and Luminance during Comparative Judgments. *Neuron, 41*, 983–993.

Priftis, K., Zorzi, M., Meneghello, F, Marenzi R, & Umiltà C. (In press). Explicit vs. implicit processing of representational space in neglect: Dissociations in accessing the mental number line. *Journal of Cognitive Neuroscience*.

Restle, F. (1970). Speed of adding and comparing numbers. *Journal of Experimental Psychology, 83*, 274–278.

Reynvoet, B., & Brysbaert, M. (1999). Single-digit and two-digit Arabic numerals address the same semantic number line. *Cognition, 72*, 191–201.

Rossetti, Y., Jacquin-Courtois, S., Rode, G., Ota, H., Michel, C., & Boisson, D. (2004). Does action make the link between number and space representation? *Psychological Science, 15*, 426–430.

Rossetti, Y., Rode, G., Pisella, L., Farne, A., Li, L., Boisson, D., & Perenin, M. T. (1998). Prism adaptation to a rightward optical deviation rehabilitates left hemispatial neglect. *Nature, 395*, 166–169.

Schwarz, W., & Keus, I. M. (2004). Moving the eyes along the mental number line: Comparing SNARC effects with saccadic and manual responses. *Perception & Psychophysics, 66*, 651–664.

Seron, X., Pesenti, M., Noël, M. P., Deloche, G., & Cornet, J. A. (1992). Images of numbers, or when 98 is upper left and 6 sky blue. *Cognition, 44*, 159–196.

Siegler, R. S., & Opfer, J. E. (2003). The development of numerical estimation: Evidence for multiple representations of numerical quantity. *Psychological Science, 14*, 237–243.

Simon, J. R. (1969). Reaction toward the source of stimulation. *Journal of Experimental Psychology, 81*, 174–176.

Vallar, G. (1998). Spatial hemineglect in humans. *Trends in Cognitive Sciences, 2*, 87–97.

Vuilleumier, P., Ortigue, S., & Brugger, P. (2004). The number space and neglect. *Cortex, 40*, 399–410.

Walsh, V. (2003). A theory of magnitude: Common cortical metrics of time, space and quantity. *Trends in Cognitive Neurosciences, 7*, 483–488.

Xu, F., & Spelke, E. S. (2000). Large number discrimination in 6-month-old infants. *Cognition, 74*, B1–B11.

Xu, F., Spelke, E. S., & Goddard, S. (2005). Number sense in human infants. *Developmental Science, 8*, 88–101.

Zebian, S. (2005). Linkages between number concepts, spatial thinking, and, directionality of writing: SNARC effect and the reverse SNARC effect in English and Arabic monoliterates, biliterates, and illiterate Arabic speakers. *Journal of Cognition and Culture, 5*, 165–190.

Zorzi, M., Priftis, K., & Umiltà, C. (2002). Brain damage: Neglect disrupts the mental number line. *Nature, 417*, 138–139.

CHAPTER 2.5

# Motor components and complexity effects in visuo-spatial processes

Robert H. Logie and Tomaso Vecchi

## Introduction

One dominant view of working memory (WM) is of a multicomponent system responsible for a large number of cognitive functions, from simple memory for words and positions to high level reasoning processes, with reference to maintenance and manipulation of information (e.g., Baddeley 1986; Baddeley & Hitch 1974; Baddeley & Logie 1999; Logie 1995, 2003). Studies of the characteristics of visuo-spatial working memory (VSWM) have gradually increased in the last decade, thus leading to the proposal that there are separate components of the cognitive architecture to support respectively temporary visual storage, temporary storage of movement sequences, and the creation and manipulation of images (e.g. Logie 1995, 1996, 2003 Vecchi, Monticelli & Cornoldi 1995; Cornoldi & Vecchi 2003). The emphasis in this work has been to explore a possible cognitive architecture for supporting cognitive tasks that involve visuo-spatial memory and on-line cognition.

The detailed characteristics of VSWM are still unclear: A number of at least partially independent subcomponents have been suggested referring both to the characteristics of the material and to the specific nature of the cognitive process. Logie and colleagues (e.g. see Logie 1995, 2003) postulated separate structures respectively for visual and dynamic spatial (i.e. movement or pathways) information. This is based on experimental, neuropsychological, and neurophysiological evidence. For example, retention of movement sequences is disrupted by concurrent arm movements but not by irrelevant visual input (e.g. Logie & Marchetti 1991; Quinn & Ralston 1986; Smyth, Pearson & Pendleton 1988), while retention of primarily visual information is disrupted by concurrent irrelevant visual input (Logie 1986; Quinn & McConnell 1996). Moreover, visual memory span appears to develop more rapidly in young children than does memory span for block sequences, and within groups of children of the same age, visual span shows low correlations with span for sequences of movements (Logie & Pearson 1997). Neuropsychological and neurophysiological studies also support the dissociation, with differential patterns of visual and spatial impairment associated with

different focal brain lesions (e.g. Beschin, Cocchini, Della Sala, & Logie 1997; Farah, Hammond, Levine, & Calvanio 1988; Hecker & Mapperson 1997; Luzzatti, Vecchi, Agazzi, Cesa-Bianchi, & Vergani 1998) or visual and spatial cognitive tasks associated with different patterns of activation observed in neuroimaging studies (e.g. Courtney, Ungerleider, Keil, & Haxby 1996; Jonides, Smith, Koeppe, Awh, Minoshima, & Mintun 1993).

One way of characterising the dissociation between visual and spatial working memory is to hypothesise a passive memory system responsible for temporary storage of information coupled with a form of visuo-spatial rehearsal. This idea draws on the fact that a similar structure has been proposed for performance of verbal serial recall tasks, specifically a phonologically based store and an active rehearsal component (see Baddeley 1986). For example, concurrent irrelevant vocalization (articulatory suppression) disrupts verbal immediate memory (e.g. Murray 1965; Levy 1971), suggesting a link between speech output and mental rehearsal of verbal sequences. Moreover speed of articulation appears to be associated with verbal memory span; Baddeley, Thomson and Buchanan (1975) demonstrated that immediate serial recall for longer words is poorer than that for shorter words, and a number of studies have demonstrated that pronunciation time is a strong predictor of verbal memory span within and between languages (Ellis & Hennelley 1980; Naveh-Benjamin & Ayres 1986).

If a similar effect were to be characteristic of immediate recall of visuo-spatial sequences, then the distance between the spatial positions in a presented sequence of targets for recall should affect the performance: the larger the distance between targets, the longer it should take to mentally rehearse the sequence of movements between them and the poorer should be recall of the sequence. Moreover, the farther apart the targets then the longer would be the physical arm movement between them. On the basis of the selective interference studies mentioned above we know that physical movement disrupts retention of movement sequences, therefore we might expect that physical movement time would be related to recall performance.

An alternative hypothesis is that the nature of verbal and visuo-spatial information might require fundamentally different cognitive processes. Verbal stimuli are necessarily processed serially, whereas visuo-spatial stimuli may be processed either serially or in parallel. This difference could have implications for the nature of the underlying components of the cognitive architecture that are necessary for task performance. Therefore, if experimental participants can retain visuo-spatial information in some form of static pattern, then the time required physically to move between the elements of that pattern would not affect memory performance. However the overall complexity, such as number of pattern elements or the regularity of their layout might limit immediate memory performance. For example, in the case of the so-called Corsi block task (DeRenzi & Nichelli 1975; Milner 1971), participants are presented with a pathway between wooden blocks arranged randomly on a board. They are then required to point to the sequence of blocks in the order of presentation. If participants attempt to retain the pathways simply by imaging a series of arrows imposed upon the array of blocks, the pathways could be retained in the form of a static pattern following ini-

tial encoding and transformations, and therefore involving no mental rehearsal of the movements. If this is the case, we might not expect a limiting effect of metric distance but rather an effect of overall pattern complexity on immediate recall performance. In contrast, if participants are attempting mentally to rehearse the movements between blocks prior to recall, then we might expect some relationship between inter-block distance, movement time and recall performance.

The hypothesis linked to distance and movement time was explored in a series of studies by Smyth and Scholey (1992, 1994) in which they presented nine squares in random positions on a computer screen and varied the distances between the squares. In several studies they failed to find a relationship between inter-square distance and recall of a pathway among the squares. However, in those studies the physical distance on the computer screen might not have been sufficiently sensitive to the effects of inter-item distance. Moreover, squares were displayed in the relevant positions by the computer rather than being presented as a sequence of movements performed by the experimenter. The fact that stimulus presentation did not involve movements and involved distances limited by the size of the computer screen could have reduced the likelihood that metric distance would have an effect on performance.

A series of studies by Kemps (1999) explored this idea using physical blocks rather than a computer display. She varied the physical distance between the blocks, and found that span was poorer when blocks were closer together. This is contrary to the result that we might expect if larger distances lead to greater difficulty in rehearsal. However in her experiments, distance between blocks was confounded with number of blocks displayed: specifically as the distance between the blocks reduced, the number of blocks displayed was increased. Therefore the effect may have arisen from the number of blocks displayed rather than the distance between them. Later experiments in the paper confirmed that this was the most likely explanation for her initial result.

It is possible to further investigate the effects of metric distance by using different variants of the Corsi blocks task or other forms of sequential visuo-spatial span varying in visual complexity. We addressed the issue of absolute metric distance and displayed movement by employing wooden blocks positioned on boards of varying size, with the experimenter pointing to blocks in the sequence to be recalled. This ensured that participants were explicitly presented with a sequence of movements between targets and that the larger distances involved substantial movements of the arm. Following this procedure we examined the effects of distance movement time and overall complexity of the array using matrices with different numbers of blocks, and sequences varying in inter-block distance.

## The effect of metric distance on visuo-spatial span

The hypothesis of an equivalence of the word-length effect for visuo-spatial processes could be investigated through the role of movement time in the execution of a span task. In order to assess the effect of movement time we devised a methodology com-

prising two different versions of a block sequence memory task, varying the distances between blocks (Large Board and Small Board). The procedure is similar to a task commonly referred to as Corsi block span (Corsi 1972; De Renzi & Nichelli 1975; Milner 1971). In addition, participants' performance was evaluated in a fast tapping task to correlate a pure measure of movement speed with the movement time obtained in the span tasks. If the metric distance hypothesis is correct we should expect a significant difference in recall performance between Small and Large Boards; better performance being linked with shorter movement times of the Small Board.

We prepared two different arrays, each of them comprising 12 wooden blocks arranged in random positions. The two patterns differed in size: in the Small Board (SB) the 12 blocks were arranged within an area of 40 cm x 50 cm; in the Large Board (LB) the 12 blocks were arranged within an area of 60 cm x 90 cm. Distances between blocks varied from 9 cm to 41 cm and from 15 cm to 75 cm for sequences in the Small and in the Large Board, respectively.

Sequences were prepared in order to maintain a constant mean distance between blocks for each movement: this measure was fixed at approximately 20 cm in the SB (mean distances varying from 20.2 to 24.2 cm), and at approximately 40 cm in the LB (mean distances varying from 40.3 to 44.9 cm). Consequently, for each span level the overall sequence distances in the LB were approximately double the overall distances in the SB. Participants were presented with sequences of increasing length until they were unable to reproduce at least two out of three sequences for each length.

Visuo-spatial span was taken as the mean of the three longest sequences correctly recalled. Figure 1 shows the mean span scores, and differences in performance were only marginally significant with the SB broadly associated with better performance. The mean time for block to block movement was calculated across all sequences correctly recalled and we found a significant effect of size indicating faster movement times with the SB.

Table 1 shows the correlations between span scores and movement times. SB and LB correlated with each other for both span scores and movement times. However, the span scores were not correlated with movement times.

These data indicated an effect of size, in favour of the SB, for the span scores and for the time to complete the tasks. However, this result is partially undermined by the absence of any correlation between span and movement time. If the better span performance in the SB was due to shorter time for mental rehearsal, and if mental rehearsal is linked to physical movement time, then movement time and span should have been negatively correlated, and this was not found.

Given previous reports of the disruptive effects of movement on tasks similar to the block sequence memory tasks, we were concerned that the lack of a link between movement time and span performance did not arise simply from insensitivity of our design. We also wanted to ensure that the modest effects of board size could be replicated, and these two issues provided the rationale for an additional experiment designed to investigate the effects of a filled delay as well as to attempt a replication of the board size effects found in the previous Experiment. To this end, we used the mate-

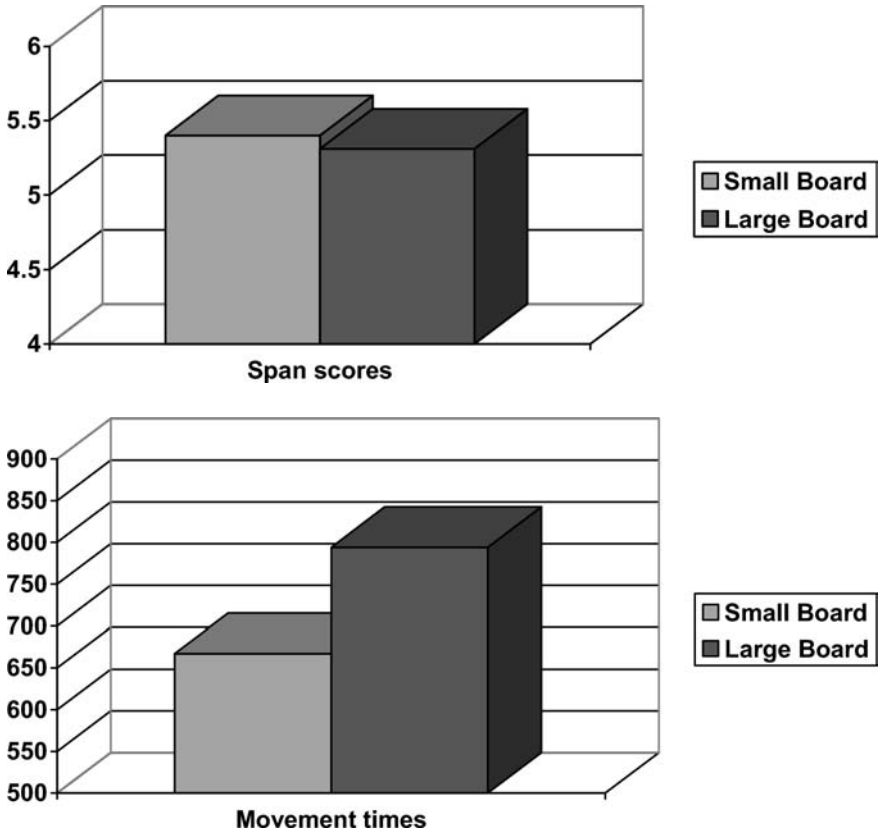



**Figure 1.** Mean span scores values (Figure 1a) and mean movement times (Figure 1B) in SB and LB.

**Table 1.** Correlations between span scores and movement times

| | | correlation coefficient | P |
|---|---|---|---|
| SB immediate (span) | LB immediate (span) | .619 | .001 |
| SB immediate (time) | LB immediate (time) | .798 | <.001 |
| SB immediate (span) | SB immediate (time) | –.090 | .673 |
| LB immediate (span) | LB immediate (time) | –.226 | .286 |

rial and procedure previously described in association with different activities during a 10-second delay. The baseline condition of an unfilled delay, in which the participants were instructed to rehearse the sequence, was compared with conditions in which the delays were filled with hand tapping or with articulatory suppression.

We found a significant effect of interference revealing that performance was highly disrupted by tapping, whereas articulatory suppression task did not disrupt perfor-

**Table 2.** Correlations between span scores and movement times

| | | correlation coefficient | P |
|---|---|---|---|
| SB (span) | LB (span) | .345 | .098 |
| SB (time) | LB (time) | .921 | <.001 |
| SB (span) | SB (time) | –.311 | .138 |
| LB (span) | LB (time) | –.054 | .802 |

mance when compared to the baseline. No differences were found between SB and LB. The effect of interference was similar when considering the mean time for block to block movement, although in this case we also reported a significant difference between SB and LB, with faster movement times with the Small Board.

Table 2 shows the correlations between span scores and movement times. SB and LB correlated with each other for movement time and only approached significance for span scores. The span scores were not correlated to movement times in either condition, thus replicating the results of the previous Experiment.

Overall, results obtained in these Experiments do not clearly support a link between movement time and span sequence, shown most clearly by the absence of any negative correlation between span scores and movement times. However, we are left with the fact that in two experiments, movement time was unrelated to block sequence span, despite the demonstration that the paradigm is sensitive to selective disruption by concurrent movement (tapping), and experiments offer limited evidence of an effect of board size. An alternative view is that the board size effect might be linked to complexity rather than to distance between blocks. It is possible for example that the large board by chance had a more complex layout than did the small board. This form of complexity is difficult to manipulate experimentally and so we chose to modify the arrays so as to vary complexity in terms of number of elements present in the arrays used in assessing the sequence span tasks.

## Movement and complexity effects in visuo-spatial processes

There is a large amount of research demonstrating the importance of the different levels of complexity, defined in terms of number of pattern elements, in performance of visuo-spatial tasks (e.g., Della Sala, Gray, Baddeley, & Wilson 1997; Kerr 1987; Logie & Pearson 1997; Vecchi 1998; Vecchi et al. 1995). Moreover, results obtained by Smyth and Scholey (1994) indicated that participants' performance on a spatial span task is reduced when the complexity of the pattern is increased by having twenty-seven blocks divided in nine groups of three blocks each, instead of having only nine separate blocks. Kemps (1999) also demonstrated that increasing complexity by increasing number of blocks presented resulted in a reduction in span performance. As with

Kemps work, matrices that clearly differ in terms of number of array elements could highlight the importance of this form of visual complexity in span sequence tasks.

It is possible to formulate two alternative hypotheses: 1) Metric distance hypothesis: The overall distance between blocks is related to span scores so that longer distances produce shorter spans; 2) Visual complexity hypothesis: Span scores are related to the overall complexity of the pattern. If the sequence of blocks is memorised as a static pattern, then the increasing complexity of the overall array pattern should reduce performance irrespective of the length of the sequence of blocks to be recalled.

Two new experiments were designed specifically to investigate the above hypotheses by using matrices differing in number of blocks and by varying the mean distance between blocks in the two matrices. We used 3×3 and 5×5 computer keypad matrices differing in number of blocks but having the same general layout.

In a first experiment, participants performed immediate spatial sequence span tasks using 3×3 and 5×5 square matrices as experimental stimuli. The keypads are illustrated in Figure 3. The overall sizes of the matrices were 12 cm × 12 cm and 20 cm × 20 cm, in the case of the 3×3 and 5×5 matrices, respectively. Distances between keys varied from 4 cm to 11 cm and from 4 cm to 22 cm for sequences in the 3×3 and in the 5×5 matrices, respectively. Sequences were prepared in order to maintain a constant mean distance between keys for each movement: this measure was fixed at approximately 6 cm in the 3×3 matrix (mean distances varying from 6 to 6.9 cm), and at approximately 12 cm in the 5×5 matrix (mean distances varying from 10.8 to 12.8 cm).

Table 3 shows the mean span scores and movement times for the two matrices. In both cases, we found significant differences between the two matrices indicating better performance and faster times for the 3×3 matrices. Span performance did not correlate in the two matrices, whereas movement times for the matrices were significantly correlated. Once again, span scores were not correlated with movement times in either condition.

Overall, this experiment showed a clear effect of matrix type, and this effect was evident on both movement time and span performance: the 3×3 matrix trials produced shorter times, but also produced longer span sequences. This result is in accordance with the metric distance hypothesis but the actual pattern of results is still unclear: Again we did not find a correlation between time and span. In this Experiment we also did not find a correlation in span performance between 3×3 and 5×5 matrices. The effect of matrix type is much stronger than that observed in the previous Experi-

**Table 3.** Mean values and standard deviations for the span scores and movement times for 3×3 and 5×5 matrices

| | **3×3** | **5×5** |
|---|---|---|
| Span | 5.11 (.65) | 4.79 (.72) |
| Time (msec) | 360 (70) | 450 (100) |

**Table 4.** Mean values and standard deviations for the span scores and movement times for 3×3 and 5×5 matrices

| | 3×3 | 5×5 |
|---|---|---|
| Span | 4.76 (.64) | 4.36 (.64) |
| Time (msec) | 290 (40) | 340 (40) |

ments, and this is consistent with the idea that the effects of visual complexity (namely the increasing number of blocks) are more important than those of metric distance.

A further Experiment was designed to explore this issue by varying visual complexity while keeping distances equivalent: The mean distance between keys for each movement was equal for both 3×3 and 5×5 matrices, fixed at approximately 6cm (distances varying from 6 cm to 6.9 cm for both matrices). If there is a metric distance effect there should be no difference in performance between the two different matrices. However, a matrix type effect would appear if the important factor is visual complexity.

Table 4 shows the mean span scores and movement times for the two matrices. As before, we found a main effect of matrix type showing better performance and faster times with the 3×3 matrices. Span performance in the 3×3 and 5×5 matrices correlated, as did movement time. The span scores were not correlated with movement times in either condition. Results from this Experiment indicate that the difference in performance between 3×3 and 5×5 matrices is due to the visual complexity of the patterns and not to the longer movement times required to perform the task. The distance between keys did affect movement time but this was unrelated to span performance. Moreover, we obtained a significant effect of movement time indicating that movement times also are related to the number of objects in the array, possibly as a result of more complex planning of movements.

## Conclusion

The experiments reported here indicate that the number of elements in an array seems to predict participants' performance in recall of sequences of those elements as well as the metric distances involved in the sequences. At the same time, concurrent movement did selectively interfere with block sequence recall. Moreover, larger distances between elements resulted in an increase in movement time and did result in poorer span, but movement time was unrelated to span levels. The increase in number of blocks affected the span levels, regardless of the manipulation of the distances. It seems that longer movement times could be related both to longer distances and to number of blocks but not to memory performance.

These results are consistent with the data reported by Smyth and Scholey (1992, 1994) in which they reported no association between span and overt movement times. They are also consistent with the Kemps (1999) result linking increased number of

blocks with lower span. In addition, our data confirmed the selective interference effects on visuo-spatial span of a spatial tapping task, consistent with some form of overlap between movement control and visuo-spatial immediate memory. Recent studies have investigated this issue confirming a specific link between motor control and visuo-spatial span performance (Cavallini, Fastame, Palladino, Rossi, & Vecchi 2004), although they also showed differences between various forms of motor control and sequential visuo-spatial tasks. In general, cognitive mechanisms underlying performance in the Corsi blocks tasks are not well understood, with evidence showing that relatively minor differences in procedure may lead to major differences in cognitve abilities (Berch, Krikorian, & Huha 1998; Vandierendock & Szmalec 2004)

Moreover, as shown in a range of previous studies, verbal and visuo-spatial working memory components seem to be independent, given the lack of any interference with visuo-spatial span from articulatory suppression. This independence has been further confirmed by recent investigations using dual tasks and selective interference paradigms, although in most cases a greater role of central, amodal processes is postulated during the execution of sequential visuo-spatial span tasks (e.g., Vandierendonck, Kemps, Fastame, & Szmalec 2004; Vecchi & Richardson 2001)

While these features of the results are clear we are left with the apparent anomaly that concurrent movement interferes with visuo-spatial memory and processing (e.g., Quinn 1988; Quinn & Ralston 1986; see Logie 1995), yet one aspect of movement, namely movement time appears to be unrelated to performance on visuo-spatial tasks. Moreover, in these experiments we obtained clear differences in movement time related to metric distance and differences in span, these two effects being quite independent. One possible resolution would be to suggest that physical movement time is a poor measure of the efficiency of the mental processes involved in planning those movements, unlike the verbal rehearsal system which appears to be more closely linked to control of speech output. For example, physical movement time is constrained not only by planning but also by physical dexterity in the control of the muscle groups involved (e.g. Bizzi & Mussa-Ivaldi 1990). Therefore, our results do not exclude the existence of a visuo-spatial rehearsal mechanism, but they do point to the need for an alternative measure of its efficiency that does not rely on physical movement.

The effects of pattern complexity, in terms of the number of pattern elements in the array, are clear in our own data and in previous studies (e.g. Kemps 1999, 2001; Kerr 1987; Logie & Pearson 1997; Vecchi 1998; Vecchi et al. 1995) but demonstrating an effect of complexity still begs a question as to why complexity might affect recall of visuo-spatial material. Certainly, a rehearsal or a maintenance component of visuo-spatial working memory would most likely have more difficulty with more complex material. It is clear that VSWM has specific characteristics that are not entirely analogous to those proposed for its auditory-verbal sibling in working memory. The effect of spatial proximity reported by De Lillo in 2004 is another variable that may affect performance in spatial span tasks and be related to a more general effect of visual complexity.

Available data suggest that immediate memory for a sequence of movements is constrained both by the distance between the elements and by the number of elements in the array on which the sequence is based. There is a suggestion too that these are independent factors, an observation that is entirely consistent with the idea that mentally represented distance for movements between elements of a path relies on one cognitive resource while immediate memory for the identification of the location of the elements for recall from a larger array relies on another, complementary resource. Although the detailed characteristics of these hypothesised systems merit further exploration, our data appear to suggest that the visuo-spatial working memory framework offers a fruitful medium within which to investigate important aspects of visuo-spatial on-line cognition.

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## References

Baddeley, A. D. (1986). *Working Memory*. Oxford: Oxford University Press.

Baddeley, A. D., & Hitch, G. J. (1974). Working memory. In G. Bower (Ed.), *The psychology of learning and motivation*, Vol. VIII (pp. 47–90). New York: Academic press.

Baddeley, A. D., & Logie, R. H. (1999). Working memory: The multiple component model. In A. Miyake & P. Shah (Eds.), *Models of working memory: Mechanisms of active maintenance and executive control* (pp. 28–61). New York: Cambridge University Press.

Baddeley, A. D., Thomson, N., & Buchanan, M. (1975). Word length and the structure of short-term memory. *Journal of Verbal Learning and Verbal Behavior, 14*, 575–589.

Berch, D. B., Krikorian, R., & Huha, E. M. (1998). The Corsi block-tapping task: Methodological and theoretical considerations. *Brain & Cognition, 38*, 317–338.

Bizzi, E. & Mussa-Ivaldi, F. A. (1990). Muscle properties and the control of arm movement. In D. Osherson, S. M. Kosslyn, & J. M. Hollerbach (Eds.), *An Invitation to Cognitive Science, Vol. 2: Visual Cognition and Action* (pp. 213–242). Cambridge, MA: MIT Press.

Beschin, N., Cocchini, G., Della Sala, S., & Logie R. H. (1997). What the eyes perceive, the brain ignores: A case of pure unilateral representational neglect. *Cortex*, *33*, 3–26.

Cavallini, E., Fastame, M. C., Palladino, P., Rossi, S., & Vecchi, T. (2004). Visuo-spatial span and cognitive functions: A theoretical analysis of the "Corsi" task. *Imagination, Cognition and Personality, 23*, 217–224.

Cornoldi, C., & Vecchi, T. (2003). *Visuo-spatial working memory and individual differences*. Hove: Psychology Press.

Corsi, P. M. (1972). *Human memory and the medial temporal region of the brain*. Doctoral dissertation, McGill University, Montreal.

Courtney, S. N., Ungerleider, L. G., Keil, K., & Haxby, J. V. (1996). Object and spatial visual working memory activate separate neural systems in human cortex. *Cerebral Cortex, 6*, 39–49.

De Lillo, C. (2004). Imposing structure in a Corsi-type task: Evidence for hierarchical organisation based on spatial proximity in serial-spatial memory. *Brain & Cognition, 55*, 415–426

Della Sala, S., Gray, C., Baddeley, A. D., & Wilson, L. (1997). *Visual Pattern* Test. Bury St. Edmunds: Thames Valley Test Company.

De Renzi, E., & Nichelli, P. (1975). Verbal and nonverbal short term memory impairment following hemispheric damage. *Cortex, 11*, 424–433.

Ellis, N. C., & Hennelley, R. A. (1980). A bilingual word length effect: Implications for intelligence testing and the relative ease of mental calculation in Welsh and English. *British Journal of Psychology, 71*, 43–52.

Farah, M. J., Hammond, K. M., Levine, D. N., & Calvanio, R. (1988). Visual and spatial mental imagery: Dissociable systems of representation. *Cognitive Psychology, 20*, 439–462.

Hecker, R., & Mapperson, B. (1997). Dissociation of visual and spatial processing in working memory. *Neuropsychologia, 35*, 599–603.

Kemps, E. (1999). Effects of complexity on visuo-spatial working memory. *European Journal of Cognitive Psychology, 11*, 335–356.

Kemps, E. (2001). Complexity effects in visuo-spatial working memory: Implications for the role of long-term memory. *Memory, 9*, 13–27.

Kerr, N. H. (1987). Locational representation in imagery: The third dimension. *Memory and Cognition, 15*, 521–530.

Jonides, J., Smith, E. E., Koeppe, R. A., Awh, E., Minoshima, S., & Mintun, M. (1993). Spatial working memory in humans revealed by PET. *Nature, 363*, 623–625.

Levy, B. A. (1971). The role of articulation in auditory and visual short-term memory. *Journal of Verbal Learning and Verbal Behavior, 10*, 123–132.

Logie, R. H. (1986). Visuo-spatial processing in working memory. *Quarterly Journal of Experimental Psychology, 38A*, 229–247

Logie, R. H. (1995). *Visuo-spatial working memory*. Hove: Lawrence Erlbaum Associates.

Logie, R. H. (1996). The seven ages of working memory. In J. T. E. Richardson, R. W. Engle, L. Hasher, R. H. Logie, E. R. Stoltzfus & R. Zacks (Eds.), *Working Memory and Human Cognition* (pp. 31–65). New York: Oxford University Press.

Logie, R. H. (2003). Spatial and Visual Working Memory: A Mental Workspace. In D. Irwin & B Ross (Eds.), *Cognitive Vision: The Psychology of Learning and Motivation*, Vol 42 (pp. 37–78). Elsevier Science (USA).

Logie, R. H., & Marchetti, C. (1991). Visuo-spatial working memory: Visual, spatial or central executive. In R. H. Logie & M. Denis (Eds.), *Mental images in human cognition* (pp. 105–115). Amsterdam: Elsevier.

Logie, R. H., & Pearson, D. G. (1997). The inner eye and the inner scribe of visuo-spatial working memory: Evidence from developmental fractionation. *European Journal of Cognitive Psychology, 9*, 241–257.

Luzzatti, C., Vecchi, T., Agazzi, D., Cesa-Bianchi, M., & Vergani, C. (1998). A neurological dissociation between preserved visual and impaired spatial processing in mental imagery. *Cortex, 34*, 461–469.

Milner, B. (1971). Interhemispheric differences in theb localization of psychological processes in man. *British Medical Bulletin, 27*, 272–277.

Murray, D. (1965). Vocalization-at-presentation, with varying presentation rates. *Quarterly Journal of Experimental Psychology, 17*, 47–56.

Naveh-Benjamin, M., & Ayres, T. J. (1986). Digit span, reading rate, and linguistic relativity. *Quarterly Journal of Experimental Psychology, 38A*, 739–751.

Pearson, D. G., Logie, R. H. & Green, C. (1996). Mental manipulation, visual working memory, and executive processes. *Psychologische Beiträge, 38*, 324–342.

Quinn, J. G. (1988). Interference effects in the visuo-spatial sketchpad. In M. Denis, J. Engelkamp, & J. T. E. Richardson (Eds.), *Cognitive and neuropsychological approaches to mental imagery* (pp. 181–189). Dordrecht: Martinus Nijhoff.

Quinn, J. G., & McConnell, J. (1996). Irrelevant pictures in visual working memory. *Quarterly Journal of Experimental Psychology, 49A*, 200–215.

Quinn, J. G., & Ralston, G. E. (1986). Movement and attention in visual working memory. *Quarterly Journal of Experimental Psychology, 38A*, 689–703.

Smyth, M. M., & Pendleton, L. R. (1990). Space and movement in working memory. *Quarterly Journal of Experimental Psychology, 42A*, 291–304.

Smyth, M. M., Pearson, N. A., & Pendleton, L. R. (1988). Movement and working memory: Patterns and positions in space. *Quarterly Journal of Experimental Psychology, 40A*, 497–514.

Smyth, M. M., & Scholey, K. A. (1992). Determining spatial span: The role of movement time and articulation rate. *Quarterly Journal of Experimental Psychology, 45A*, 479–502.

Smyth, M. M., & Scholey, K. A. (1994). Characteristics of spatial memory span: Is there an analogy to the word length effect based on movement time? *Quarterly Journal of Experimental Psychology, 47A*, 91–117.

Vandierendonck, A., Kemps, E., Fastame, M. C., & Szmalec, A. (2004). Working memory components of the Corsi blocks task. *British Journal of Psychology, 95*, 57–79.

Vandierendonck, A., & Szmalec, A. (2004). An asymmetry in the visuo-spatial demands of forward and backward recall in the Corsi blocks task. *Imagination, Cognition and Personality, 23*, 225–231.

Vecchi, T. (1998). Visuospatial imagery in congenitally totally blind people. *Memory, 6*, 91–102.

Vecchi, T., Monticelli, M. L., & Cornoldi, C. (1995). Visuo-spatial working memory: Structures and variables affecting a capacity measure. *Neuropsychologia, 33*, 1549–1564.

Vecchi, T., & Richardson, J. T. E. (2001). Measures of visuospatial short-term memory: The Knox Cube Imitation Test and the Corsi Blocks Test compared. *Brain & Cognition, 46*, 291–295.

SECTION III

# Aging and visuo-spatial abilities

CHAPTER 3.1

# Aging and Visuo-spatial working memory

Elena Cavallini and Tomaso Vecchi

## Introduction

Studies on aging and cognition show that human aging is associated with lower performance in a number of different cognitive tasks (Craik & Salthouse 1992, 2000). Psychometric studies in this field have been growing in the last decade probably due to the increase in the elderly population. The researchers' aim has been to understand the changes related to aging and over the last 15–20 years, a number of multivariate analytical procedures have been used in order to investigate the nature of the age-related effects on different cognitive variables. Some of the models, developed to localize age differences between individuals in a hierarchical structure of cognitive abilities, indicate that aging has generally a negative influence especially on speed and memory factors. On the contrary it seems to have a positive influence on the vocabulary factor (Salthouse & Ferrer-Caja 2003; Salthouse 2004). Concerning the speed variable, one of the most reliable findings in cognitive research is that older adults are slower than younger adults in performing speeded cognitive tasks (Carella & Hale 1994; Salthouse 1996). Regarding memory, many studies have reported age-related differences in long term episodic memory and in working memory (see, e.g., Anderson & Craik 2000; Zacks, Hasher & Li 2000, for reviews). Moreover, decline in memory is greater in tests evaluating a combination of items (binding, context, or associative learning) than in tests assessing individual peculiarities or item information (Benjamin & Craik 2001; Mitchell, Johnson, Raye, Mather, & D'Esposito 2000). Indeed elderly individuals have greater difficulties in creating relations amongst different features.

Given their importance, the two most commonly studied indicators of aging are the measure of speed processing and the measure of working memory (Baddeley 1986). Their influence is not limited to cognitive aging research, there are also important neurobiological and neuropsychological constructs. For example perceptual speed of processing is highly sensitive to both brain damage and dementia and to normal age-related decline in cognition (Lezak 1995). Working memory deficits are similarly involved in frontal dysfunction (Smith, Geva & Maeshuets, in press), Alzheimer's disease and normal cognitive aging (Belleville, Perts, & Malenfant 1996; Reuter-Lorenz 2000).

Another important feature of cognitive aging concerns the effects of experience. Salthouse and colleagues (Salthouse 1991; Salthouse, Babcok, Skovronek, Mitchell, & Palmon 1990) suggested that experience and aging could be considered as independent factors, the first being connected with the level of expertise determining performance whereas the other producing the cognitive age-related decline. Most recent data (Hultsch, Hertzog, Small, & Dixon 1999; Masunaga & Horn 2001) are likely to question this hypothesis and suggest that age-related decline could be slowed down by intensive practice.

If on one hand data showing memory decline in old people are continuously reported, on the other hand several studies report that performance in certain task domains seems to be more sensitive to age than others (Mayr, Kliegl, & Krampe 1996; Sliwinski 1997). Data from several studies show that aging affects the visuo-spatial domain to a greater extent than verbal performance (Jenkins, Myerson, Joerding, & Hale 2000a; Jenkins, Myerson, Joerding, Hale, & Fry 2000b). Indeed visuo-spatial processes seem to decline more abruptly than verbal processes in later life. The encoding of spatial information is involved in a huge number of daily activities. For example navigational behavior, such as learning new routes or driving a car, involves the encoding of visuo-spatial information. Besides, the use of mental imagery is very important in several mental processes: it enhances cognitive efficiency, whilst being involved in topographical memory as well. Given the implication of visuo-spatial working memory (VSWM) in performing many human activities, it is easy to imagine that a decline in this domain can determine a decrease in a number of cognitive abilities. Understanding the nature of the decay in visual spatial abilities may reveal new information about the architecture of working memory as well as identifying the cognitive modifications related to aging. Provided that aging is a biological phenomenon affecting the organism at both structural and functional levels, to comprehend the functional modifications, it is very important to study their anatomical and physiological correlates as well.

Several studies have been carried out in order to examine working memory and its components, particularly in the field of aging. In general, the literature investigating visuo-spatial abilities across the life span of invidivuals highlights that aging has a greater impact on this particular subsystem of working memory. It seems that age affects VSWM and that this effect is progressive and linear (Bruyer & Scalquin 1999). Although some studies (Hale & Myerson 1996; Lawrence, Myerson, & Hale 1999; Myerson, Hale, Rhee, & Jenkins 1999; Jenkins et al. 2000a) suggest age-related differences between visuo-spatial and verbal encoding processes, others show an equivalent decline in both domains (Park, Lautenschlager, Hedden, Davidson, Smith, & Smith 2002; Reuter-Lorenz 2000, for an overview of these issues). The data relevant to the differences between younger and older adults are not homogeneous either. The diversity of findings could be due to the characteristics of the task – like familiarity and complexity – which sometimes makes interpreting aging data more difficult.

Initial studies found that visuo-spatial abilities' decline is more pronounced than verbal decline (Arenberg 1978). The interpretation of these data was limited by the absence of appropriate tools for measuring visuo-spatial processes, compared to verbal

abilities. The tasks employed in assessing visuo-spatial encoding were often more difficult to understand, being complex and unfamiliar to subjects. The lack of familiarity and other features of the task are considered to be the main causes for the decline in elderly people's performance (Baltes & Baltes 1990). It seems that during their lifetime people may acquire greater expertise for verbal processing than for visuo-spatial processing and that old people may be lacking in everyday experience with visuo-spatial tasks. Familiarity influences old people more than young people, and in addition to complexity, it can determine a more pronounced decay. In a recent research on familiarity, where the familiarity variable was manipulated and visual and verbal tasks were similar, results showed larger age-related deficits in visuo-spatial tasks. Old people had in general greater difficulties in learning new information than younger adults, but the most evident reduction was found in visuo-spatial abilities (Jenkins et al. 2000a). This result suggests that even when the verbal task is unfamiliar the age-related decline is more evident in visuo-spatial encoding.

Task complexity is another important factor associated with performance decline during aging. It seems that the elaboration of a limited amount of stimuli is preserved in the elderly, however when the task is more complex there is a decrease in the old people's performance. Recent studies in the visuo-spatial field found that healthy older adults are likely to maintain the ability of encoding spatial information for a fairly small number of items (Olson, Zhang, Mitchell, Johnson, Bloise, & Higgins 2004). Elderly people begin to show deficits as the amount of information increases (Chalfonte & Johnson 1996). Complexity refers not only to the number of items but also to the typology of information that has to be encoded. A simple task could require a subject to memorize either the item or the location information but a more difficult trial could require moemorization of both at the same time. Older adults are impaired on combination tasks, namely they differ from younger adults in creating relationships among several features (e.g. item and location) (Mitchell et al. 2000). It seems that in both younger and older adults individual differences increase systematically with task difficulty (Zhen, Myerson, & Hale 2000) but the elderly are more sensitive to the complexity variable than younger people (Chen, Hale, & Myerson 2003).

Moreover, elderly people have problems related to processing speed; they perform tasks slower than younger adults. Processing speed represents another approach in explaining age differences in all cognitive tasks and particularly in the visuo-spatial domain (Hale & Myerson 1996; Lawrence et al. 1999). Although older adults show difficulties in the trials in which they are asked to produce answers quickly, their performance is very similar to that of the younger adults in self paced tasks. Thus when they are free to decide how much time they spend performing a task, the age-related differences are likely to decrease (Sharps & Gollin 1987). The hypothesis of a reduction in processing speed is been shown to be crucial to interpreting the VSWM decay in several kinds of tasks, such as those that require manipulation of mental images or the elaboration of spatial locations. Given the importance of this variable, its role is also relevant in understanding cognitive aging.

The name visuo-spatial encoding is related to a variety of tasks such as recall and recognition of faces and spatial perception. Our attention will be focused on three sectors in which VSWM is particularly involved: spatial orientation, visuo-spatial location and mental rotation. A literature analysis of these fields should allow us to clarify the nature of the decay and the role played by the different variables.

Only relatively few studies have systematically investigated spatial orientation abilities because of the difficulties in creating ecologically valid evaluations. It is, in fact, rather difficult to both control for the external environment and obtain a laboratory setting similar to the real world. Studies on route-learning and topographical memory show that older adults have self-perceived problems in navigation and develop behavioral patterns to avoid unfamiliar routes and places (Burns 1999). Recent data on navigational/route finding skills, obtained from healthy old people, highlight age-related differences (Newman & Kaszniak 2000; Moffat, Zonderman, & Resnick 2001). In general elderly people have more difficulty than young people in learning and remembering routes through new environments. Furthermore, it is interesting to note that clinically relevant impairments in navigational skills are often present in the early stages of dementia (Klein, Steinberg, Galik, Steele, Sheppard, Warren, Rosenblatt, & Lyketsos 1999) and in several cases they contribute to diagnosis (Morris 1993). A recent study, employing a virtual environment technology (Moffat et al. 2001), confirms the data of prior ecological studies in which elderly people showed objective route learning and navigation impairments (Kirasik 1991; Kirasik, Allen, & Haggerty 1992). Particularly Kirasic (1991) found that the complexity of the task influenced the increase in age-related differences. Old people had difficulties in navigating in big places; while their performance was very similar to that of young adults when the place was smaller, such as their local grocery store. It appears that there are age-related differences in unfamiliar situations too (Ohta 1983; Kirasik 1991). The elderly obtain an advantage from familiar places provided that their dimension is limited. Indeed familiarity can facilitate old people's performance although the influence of complexity tends to be more relevant. The use of virtual environment technologies to investigate spatial navigation in older subjects proved that, compared to younger adults, older participants were slower in performing each task, traversed a longer distance and made more spatial memory errors (Moffat et al. 2001). Also in this case the processing speed was particularly important in highlighting age differences.

The recall of visuo-spatial information is frequently studied by using abstract material, complex scenes or other stimuli like matrices that require a subject to memorize the location of items. Most of these studies show a decline in performance as people age. Arenberg (1978) found that old people have greater difficulty in reproducing geometric figures on the basis of long term memory. A similar result was obtained in another study in which participants were required to recognize items presented to them just before the task (Reige & Inman 1981). Age-related differences in VSWM appear in spatial location tasks as well. It is interesting to note that there are no significant age deficits in working memory for visual features (form and appearance) but old people are impaired in encoding processes for spatial locations (Chen et al. 2003) and

particularly in those encoding processes that create a relationship amongst different features such as item and location (Mitchell et al. 2000). Such data are in line with earlier studies in which participants were required to memorize spatial positions on maps (Zelinski & Light 1988) or on geometric figures (Cherry & Park 1989); the effects of aging were always evident. More recently Olson et al.'s (2004) study in which they compared young and old adults' memory for location information after brief intervals, showed that initial encoding of spatial information for a relatively small number of items is largely spared in older participants and that the representation of spatial information persists over short intervals. It is reasonable to assume that the deficits in memory for spatial information grow as the number of items or the retention interval increase (Chalfonte & Johnson 1996). When the complexity of the task is raised, elderly people show a poorer performance (Chen et al. 2003). Also the processing speed influences the older adults' performance, indeed they perform the spatial location tasks more slowly than younger people. In a recent research the authors found that the age-related slowing was particularly pronounced in the visuo-spatial domain rather than in the verbal one (Jenkins et al. 2000b).

Another aspect that tends to decline with age and in which the speed variable is particularly relevant is the ability to generate and manipulate mental images (Dror & Kosslyn 1994). In general in these tasks participants are asked to perform mental rotations of previously presented stimuli in order to verify the similarity with another stimulus. It seems that the elderly people's performance in mental visual rotation tasks is particularly related to response time. This effect was well studied by Gaylord and March (1975) who employed an interesting paradigm used by Shepard and Meltzer (1971). Pairs of figures, different by degree of rotation, were presented to participants who had to judge the similarity of the stimuli. The time needed tended to increase on the basis of a greater angular disparity between the two figures. Old people needed more time to carry out the tasks and produced more errors. More recent studies, using similar tools, have reported similar results (Dror & Kosylin 1994; Hertzog & Rympa 1991). These data suggest that processing speed can be considered an important variable affecting the performance of elderly people.

Old people show a decreased ability to perform visuo-spatial tasks. Several variables can be considered relevant in determining the decay, such as familiarity and complexity. The literature suggests that a task's familiarity cannot be considered as a relevant factor justifying the different decay of verbal and visuo-spatial components, however it is an important variable that highlights the age-related differences in VSWM. Thus decreased familiarity and increased complexity make the elderly people's visuo-spatial performance worse. A great influence seems to be attributed to a decrease in processing time given the results obtained from studies based on mental rotation tasks, visual position tasks and also verbal tasks. The importance of speed has been associated with the assumption that the central components of working memory are generally more affected by aging. Formerly Welford (1958) introduced the hypothesis that the ability to coordinate and organize information in memory is more impaired in later life. Although this idea was not originally related to the WM system

it is consistent with the assumption of a selective decline of central executive structures (Baddeley 1986). The idea of a selective impairment of WM functions has been studied over years in more detail by employing different kinds of materials (verbal and visuo-spatial) and in association with different theoretical assumptions. In particular in the last few years, a new kind of research has been developed in order to investigate in greater detail the nature of the administered task and to clarify the effects of aging on the processes involved in input processing. The literature in this field is likely to emphasize the distinction between the storage and manipulation processes of information both in the verbal and visuo-spatial domains and to highlight a different trend for the two abilities in later life. Passive storage refers to the recalling of a limited amount of information in the same format in which it has been processed, stored or encoded. However the active processes refer to the operations – such as modification, transformation, integration of stimuli – that are required to carry out a task. This distinction is particularly useful whether explaining the modifications of VSWM during a person's lifetime or the functioning and architecture of the memory system.

In the next paragraphs this issue will be investigated by taking several recent studies into consideration. In particular, the latest research where we developed tools for the assessment of the passive and active processes, will be discussed both from the cognitive aging perspective and highlighting the different nature of the working memory components.

## An interpretation of age differences in VSWM: Active processes

It is well known that physical changes in the brain influence mental abilities. It would be easy to think that the effects are uniform and global but although this may in part be true, aging has also more selective effects on mental abilities. Not only are there age-related differences in the verbal and visuo-spatial components but it also seems that older adults have greater difficulties in the manipulation of information. Gick, Craik, & Morris (1988) found that the performance of the elderly was not influenced by the passive memory load but by an increase of executive functions. The decline in aging would be more pronounced in those tasks that imply the active encoding of information rather than in tasks requiring the storage of information without performing other operations or transformations. These selective effects are confirmed by studies on visuo-spatial performance. For example Salthouse & Mitchell (1989) distinguished between a structural and an operational capacity in WM functions. The former refers to the number of information units that can be encoded at the same time whilst the operational capacity is meant to be the number of processing operations. The latter implies that one or more operations can be performed while the products of the other are still present. Thanks to the use of two different tasks, assessing the respective capacities in the visuo-spatial domain, the researchers achieved results consistent with the hypothesis that operational capacity is more sensitive to aging.

A similar selective impairment was found by two other authors although based on a different theoretical perspective. Mayr and Kliegl (1993; Mayr, Kliegl, & Krampe 1996) proposed a distinction between sequential and coordination complexity and indicated that the integration and coordination of information are more greatly affected by age. Taken together, these results suggest that old people show a selective impairment in visuo-spatial tasks that require the manipulation of information. Unfortunately the data are not conclusive because when Salthouse, Babcock, & Shaw (1991) tried to confirm earlier findings, they did not find a different age-related trend for the two capacities. The discrepancy between the two studies may reflect a problem in the tools used. In the second study the researchers employed less familiar tools and a more complex experimental procedure; indeed participants were required to memorize stimuli presented on one of four quadrants of a computer screen. Later they had to remember the stimuli (passive task) and indicate the product of the stimuli which appeared on each quadrant (active task). The lack of an age effect could be due to the old people's unfamiliarity with this kind of task and/or to the unclear encoding processes required by these tools.

These findings suggest how important it is to develop adequate tools in order to asses visuo-spatial processes, in particular active ones. Although over the past few years several passive tasks have been created, there is an evident difficulty in finding procedures for the assessment of manipulation processes in aging.

The studies conducted by Vecchi and Richardson (2000; Richardson & Vecchi 2002) developed experimental procedures for assessing active visuo-spatial processing. The aim of their work was to produce a task in which the passive load was minimal in the presence of modifications in the active load. They developed a task, called Jigsaw Puzzle Test (JPT), in which participants are shown fragmented pictures of familiar objects selected from the Snodgrass and Vanderwat (1980) standardized set. The objects are divided into four, six, or nine numbered pieces and are arranged in jumbled configurations. Participants are required to solve the jigsaw puzzle by writing the numbers corresponding to the correct fragments on a response grid. Given that fragments are always in full view, the passive load is minimal. On the basis of several investigations it is possible to consider the task an important tool able to investigate age differences in active visuo-spatial abilities. Moreover it was revealed to be particularly useful in the assessment of normal aging (Richardson & Vecchi 2002; Vecchi & Cornoldi 1999) and of neuropsychological patients (Vecchi, Saveriano, & Paciaroni 1998/1999).

When older adults are compared to younger adults, all studies employing the JPT, have shown that the elderly make more errors, need more time to perform the task and their performance is usually worse. These results confirm the sensitivity of the test in detecting age differences and the difficulty older adults have in the active manipulation of information but not in the passive storage.

The distinction between the two capacities appears to have relevant implications for the architecture of WM. Indeed the studies employing either active tools or passive tasks indicate that the first tend to group together, although loading is lower for the verbal active tasks. On the contrary, passive tasks tend to be differentiated on the

basis of the tasks' characteristics, verbal or visuo-spatial. These data suggest that although a degree of modality-specific processes is present at all levels, the extent to which the processes are differentiated is inversely proportional to the growth of the active load (Vecchi & Cornoldi 1999). Richardson and Vecchi (2002) strengthened the hypothesis of differentiation between process-dependent (passive vs. active) and information-dependent activities (verbal vs. visuo-spatial). The researchers employed a set of tasks evaluating the passive and active processes in the verbal and visuo-spatial domains in order to investigate in more detail the characteristics of the tools, particularly the JPT. The results of the factorial analysis were very interesting: three different factors were found. The first was related to verbal processes, the second to active visuo-spatial processing and the third to passive visuo-spatial processes. Thus it seems that modality-specific effects are present at higher levels of processing. Also in this study the JPT was capable of detecting the age differences in the process involving the active manipulation of information.

The development of adequate tools seems to allow an interpretation of the discrepancies that can sometimes emerge from studies on VSWM, for example those obtained by Salthouse and colleagues (Salthouse & Mitchell 1989; Salthouse, Babcock, & Shaw 1991). Particular attention has to be paid to the characteristics of the task administered. As previously discussed, some of the tools' features can greatly influence the performance of elderly people. That is why we must be sure that the distinction between the two processes is related to a qualitative difference and not to a quantitative one. Indeed after a superficial assessment it may seem that the older adults' poorer perfromance in the two tasks is due to the characteristics of the task, such as its complexity, rather than to the decay of the information manipulation process. In the next section this issue will be discussed in order to clarify the age differences in VSWM particularly in the active visuo-spatial process.

## Can complexity explain the age differences between passive storage and active manipulation?

Working memory is generally differentiated from previous definitions of short term memory because there is a tendency to distinguish between on the one hand the simultaneous storage and processing of information and on the other the storage of information.

Several studies carried out in the field of visuo-spatial working memory and aimed at studying individual differences, appear to be in line with the hypothesis of a different nature of working memory (see Cornoldi & Vecchi 2003). On the basis of previously reported results it seems that increased age is associated with a more evident decline in the active processing capacities. Another recent study is consistent with the hypothesis of a different trend of active abilities for both verbal and visuo-spatial components during a person's life span (Vecchi, Richardson, & Cavallini 2005). But the features of active tasks tend to pose an important and interesting question. The instruments in-

volving the manipulation of information are often more complex and difficult than passive ones. It is well known that the complexity of a task is one of the main factors influencing elderly people's performance. An interpretation of age differences in performing active visuo-spatial tasks could be related to the greater difficulty in employing active tools. Vecchi et al. (2005) investigated this issue employing a modified version of the JPT (Vecchi & Richardson 2000; Richardson & Vecchi 2002). The analysis of the problem implied the possibility not only of comparing active vs. passive tasks but also modifying the passive task to make it more complex than the active one, thus controlling for complexity. The authors modified the original version of JPT and incorporated in the same experimental trial both an active and a passive task. They used a dual-task paradigm in which participants were asked to remember the original spatial positions of the stimuli and then to manipulate and integrate the stimuli to produce a different configuration. The two tasks could be directly compared because the same stimuli were employed simultaneously for both the passive and the active task. Participants were first asked to solve a puzzle (as described above) (which represents the manipulation of information) and then to place the pieces on a new response grid in the same locations as had been presented in the original configuration. In this case they actually held the fragments in their hands. The results show that the effects of aging are more evident in active tasks even if less complex than passive ones. Similar data were obtained from a study using a verbal task. Participants were presented four-word sequences, then six-word sequences, and finally nine-word sequences. In the active task they were required to recall the words in alphabetical order. After an interval of 10 s, participants had to recall the words in the order in which they had originally been presented. Although the passive task emerged as the more difficult one, it also revealed itself to be more sensitive to aging. In both studies the active tasks were easier but the differences among the three age groups (young adults, middle-aged adults and elderly people) were more evident in this task rather than in the passive one.

It is interesting to note that the dual-task paradigm also permits the evaluation of the variable that can affect complexity i.e. the number of puzzle pieces. The results show that the increase in the number of fragments has more influence on the passive task than the active one.

The results confirm the hypothesis that aging affects the tasks requiring active processing more than the tasks requiring the passive storage of information (Gick et al. 1988; Salthouse & Mitchell 1989; Vecchi & Cornoldi 1999).

Taken together, the data suggest that the difference between passive storage and active manipulation refers to a qualitative distinction and should not be confused with the quantitative variable of task complexity. By considering the characteristics of the task it becomes possible to interpret cognitive decline without confusing the influence of different variables. The research on cognitive aging needs to pay particular attention to several factors that could affect the performance of the elderly. Another relevant aspect of VSWM studies in the field of aging refers to the role of experience. The relationship between practice effects and VSWM is very important in understanding cognitive decline in later life and can help in interpreting data when results are

not homogenous.It is thus necessary to further investigate the role of expertise in visuo-spatial performance.

## The influence of expertise on VSWM aging research

As previously shown, the literature investigating the nature of age-related decline indicates a selective influence of aging on cognition, and VSWM appears to be one of the most age sensitive domains. Although cognitive abilities tend to decrease with age, presumably reflecting a gradual decline in cognitive resources such as speed of processing and working memory capacity, some deficits related to age are not always evident in work-related tasks (Salthouse & Maurer 1996). The discrepancy between laboratory experiments and daily life can reflect the influence of experience and knowledge. The relationship between aging and expertise is relevant to research because it could help to explain the contrasting data regarding memory decline. The effect of professional experience on VSWM poses two interesting questions. The first concerns whether visuo-spatial expertise can improve visuo-spatial performance in an experimental setting. Several studies confirm that carrying out related activities in daily life allows people to develop visuo-spatial capacities and perform better in domain specific tasks in a laboratory setting. This result emerged for example in studies with architects (Salthouse et al. 1990), graphic designers (Linderberger, Kliegl, & Baltes 1992) and pilots (Morrow, Menard, Stine-Morrow, Teller, & Bryant 2001). It seems that their experience affects performance in several ways. It may be that skills that have become automatized require less cognitive resources making the task easier to solve (Salthouse 1995). It is also possible that further compensatory mechanisms are involved where older participants knowledgable in this field may individuate a decline in their capacities and compensate by employing strategies based on their expertise (Dixon & Backman 1995; Salthouse 1995).

The second issue is more complex and the data are not always homogenous. Can expertise mitigate age decline? The question is whether practice in a specific activity that involves visuo-spatial abilities can reduce aging decay. Salthouse and collaborators (Salthouse et al. 1990; Salthouse 1991) tried to answer this question by formulating two hypotheses: "differential preservation" or "preserved differentiation". The differential preservation hypothesis indicates that the differences between good and bad imagery users increase throughout life because of a selective maintenance of this ability in the good imagery users. Following this hypothesis the discrepancy would tend to become increasingly evident with aging, but expertise would mediate and mitigate the effect of old age. The preserved differentiation hypothesis suggests that individual differences tend to remain the same throughout life. In this case the expertise would affect the performance level but without lessening the cognitive aging process. Salthouse and colleagues (1990) compared the performance of architects to that of people who had carried out activities not related to the visuo-spatial capacity, considering several age groups. The architects were found to outperform non-architects at all ages. It is inter-

esting to note that the differences between the two kinds of workers did not change across their life span. The authors (Salthouse et al. 1990) concluded that experience can affect performance but not age decline (i.e. the preserved differentiation hypothesis). Similar data were found by Linderberger et al. (1992) who investigated the role of professional experience of graphic designers on imagery-based memory performance. Participants were tested with different kinds of tasks and were trained to use the Loci Method (a technique that requires visuo-spatial abilities). Older graphic designers obtained a higher level of memory performance than older control participants, but were not able to reach the level of performance displayed by younger participants. Also in this study advantages associated with criterion-relevant abilities (talent) and experience could attenuate but not eliminate age differences. A more recent study (Cavallini, Vecchi, & Cornoldi, in preparation) was aimed at replicating results obtianed by Salthouse (Salthouse et al. 1990) both in the visuo-spatial domain and with people who had developed experience in the verbal field. The researchers compared the performance of architects and literary people with that of control participants on both verbal and visuo-spatial tasks. Expertise makes the level of performance higher especially in the visuo-spatial field; indeed architects outperformed control groups at all ages. Also literary people tended to perform better. Although the benefits of expertise occurred for participants of all ages even for older adults, the age-related differences were not reduced by professional experience. Overall results are consistent with the preserved differentiation hypothesis in the two domains of working memory. Moreover, professional experience influenced only the performance in those tasks associated with the specific expertise. This data appears to suggest that the experts are more likely to outperform novices on profession-related tasks. Indeed, architects performed better than normal participants in visuo-spatial tasks but not in verbal ones and literary people only outperformed the control group in tasks requiring verbal capacities. The experts may be able to use highly practiced skills and draw upon strategies in specific but not in general tasks. Thus, expertise can affect performance when the task is highly domain relevant.

If professional experience cannot modulate age decline, we could conclude that it is more likely that neurophysiological losses related to aging are involved.

Results are very important for a number of different reasons as well as having certain methodological consequences. Firstly they suggest the need to develop longitudinal studies able to investigate the role of experience and to further disentangle factors such as talent, experience and aging. Secondly it is very important to consider the effects of experience and practice because they may influence the results and account for non-homogenous findings.

## Conclusion

Taken together these data show an evident age related decline in visuo-spatial abilities. This decline was found in nearly all experimental situations employing different tools.

The analysis of VSWM throughout life emphasizes two important aspects. First, aging tends to affect the tasks requiring the manipulation of information more than those involving storage processes. The distinction between passive and active abilities in the visuo-spatial domain is particularly important because it helps to explain cognitive modifications due to aging as well as other individual differences such as pathological conditions. The elderly show difficulties in manipulation and transformation of information. On the contrary when they have to perform tasks involving only resource maintenance their performance is often similar to that of younger adults. Apparently the cause of the different performance in the two tasks could be attributed to the characteristics of the tools employed. Indeed the qualitative difference between the passive and active tasks could be confused with another variable that is often accountable for memory impairments i.e. complexity, given that the active tasks are usually more complex than the passive ones. Recent studies have tried to solve the issue by manipulating this variable. Even when active processes are investigated using simpler experimental procedures, older adults do not carry out the tasks as well as younger adults. These data confirm the recent hypothesis of a greater influence of aging on active processes.

Another interesting aspect that emerges from studies on VSWM concerns the relationship between age and experience and its effect on cognitive performance. The results in the visuo-spatial field suggest that they are independent variables that do not interact with each other. Expertise improves the level of performance of people of all ages but it seems to have no influence on the effects of aging. Although elderly people expert in the visuo-spatial domain show a better performance compared with non experts of the same age, the decay of visuo-spatial abilities is still present. For this reason it is possible to suppose that other factors, such as neurological and physiological ones, are involved in the aging process.

From a cognitive aging perspective, visuo-spatial studies are relevant also in order to understand the architecture of working memory and the nature of the processes involved. In particular the distinction between storage processes, active manipulation and the selective implication of verbal and visuo-spatial abilities appears to strengthen the hypothesis of the existence and of an interaction between the process-dependent and information-dependent dimensions of WM.

## References

Anderson, N. D., & Craik, F. I. M. (2000). Memory in the aging brain. In E. Tulving & F. I. M. Craik (Eds.), *The Oxford handbook of memory* (pp. 411–425). New York: Oxford University Press.

Arenberg, D. (1978). Differences and changes with age in the Benton Visual Retention Test. *Journal of Gerontology*, *33*, 534–540.

Baddeley, A. (1986). *Working memory*. Oxford, England: Clarendon Press.

Baltes, P. B., & Baltes, M. M. (1990). *Successful aging*. Cambridge: Cambridge University Press.

Belleville, S., Perts, I., & Malenfant, D. (1996). Examination of the working memory components in normal aging and in dementia of the Alzheimer type. *Neuropsychologia*, *34*, 195–207.

Benjamin, A. S., & Craik, F. I. M. (2001). Parallel effects of aging and time pressure on memory for source: Evidence from the spacing effect. *Memory and Cognition*, *29*, 691–697.

Bruyer, R., & Scalquin, J.-C. (1999). Assessment of visuospatial short-term memory and effect of aging. *European Review of Applied Psychology/Revue Europeene de Psychologie Appliquee*, *49* (3), 175–180.

Burns, P. C. (1999). Navigation and mobility for older drivers. *Journal of Gerontology Social Science*, *54*, 49–55.

Carella, J., & Hale, S. (1994). The rise and fall of information processing rates over the life span. *Acta Psychologica*, *86*, 109–197.

Cavallini, E., Vecchi, T., & Cornoldi, C. (in preparation). Experience effects on verbal and visuo-spatial abilities across life.

Chalfonte, B. L., & Johnson, M. K. (1996). Feature memory and binding in young and older adults. *Memory and Cognition*, *24*, 403–416.

Chen, J., S. Hale, & Myerson, J. (2003). Effects of domain, retention interval, and information load on young and older adults' visuospatial working memory. *Aging, Neuropsychology, and Cognition*, *10* (2), 122–133.

Cherry, K. E., & Park, D. C. (1989). Age-related differences in three-dimensional spatial memory. *Journal of Gerontology: Psychological Sciences*, *44*, 16–22.

Craik, F. I. M, & Salthouse, T. A. (Eds.). (1992). *The handbook of aging and cognition*. Hillsdale, NJ: Lawrence Erlbaum Associates Inc.

Craik, F. I. M., & Salthouse, T. A. (Eds.). (2000). *The handbook of aging and cognition* (2end ed.). Hillsdale, NJ: Lawrence Erlbaum Associates Inc.

Dixon, R. A., & Backman, L. (1995). *Compensating for psychological deficits and declines: Managing losses and promoting gains*. Mahwah, NJ: Erlbaum.

Dror, I. E., & Kosslyn, S. M. (1994). Mental imagery and aging. *Psychology and Aging*, *9*, 90–102.

Gaylord, S. A., & March, G. R. (1975). Age differences in the speed of a spatial cognitive process. *Journal of Gerontology*, *30*, 674–678.

Gick, M. L., Craik, F. I. M., & Morris, M. G. (1988). Task complexity and age differences in working memory. *Memory and Cognition*, *16*, 353–361.

Hale, S., & Myerson, J. (1996). Experimental evidence for differential slowing in the lexical and nonlexical domains. *Aging, Neuropsychology, and Cognition*, *3*, 154–165.

Hertzog, C., & Rympa, B. (1991). Age differences in components of mental-rotation task performance. *Bulletin of Psychonomic Society*, *29*, 209–212.

Hultsch, D. F., Hertzog, C., Small, B. J., & Dixon, R. A. (1999). Use it or lose it: Engaged lifestyle as a buffer of cognitive decline in aging? *Psychology and Aging*, *14*, 254–263.

Jenkins, L., Myerson, J., Joerding, J. A., & Hale, S. (2000a). Converging evidence that visuo-spatial cognition is more age-sensitive than verbal cognition. *Psychology and Aging*, *15*, 157–175.

Jenkins, L., Myerson, J., Hale, S., & Fry, A. F. (2000b). Individual and developmental differences in working memory across the life span. *Psychonomic Bulletin and Review*, *6*, 28–40.

Kirasik, K. C., Allen, G. L., & Haggerty, D. (1992). Age-related differences in adults' macrospatial cognitive processes. *Experimental Aging Research*, *18* (1–2), 33–39.

Kirasik, K. C. (1991). Spatial cognition and behavior in young and elderly people: Implications for learning new environments. *Psychology and Aging*, *6* (1), 10–18.

Klein, D. A., Steinberg, M., Galik, E., Steele, C., Sheppard, J. M., Warren, A., Rosenblatt, A., & Lyketsos, C. G. (1999). Wandering behaviour in community-residing persons with dementia. *International Journal of Geriatric and Psychiatry*, *14* (4), 272–279.

Lawrence, B., Myerson, J., & Hale, S. (1999). Differential decline of verbal and visuo-spatial processing speed across the adult life span. *Aging, Neuropsychology, and Cognition*, *5*, 129–146.

Lezak, M. D. (1995). *Neuropsychological assessment* (3rd ed.). New York: Oxford University Press.

Linderberger, U., Kliegl, R., & Baltes, P. B. (1992). Professional expertise does not eliminate age differences in imagery-based memory performance during adulthood. *Psychology and Aging*, *7* (4), 585–593.

Masunaga, H., & Horn, J. (2001). Expertise and age-related changes in components of intelligence. *Psychology and Aging*, *16*, 293–311.

Mayr, U., Kliegl, R., & Krampe, R. T. (1996). Sequential and coordinative processing dynamics in figural transformations across the life span. *Cognition*, *59*, 61–90.

Mitchell, K. J., Johnson, M. K., Raye, C. L., Mather, M., & D'Esposito, M. (2000). Aging and reflective process of working memory: Binding and test load deficits. *Psychology and Aging*, *15*, 527–541.

Moffat, S. D., Zonderman, A. B., & Resnick, S. M. (2001). Age differences in spatial memory in a virtual environment navigation task. *Neurobiology of aging*, *22*, 787–796.

Morris, J. C. (1993). The clinical dementia rating (CDR): Current version and scoring rules. *Neurology*, *43*, 2412–2414.

Morrow, D. G., Menard, W. E., Stine-Morrow, E. A. L., Teller, T., & Bryant D. (2001). The influence of expertise and task factors on age differences in pilot communication. *Psychology and Aging*, *16* (1), 3–46.

Myerson, J., Hale, S., Rhee, S. H., & Jenkins L. (1999). Selective interference with verbal and spatial working memory in young and older adults. *Journal of Gerontology: Psychosocial Science*, *3*, 161–164.

Newman, M., & Kaszniak, A. (2000). Spatial memory and aging: Performance on a human analog of the Morris water maze. *Aging, Neuropsychology, and Cognition*, *7* (2), 86–93.

Ohta, R. J. (1983). Spatial orientation in elderly: The current status of understanding. In H. Pick & L. Acredolo (Eds.), *Spatial orientation: Theory, research and application*. New York: Plenum Press.

Olson, I. R., Zhang, J. X., Mitchell, K. J., Johnson, M. K., Bloise, S. M., & Higgins J. A. (2004). Preserved spatial memory over brief intervals in older adults. *Psychology and Aging*, *19* (2), 310–317.

Park, D. C., Lautenschlager, G., Hedden, T., Davidson, N. S., Smith, A. D., & Smith, P. K. (2002). Models of visuo-spatial and verbal memory across the adult life span. *Psychology and Aging*, *17* (2), 299–320.

Reige, W. H., & Inman, V. (1981). Age differences in nonverbal memory tasks. *Journal of Gerontology*, *36*, 51–58.

Reuter-Lorenz, P. A. (2000). Cognitive neuropsychology of the aging brain. In D. C. Park & N. Schwarz (Eds.), *Cognitive aging: A primer* (pp. 3–114). Philadelphia: Psychology Press.

Richardson, J. T. E., & Vecchi, T. (2002). Ajigsaw-puzzle imagery task for assessing active visuospatial processes in old and young people. *Behavior Research Methods, Instruments and Computers*, *34*, 69–82.

Salthouse, T. A. (1991). *Theoretical perspectives on cognitive aging*. Hillsdale, NJ: Lawrence Erlbaum Associates Inc.

Salthouse, T. A. (1995). Refining the concept of psychological compensation. In R. A. Dixon & L. Backman (Eds.), *Compensating for psychological deficits and declines: Managing losses and promoting gains* (pp. 21–34). Mahwah, NJ: Erlbaum.

Salthouse, T. A., & J. J. Maurer (1996). Aging, job performance, and career development. In J. E. Birren & K. W. Schaie (Eds.), *Handbook of the psychology of aging* (4th ed.) (pp. 353–364). New York: Academic Press.

Salthouse, T. A., & Mitchell, D. R. D. (1989). Structural and operational capacities in integrative spatial ability. *Psychology and Aging*, *4*, 18–25.

Salthouse, T. A., Babcock, R. L., & Shaw, R. L. (1991). Effects of adult age on structural and operational capacities in working memory. *Psychology and Aging*, *6*, 118–127.

Salthouse, T. A., Babcok, R. L., Skovronek, E., Mitchell, D. R. D., & Palmon, R. (1990). Age and experience effects in spatial visualization. *Developmental Psychology*, *26*, 128–136.

Salthouse, T. A., & Ferrer-Caja, E. (2003). What needs to be explained to account for age-related effects on multiple cognitive variables? *Psychology and Aging*, *18* (1), 91–110.

Salthouse, T. A. (1996). The processing-speed theory of adult age differences in cognition. *Psychological Review*, *103*, 403–428.

Salthouse, T. A. (2004). Localizing age-related individual differences in a hierarchical structure. *Intelligence*, *32*, 541–561.

Sharps, M. J., & Gollin, E. S. (1987). Speed and accuracy of mental image rotation in young and elderly adults. *Journal of Gerontology*, *42*, 342–344.

Shepard, R. N., & Meltzer, J. (1971). Mental rotation of three-dimensional objects. *Science*, *171*, 701–703.

Sliwinski, M. (1997). Aging and counting speed: Evidence for process-specific slowing. *Psychology and Aging, 12*, 38–49.

Smith, E. E., Geva, A., & Maeshuets, C. (in press). Working memory: Findings from neuroimaging and patient studies. In F. Boller & J. Grafman (Eds.), *Handbook of neuropsychology* (2nd ed.)

Snodgrass, J. G., & Vanderwat, M. (1980). A standardized set of 260 pictures: Norms for name agreement, image agreement, familiarity, and visual complexity. *Journal of Experimental Psychology: Human Learning and Memory*, *6*, 174–215.

Vecchi, T., & Cornoldi, C. (1999). Passive storage and active manipulation in visuo-spatial working memory: Further evidence from the study of age differences. *European Journal of Cognitive Psychology*, *11*, 391–406.

Vecchi, T., & Richardson, J. T. E. (2000). Active processing in visuo-spatial working memory. *Cahiers de Psychologie Cognitive*, *19*, 3–32.

Vecchi, T., Richardson, J. T. E. & Cavallini, E. (2005). Passive storage versus active processing in working memory: Evidence from age-related variations in performance. *European Journal of Cognitive Psychology, 17*, 521–539.

Vecchi, T., Saveriano, V. & Paciaroni, L. (1998/1999). Storage and processing working memoryfunctions in Alzheime-type dmentia. *Behavioural Neurology*, *11*, 227–231.

Welford, A. T. (1958). *Ageing and human skill*. London: Oxford University Press.

Zacks, R. T., Hasher, L., & Li, K. Z. H. (2000). Human memory. In F. I. M. Craik & T. A. Salhouse (Eds.), *The handbook of aging and cognition* (2end ed., pp. 293–357). Mahwah, Nj: Erlbaum.

Zelinski, E. M., & Light, L. L. (1988). Young and older adults' use of context in spatial memory. *Psychology and Aging*, *3*, 99–101.

Zhen, Y., Myerson, J., & Hale, S. (2000). Age and individual differences in visuospatial processing speed: Testing the magnification hypothesis. *Psychonomic Bulletin and Review*, *7* (1), 113–120.

CHAPTER 3.2

# Imagery and aging

Paola Palladino and Rossana De Beni

## Introduction

How miserable would our life be without being able to imagine the beloved smile of a friend or the light of a sunny summer's day on a raining monday morning? Visual mental imagery allows people to temporarily access figural aspects of a previous experience such as color, shape and the structure of objects, sites and scenes (Denis 1991).

Mental imagery is a fascinating field where the subjective introspectionist approach to psychology encounters cognitive science in an attempt to answer, using an experimental approach, some of the most compelling questions about the mind and its functions.

If defining mental imagery may be rather easy when it refers to everyday and subjective experiences, problems arise when an operationalized definition is required and specific parameters of what is and what is not a mental image are needed.

A task analysis approach presents imagery processing as being a composit of a number of different processes. The study of mental rotation tasks has highlighted that imagery is not a unitary function but has a complex underlying structure (e.g. see Dror & Kosslyn 1994; Kosslyn 1980; Kosslyn & Koenig 1992; Sharps & Gollin 1987; Shepard & Metzler 1971). First, the mental image must be generated, activating stored information in the short term memory system, such as the visuo-spatial sketch pad (Baddeley & Hitch 1974) or a visual buffer (Kosslyn 1980). Then the mental image must be maintained, contrasting the spontaneous decaying process with continous effort. A further image scanning process may be initiated whilst in short term memory and finally an image transformation (for example a rotation) may also take place.

The independence of these processes emerged when studied from a developmental perspective. For example, younger children showed a poorer performance on all processes but maintenance, when compared to older children and young adults (Kosslyn, Margolis, Barrett Goldknopf, & Daly 1990).

Historically (Galton 1883) images have also been classed according to their phenomenological characteristics, such as number, detail, quality and vividness.

Classifications of visual mental images have been proposed according to distinct categories (Cornoldi, De Beni, & Pra Baldi 1989; De Beni & Pazzaglia 1995; Einstein &

McDaniell 1987). Cornoldi et al. (1989) proposed a distinction between general, specific and autobiographical mental images. General images represent a skeleton visual image of a prototypical object without reference to a particular example. By contrast, a specific image is a visual representation of a single, detailed and well-defined example of a concept. Autobiographical, also called self-referred, images correspond to the visual representation of an object connected to an autobiographical episode. Cornoldi et al. (1989) found that participants were able to classify their images according to these three categories, and to evoke, on the experimenter's request, only images belonging to one particular category.

General, specific and autobiographical images were found to differ in several respects (Cornoldi et al. 1989). General images were the most often evoked but specific images were rated highest in vividness. Furthermore the autobiographical images took the longest times to be generated.

De Beni & Pazzaglia (1995) collected evidence for the existence of different kinds of mental images: general, contextual, specific and self-referred images. Contextual images were images of objects in their usual contexts. They examined the relationship between the type of image and the ease with which it would be remembered. Contextual, specific and self referred image descriptions were richer in detail and more frequently recalled than general images. Furthermore, the former are sensitive to a variation in generation time.

Kosslyn (1994) reported neuropsychological evidence supporting the distinction between the different types of images. A different hemispheric specialisation has been associated with the generation of different types of image (Kosslyn et al. 1995). The right hemisphere is involved in the generation of prototypical images, whereas the left hemisphere is deputed to the generation of both prototypical and exemplar images. A functional Magnetic Resonance Imaging (fMRI) study (Gardini, Cornoldi, De Beni, Bromiley, & Venneri 2004), carried out on the generation of general and specific mental images, showed that general images activated a bilateral pattern involving the parietal and occipital areas, including the visual associative cortex, areas deputed to visuo-spatial processing and formation of gestalt like object representations (Lee, Mumford, Romero, & Lamme 1998). By contrast, specific images activated the frontal areas and the medial dorsal nucleus of the right thalamus, linked to attention to visual detail (LaBerge 2000). Further evidence consistently suggests that the two types of image are equally rich in visual details (Gardini, De Beni, Cornoldi, & Venneri 2005). Exclusively, the generation of episodic autobiographical mental images involved left medio-temporal areas (the parahippocampal gyrus) associated with episodic memory retrieval (Gardini et al. 2005).

Recently Baddeley and Andrade (2000) investigated the vividness of mental images in order to establish its relationship to both Working Memory (WM) and Long Term Memory (LTM). Previous studies attempting to relate individual differences in vividness rating and memory performance have been quite inconsistent (e.g. see Di Vesta, Ingersoll & Sunshine 1971). However a within subjects design could be a methodological device to calibrate the subjective scale used and, if accompanied by a simplification

of the judgements requested, it could overcome previous inconsistencies. The authors were, in fact, able to find consistent results across several experiments showing that perceived vividness of mental images decreases in the interfering conditions i.e. when a counting or a spatial tapping task was performed during imagery and rating tasks. They also consistently demonstrated that vividness ratings decreased when referred to new images (like bizarre images or dynamic images). The authors concluded that vividness ratings of novel mental images depend upon the working memory system whilst in the case of images from LTM other determinants influence their vividness.

Research on mental imagery in aging has mainly developed following the two directions described above i.e. the analysis of different imagery processes in visual imagery tasks, such as mental rotation tasks, and the study of the mental imagery's phenomenological characteristics such as type of image, number and quality of details and vividness, also in association with memory skills and performance.

## Aging and imagery processes

An interesting and effective approach to the study of mental imagery in aging has been the separate exam of each single process that composes the more complex mental imagery process such as for example in the mental rotation task.

Dror and Kosslyn (1994) administered four tasks to young and old people based on the tasks used by Kosslyn et al. (1990) to study the development of imagery processes, image generation, maintenance, scanning and rotation. In the image generation condition participants were required to form an image of a block letter within four brackets and decide whether the letter would cover an X mark placed within the brackets. In the image maintenance condition participants studied a pattern that appeared within four brackets and was then removed. The task was again to decide whether the pattern would cover an X mark placed within the brackets but participants were required to maintain the mental image of the pattern for a longer time (2,500 ms). In the image scanning condition participants were asked to study a rectangular ring and, when it disappeared, to scan the mental image in order to decide whether the arrow on the screen pointed to a filled or an empty square composing the rectangular ring. Finally, in the image rotation condition participants were required to decide whether two shapes were identical, regardless of their orientation. Both error rate and response time were considered in the data analyses. The authors suggested the existence of two phases in image generation: in the first, a stored description of the object shape is accessed and activated from long-term memory; in the second, each part of the object is visualised and put into the correct relative position. The older people were less efficient in image activation but their ability to add successive segments to their images was comparable to that of younger people. Older and younger participants did not differ in their image maintenance ability showing a similar increase in response times and error rates relative to the increasing image complexity. Furthermore no difference between age groups was found in the scanning task. Groups showed a similar increase in

scanning relative to the increase in distance. Finally in the rotation task elderly participants were relatively slower than the younger participants when the amount of rotation required increased. The results indicate that generation and rotation are sensitive to aging whereas maintenance and scanning appear to work in the elderly as efficiently as in the younger participants.

The attempt to distinguish between imagery processes and to understand the specific sensitivity to aging in a mental image rotation task is an interesting way to approach the study of age-related differences in mental imagery. However, despite the rigorous analytic approach, results of the few studies on this subject are far from consistent. For example, Johnson & Rybash (1993) found elderly people rather impaired in maintaining mental images compared to younger people. Brown, Kosslyn and Dror (1998), using the same task as Dror and Kosslyn (1994), were unable to replicate the absence of differences between age groups in the mental image scanning task. In fact they observed an age related decline in the task, both for error rates and response time. Results consistent with Dror and Kosslyn (1994) were obtained by Bruyer and Scailquin (2000) who found an aging effect only in the first phase i.e. activation of representations from long-term memory.

A general age related decline was found by Briggs, Raz and Marks (1999) in image generation and rotation tasks. They measured response time and accuracy in tasks that required either perceptual speed or mental imagery processing thus allowing a distinction between generation and rotation processes. The study was also aimed at verifing whether sensorimotor speed or working memory or both could explain the mental imagery age related decline. Results were not completely comparable across the two dependent variables examined. In fact an increase in response time was related to the increase in age for all perceptual and mental imagery tasks whereas the analysis of accuracy demonstrated a dissociation between perception and imagery tasks since only the latter were sensitive to age. Furthermore comparing perceptual speed with working memory it emerged that only the latter significantly mediated age related differences in mental imagery processing.

When the imagery task is not a mental rotation and mental imagery processes are not isolated but performance is examined unitarily, older participants are invariably less efficient than younger participants (Craik & Dirkx 1992) although to different extents depending on the task. When the tasks presented (the Brook Letter test, the East-West test and the Clock test) vary on many aspects (e.g. material, procedure, memory, processing requests etc.) results obtained are "difficult to interpret" (Dror & Kosslyn 1994:91) yet, at present, they suggest that "imagery changes over age in nonintuitive ways" (Dror & Kosslyn 1994:91).

Taken together results from the mental rotation field were aimed at demonstrating the different impact of age decline on the processes involved in complex imagery tasks. However due to both the paucity of studies and the lack of consistency in the results obtained it is, as yet, not possible to give a definitive answer to the nature of the imagery process and its sensitivity to aging relative to different tasks and processing requests. For what specifically concerns the mental rotation task, there are converging data sup-

porting an aging decline in the image generation process and its independence from the image maintenance process that is not affected by aging. Data on scanning and manipulation processes of the mental rotation task in aging are still rather inconsistent.

## Type of images and aging

Images have been systematically classified according to their properties and effects on memory (see for example, Cornoldi et al. 1989; De Beni & Pazzaglia 1995; Einstein & McDaniell 1987). General, contextual, specific and self-referred images have been described by participants asked to spontaneously generate mental images from concrete nouns and maintain them for a set period of time (De Beni & Pazzaglia 1995). Contextual, specific and self-referred image descriptions are richer in detail and more frequently recalled than general images. Furthermore, the former are sensitive to an increase in generation time.

De Beni, Pazzaglia and Gardini (2005) investigated generation and maintenance of visual mental images as a function of age and type of image. They examined age-related differences on image generation and maintenance according to types of image. As research on mental rotation showed a dissociation between generation and maintenance in relation to aging sensitivity (e.g. Bruyer & Scailquin 2000; Dror & Kosslyn 1994), the authors hypothesised that older people would show a longer generation time than younger participants but would be equal in maintenance time. In this case, as further support for the independence of the two processes, a low correlation between generation and maintenance times could be expected.

A further aim was to verify if general, specific, contextual and episodic-autobiographical images have different generation and maintenance times. The shortest generation time would be expected for general images (as showed by Cornoldi et al. 1989) considering their peculiar generation process (Kosslyn 1994), and the longest for episodic autobiographical images (De Beni & Pazzaglia 1995) since a long term memory search would be a necessary additional step in the process. The comparison between different types of images is substantially the comparison between very simple and prototypical images (general images) and more complex and detailed images, such as those containing specific details (specific images), a spatial context (contextual images), or a reference to episodic autobiographical memory (episodic autobiographical images).

In a first experiment two groups, one of young (22 years old on average) and one of older (69 years old on average) participants were asked to generate and maintain general, specific, contextual and episodic autobiographical images. Participants were presented 40 two-syllable, high imagery-value and medium-high frequency words, one word at a time, grouped in four lists of 10 items each. They were required to generate a different type of image for each list of ten words and they were told which type of image (general, specific, contextual or episodic-autobiographical) to evoke. A training session was given in which the experimenter explained the differences between general,

specific, contextual and episodic-autobiographical images, providing some examples for each category to make sure participants understood the task requirements and the differences between image types.

The words appeared on the centre of a computer screen and participants had to press the keyboard space bar twice: the first press indicated the generation time and was made when the corresponding image had been evoked; the second press measured the maintenance time and indicated when the image disappeared. Following the procedure described in Cocude, Charlot, and Denis (1997), generation time was defined as the interval between word presentation and the participant's response i.e. pressing the computer key indicating that an image had been formed and was currently present in mind. Maintenance time was defined as the time between the first response, indicating that an image had been formed, and the second key tap, meaning that the image was no longer available for conscious inspection, or was drastically altered.

Results obtained support an effect of aging on the generation of visual mental imagery since older participants showed a longer generation time than younger participants. In contrast the effect of age and interaction between age and type of image were not significant when maintenance time was analysed.

The lack of a significant correlation between generation and maintenance time further supports the independence of the two processes whereas the correlation between the four types of images was high.

In a second experiment, number and processing time of image transformation was examined with a procedure similar to that used in the previous experiment. Participants were again required to generate a type of image for each of the 40 words, the same used in the previous experiment, and to press a button when the image was generated. But they also had to press a button each time the image changed in colour, size, and richness of detail thus becoming a different type of image from the first one generated.

Again two groups, one of young (22 years old on average) and one of older (72 years old on average) participants were compared.

Results replicated the previous findings showing no age effect for the image maintenance process but also no age effect on image transformation, neither in the number nor in the time taken for transformation. Both the older and younger participants produced a lower number of transformations and the shortest maintenance time with general images, whilst episodic-autobiographical images were maintained the longest by the older people. Authors concluded that maintenance and transformation processes share some common mechanisms and are not subject to age decline.

Although these results could have been strengthened by asking participants to give a brief description of each generated image in order to control for the resulting type of image, they should be considered with interest.

In fact these results extend the dissociation between generation and maintenance processes and their sensitivity to the age effect to tasks quite different from the classical mental imagery tasks, such as the mental rotation task. In De Beni et al. (2005) more familiar and ecological stimuli were presented and participants generated mental im-

ages referring to long term memory representations of each specific object whose noun appeared on the computer screen.

Results were consistent in highlighting a process-specific aging effect even though both the material and procedure used were rather different from that used in research on mental rotation. Older participants were shown to be less efficient in the image generation tasks that require an image activatin from short/long term memory. Less clear and consistent with research on mental rotation are the results on mental image manipulation. With a less artificial task older participants showed to do as well as younger participants, both in terms of number of manipulations and time spent on it. However this was the case for spontaneous manipulations vs. required manipulations (in mental rotation tasks).

Furthermore it should be mentioned that results of a study on the neural substrates of age related decline in mental imagery in which image generation and maintenance were examined with separate tasks, did not allow a strengthening of the picture (Raz, Briggs, Marks & Acker 1999). Raz et al. (1999) obtained data from the magnetic resonance imaging (MRI) of 85 participants involved in imagery tasks. Contrary to what expected reduction in the volume of the dorsolateral prefrontal cortex and not of the modality-specific posterior visual region mediated age-related decline in mental imagery tasks. There was no relationship between the size of any of the specific brain regions that are usually associated with mental imagery processes and therefore no evidence sustaining a selective effect of aging on generation and maintenance processes.

## Imagery and memory in aging

Given that the helpful role of mental imagery in supporting various cognitive processes is well known, and also quite a common experience (Richardson 1980), it is reasonable to hypothesise that less efficient mental imagery processes could contribute to older adults performing poorly in many tasks. For example, older adults could be disadvantaged by a mental imagery deficiency in remembering concrete words since their superiority in a recall test compared to abstract words has been attributed to the higher imagery potential of concrete words (see for example Paivio 1971, 1986). In fact, older adults have repeatedly shown little or no advantage in recalling concrete word lists, even after imagery mnemonic instruction (Dirkx & Craik 1992; Isingrini, Fontaine, Métras, Bonneau, & Rey 1994; Richardson & Rossan 1994; but see also Mason & Smith 1977; Witte & Freund 1976). However, with a paradigm of selective interference, Dirkx and Craik (1992), were unable to demonstrate a lower involvement of visual imagery in the older adults' memory processes for concrete words since the visual interference was equally disruptive for the recall of both age groups, young and old.

If stimulated towards a more systematic and strategic use of mental imagery, older adults seem to be aided in memory tasks but, if untrained, or simply instructed, older

adults often seem to gain no advantage from the use of mental imagery processes for related memory tasks (Floyd & Scogin 1998; Verhaeghen, Marcoen, & Goossens 1993).

A useful approach to increase understanding in this field could be to examine the potential causes of aging decline in mental imagery.

A first hypothesis to be tested could be that the difficulty shown by older adults in imagery processes is referable to a deficit in the available cognitive resources, as pointed out by Craik and Byrd (1982). They hypothesized that older adults have difficulty in generating a mental image because it places heavy demands on cognitive processing resources, which are more limited in the elderly.

Another hypothesis could link mental imagery tasks with working memory tasks. The poor performance in the latter is attributed to poor inhibitory processes that allow irrelevant information to overload memory. Research examining working memory performance in older adults shows that they allow irrelevant thoughts to continue or reach conspicuous activation thus interfering significantly with the memory of more relevant material (see for example, De Beni & Palladino 2003; Hartman & Hasher 1991; Hasher & Zacks 1988; Hasher, Quig, & May 1997; Palladino & De Beni 1999). This interpretation could be extended to explain age limitations on memory performance as a function of imagery processing. In fact, it is possible to hypothesise that older adults generate mental images that are not only qualitatively different from the younger adults' images as observed by De Beni et al. (2005) but, in particular, are associated to the generation of irrelevant information. The difficulty in controlling irrelevant thoughts could interfere with the image generation and maintenance processes, reducing the benefit that visual coding normally produces in memory.

Considering that there are various kinds of mental images and that they can be grouped in categories with different properties and different effects on memory (see for example, Cornoldi et al. 1989; De Beni & Pazzaglia 1995; Einstein & McDaniell 1987), it is reasonable to hypothesise that besides age-related differences in the type of preferred images generated, older adults could show poor memory performance associated to imagery coding as a consequence of a failure in controling for irrelevant information during generation and maintenance of mental images in working memory. Palladino & De Beni (2003, 2005) conducted a series of experiments to investigate this hypothesis. In a first study, two experiments were conducted in which mental images spontaneously generated from a list of concrete high-imagery words were described by participants from different age groups (Palladino & De Beni 2003). The procedure allowed participants to freely generate the type of image they preferred.

All mental image descriptions were systematically analysed by two independent judges by classifying the images according to their type, and further distinguishing between image details affecting an increase in the goodness and specification of the image, and those that did not contribute to describing the image but simply overloaded memory. Four types of images were considered according to the literature (Cornoldi et al. 1989; De Beni & Pazzaglia 1995): General, Specific, Contextual and Self-referred images.

The relationship between type of image, their relevant and irrelevant details and their final recall was investigated and compared between four age groups, 21, 61, 69 and 75 years on average.

Results showed that older participants generated self-referred and general images more frequently than younger participants, but generated specific and contextual images less frequently than younger participants. Therefore aging affects the preference for the type of image spontaneously generated.

In accordance with the inhibitory hypothesis age-related differences were also observed in the number of details generated associated with the images. Older participants produced a higher number of irrelevant details though their image descriptions were equally rich of relevant detail to those of the young participants. As expected the older adults' final recall was poorer than the younger adults' one.

From these results the authors could speculate that the older adults' poor recall is due to the interference generated by a high number of irrelevant details that appear in their image description. However the indirect nature of the relation between irrelevant details and final recall does not allow for further speculations in this direction.

The second experiment was aimed at testing more directly the relationship between irrelevant details and memory performance controlling for the generation of irrelevant information.

The same task as for the previous experiment was presented to different age groups, but in two different conditions, i.e. giving either 20 or 40 seconds generation time for each word. The authors believed that a reduction in the available time in which to generate and describe the images could reduce the opportunity to generate irrelevant thoughts. The authors hypothesised that irrelevant thoughts could be responsible for poor memory performance, hence a time reduction, decreasing irrelevant thoughts, should improve final recall.

However, according to the results of Cornoldi et al. (1989) and De Beni & Pazzaglia (1995), the type of image could be sensitive to time constraints and the faster rate proposed (20 seconds per word) should induce less memorable types of images, such as general images. Therefore, if the reduction of time generation is shown to influence irrelevant detail production and thus reduce interference improving memory recall it could also decrease image specification and relevant details and thus increase general image production, known to depress memory recall. Results should therefore depend on the relative relevance of the two factors examined (i.e. type of image and number of irrelevant details) on recall since they are expected to affect it in opposite ways. A potential risk was also that the opposite effects would reciprocally eliminate each other producing a null effect.

Despite the complex plot of potentially different scenarios results obtained were rather clear in showing that the manipulation of generation time affected irrelevant detail production and final recall in accordance with the hypothesis.

The manipulation of generation time was effective in modifying the production of irrelevant details in older adults, from an average of 11 details in the 40 seconds condition, to an average of 3.7 details in the 20 seconds condition. No difference between

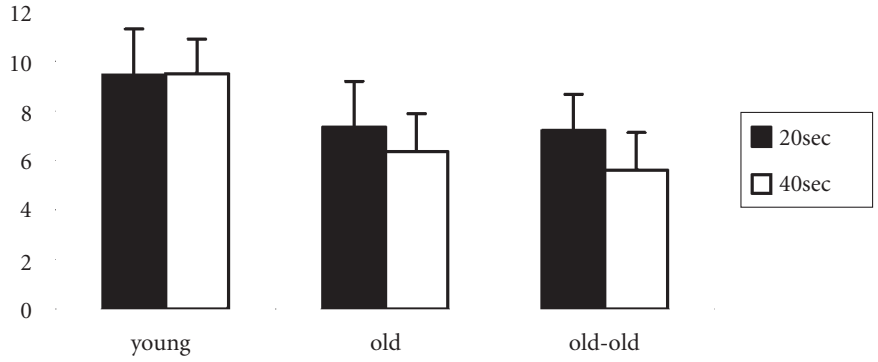



**Figure 1.** Total number of words recalled by the age groups. (Palladino & De Beni 2003)

time conditions was observed in the younger participants who produced about 1 irrelevant detail on average in both conditions. However, in the 40 seconds condition the three groups produced a comparable number of relevant details whereas, with 20 seconds, the older participants' number of relevant details decreased from approximately 40 to 24. This reduction in relevant details was probably a consequence of an increase in general images when less time was available (20 second condition) and a decrease of self-referred images.

The reduction of generation time could have boosted the older participants' recall only if irrelevant details were a more crucial factor in determining memory performance than the type of image and relevant details.

The memory recall test showed that old-old participants recalled less items than the young but, surprisingly, only when they had more time to generate and describe the images, (see Figure 1). It must be noted that in this condition (40 seconds) the older participants produced a significantly higher number of irrelevant details.

Although an explanation could be that the old-old participants in this condition produced more irrelevant details that interfered with memory and reduced performance, results could have been affected by a time delay between the beginning and the end of the presentation. The forty seconds delay for each word increased the interval between the beginning and the end of the presentation by about 300 seconds, thus double, the total time spent for image generation in the 20 seconds condition. If the poorer performance of the older participants with 40 seconds is due to the increase in the delay they should have a worse recall of the first, and hence more distant, words. The comparison between recall of the first, central and last words of the list, showed no interaction with age group. The last words presented were recalled better than the first and centrally positioned words in both conditions. This result allows to exclude that the benefit produced by the shorter time generation for older adults was due to a short delay between word presentation and recall.

In conclusion the authors were able to demonstrate that irrelevant details (generating interference) are strongly related to the older adults' poor memory performance

when a spontaneous image generation task is performed in association with a final recall. The results extend the inhibitory control hypothesis, which has received consistent support from several domains and different experimental designs, to explain age-related differences in memory performance following an imagery encoding phase (e.g. De Beni & Palladino 2003; Hasher & Zacks 1988; Hasher, Quig, & May 1997; Palladino & De Beni 1999). However, the inhibitory mechanism examined by Palladino & De Beni (2003) does not seem to be specifically related to imagery processes but, as the nature of irrelevant thoughts examined was quite heterogeneous (not mainly visual), it seems to be a more general mechanism controlling interference in various memory tasks.

A further step in order to better understand the aging effects on spontaneous image generation and their relationship with memory recall was conducted with the following study articulated in two experiments (Palladino & De Beni 2005). Authors were interested in replicating previous results in an experimental situation in which the process of image generation was better controlled for between participants and age groups. Participants were instructed to generate previously defined types of images that were extensively exemplified and specified.

In a first experiment two imagery conditions (generation of a specific or a self-referred image) were compared to a rehearsal strategy condition in which participants were instructed to rehearse the word presented until a new word was pronounced. Twenty seconds per word was the time constraint common to all three conditions. The authors' expectations were to highlight a reduction of the aging effect when a less efficient but more controlled for interference strategy (rehearsal) was applied.

A first analysis conducted on the real type of image generated showed that older participants met difficulties in generating both specific and autobiographic images. In fact, for example, old participants instructed to generate self-referred images, failed for more than 5 words on average out of the 15 presented.

The analysis of details distinguished not only between relevant and irrelevant but also between specific and self-referred images. Younger participants produced specific images richer of relevant details than old participants but their self-referred images were as rich as those of the older participants. However the older participants' self-referred images were described with more irrelevant details than the same type of image described by the younger participants.

The analysis of the number of words recalled showed no significant difference between age groups for both rehearsal and specific image generation conditions since the young recalled respectively one and two words more than the older participants. But given the instruction to generate self-referred images the young recalled a significantly higher number of words than the older participants, approximately 3 words more on average. The comparisons within each age groups between the three conditions showed no condition effect.

Compared to the imagery condition the rehearsal strategy allowed old participants to obtain a recall performance comparable to that of the young participants. When instead they were required to generate and describe mental images they showed some

difficulties, producing a higher number of irrelevant details and showing a poorer recall performance than that of the younger participants. These results demonstrate that the imagery strategy is not as effective for older adults since, besides inducing irrelevant details, it is not completed successfully. However it must be noticed that the use of imagery also for the younger participants did not increase their performance to such an extent as to be significantly different from rehearsal.

These results therefore suggest that the request to generate a well defined type of image appears to be rather different from the spontaneous generation of an image even if it is of the same type.

In a following experiment Palladino & De Beni (2005) aimed to directly examine the relationship between type of image and memory with an image generation procedure more spontaneous than the one used in the previous experiment. Therefore they instructed participants to generate both specific and self-referred images according to their liking.

This procedure allowed to directly relate the details to the type of image in order to examine the direct relationship between type of image, related details and memory performance. The current experiment differed from the previous one in two other ways: after the final recall participants were invited to focus on the images generated and try to shortly describe each one. The aim was to test the role of images as a cue to recall when the reference to the image generation process was controlled for (Richardson & Rossan 1994).

Furthermore irrelevant details were classed as either associated or confabulatory: the former being a type of detail that is not useful in describing the image but is semantically associated with it, whilst the latter is a type of detail arbitrarily associated with the object. It was thus possible to distinguish between irrelevant details that arise from a rich description of the object's semantic context from details that represent intrusive, unrelated thoughts.

Results showed that in a spontaneous generation condition young participants generated a comparable number of specific and self-referred images whereas older participants produced a higher number of self-referred images in a proportion of about 1/3–1/4 of specific images.

The mean number of relevant details is higher for the younger than for the older participants but, calculated as a proportion of the number of specific/self-referred images generated, this effect is comparable for both specific and self-referred images. The mean number of irrelevant details is low and comparable between groups when related details are considered. However older adults produced a higher number of confabulatory irrelevant details than younger participants both for specific and for self-referred images, although higher for self-referred than for specific images. The mean number of confabulatory irrelevant details per image was between approximately 1.5 and 2.5 for older participants and .14 and .40 for younger participants.

The older participants' recall performance was lower, recalling about half of the words presented, proportionally comparable between specific and self-referred images,

than the younger participants, whose recall was about 65–70% of the material. Similar effects were obtained on the recall performance cued by images.

Results are consistent with those obtained in previous experiments showing the older adults' poor recall of concrete words with imagery instructions. The quality of the images generated by the older adults was different from that of the younger adults. They showed a greater preference for spontaneously generated self-referred images rather than specific images. Their images were less rich in relevant details and more frequently endorsed with irrelevant confabulatory details than the younger participants' descriptions. It could be suggested that self-referred images elicit personal memories and structured memory associations that are less controllable. However, this was not the case since the proportion of confabulatory and relevant details was observed to the same extent in both the older participants' specific and self-referred image descriptions. Furthermore no imagery cue advantage in the recall performance was observed for either age group. However the lack of advantage could be due to the fact that the imagery cue recall condition was always presented after the free recall and the order of presentation was not counterbalanced.

The two studies described here investigated the relationship between image type, the associated production of details and memory in aging. Their specific contribution to the field is the use of more familiar and ecologically valid tasks than the classic imagery tasks (e.g. mental rotation) since participants are asked to spontaneously generate mental images, avoiding artificial constraints that are showed to decrease performance particularly in older adults (e.g. Baltes, Dittman-Kohli, & Dixon 1984; Richardson & Rossan 1994).

These studies consistently showed that older participants preferentially generated self-referred images whereas younger participants preferred specific images. However, the type of image did not seem responsible for the memory decrease apparent with aging since when image type was directly related to recall no effect was observed. On the contrary, irrelevant details appeared rather critical in reducing memory performance in older participants. When irrelevant details are reduced the older participants' memory performance showed a benefit although final recall was not yet comparable with that of the younger group.

Therefore it appears that imagery processes acquire certain peculiarities with aging probably related to a specific life-period condition (e.g. Rubin & Schulkind 1997). One of these peculiarities (i.e. type of image) did not show an adverse effect on mental efficiency (for example memory) but appeared only as qualitative specifications. However older participants showed a phenomenon which was completely absent from the younger group: the production of irrelevant details in image description. This phenomenon could be associated to the evidence of an increase in interfering thoughts with aging and seems to have a negative effect on memory performance in accordance with the inhibitory control hypothesis. In fact older participants are advantaged by imagery conditions that constrain irrelevant details production. However the reduction of irrelevant details was not completely efficient since older adults still showed a worse

performance than younger adults suggesting that poor recall depends on more than just the difficulty in controlling interference.

## Conclusion

Some preliminary conclusions could be drawn from the main results of research on imagery and aging, although with caution due to the relatively small number of studies that have been conducted on this subject.

The majority of the studies examined in the present chapter are consistent with a view of mental imagery as a complex process which a position of unitary continuous decline with aging is not able to adequately represent. Furthermore the effects of aging on the mental imagery process appears to be sensitive to familiarity and the ecology of the experimental situation and tasks, maybe more so than for other cognitive processes (see Palladino & De Beni 2003, 2005; Richardson & Rossan 1994).

Results that are consistent across different experimental approaches (for example, more vs. less ecological and with the presentation of different imagery tasks) must be considered particularly valuable. This is the case for the specific impairment showed by older adults in the image generation process and the absence of a deficit in the image maintenance process which have both been repeatedly demonstrated using different experimental designs and tasks (Brown et al. 1998; Bruyer & Scailquin 2000; Dror & Kosslyn 1994; De Beni et al. 2005). Thus aging seems to affect specific imagery processes such as image generation or activation but not others, such as for example image maintenance.

However a phenomenological research perspective seems to show that imagery processes, generation and maintenance, undergo qualitative changes one of which appears to be related to a memory gain based on imagery coding. Relatively few studies have examined the changes of type and quality of mental images in different age groups. They have consistently shown that the increase in age is associated with a preference in spontaneously generating the autobiographical type of images and a difficulty in image description represented by the production of a greater number of irrelevant details (Palladino & De Beni 2003, 2005). The difficulty in controlling irrelevant thoughts observed with aging (e.g. Hasher & Zacks 1988) appears to be involved in the imagery description process and to be related to memory recall. Therefore the benefit of imagery coding seems to be reduced by the difficulty in controlling irrelevant thoughts which have been shown to influence the older adults' working memory performance and cognitive tasks related to working memory (e.g. De Beni & Palladino 2003). On the other hand Baddeley and Andrade (2000) demonstrated that another phenomenological feature, i.e. perceived vividness of mental images, is dependent on working memory and long term memory efficiency.

The future directions of the field could be, of course, to strengthen and expand current results but also to integrate a purely experimental approach with a phenomenological perspective in order to more effectively study the imagery process with

a clear awareness of its potential dependency on cognitive structures and processes constraints.

## References


Baddeley A. D. & Andrade, J. (2000). Working memory and the vividness of imagery. *Journal of Experimental Psychology: General*, *129*, 126–145.

Baddeley A. D. & Hitch G. (1974). Working Memory. In G. A. Bower (Ed.), *Recent advances in learning and motivation, 8*. New York: Academic Press.

Baltes, P. B., Dittmann-Kohli, F., & Dixon, R. A. (1984). New perspectives on the development of intelligence in adulthood: Toward a dual-process conception and a model of selective optimization with compensation. In P. B. Baltes & O. G. Brim Jr. (Eds.), *Life span delopment and behavior*, Vol. 6 (pp. 33–76). Orlando, FL: Academic Press.

Briggs, S. D., Raz, N., & Marks, W. (1999). Age-related deficits in generation and manipulation of mental images: I. The role of sensorimotor speed and working memory. *Psychology and Aging, 14*, 427–435.

Brown, H. D., Kosslyn, S. M., & Dror, I. E. (1998). Aging and scanning of imagined and perceived visual images. *Experimental Aging Research*, *24*, 181–194.

Bruyer, R., & Scailquin, J. C. (2000). Effects of aging on the generation of mental images. *Experimental Aging Research*, 26, 337–51.

Cocude, M., Charlot, V., & Denis, M. (1997). Latency and duration of visual mental images in normal and depressed subjects. *Journal of Mental Imagery, 21*, 127–142.

Cornoldi, C., De Beni, R., & Pra Baldi, A. (1989). Generation and retrieval of general, specific and autobiographic images representing concrete nouns. *Acta Psychologica*, *72*, 25–39.

Craik, F. I. M., & Dirkx, E. (1992). Age-related differences in three tests of visual imagery. *Psychology and Aging*, *7*, 661–665.

Craik, F. I. M., & Byrd, M. (1982). Aging and cognitive deficits: The role of attentional resources. In F. I. M. Craik & S. E. Trehub (Eds.), *Aging and cognitive processes* (pp. 191–211). New York: Plenum.

De Beni, R., & Palladino, P. (2003). Decline in Working Memory Performances With Aging: Intrusion Errors Analyses. *Memory*, *12,* 75–89.

De Beni, R., & Pazzaglia, F. (1995). Memory for different kinds of mental images: Role of contextual and autobiographic variables. *Neuropsychologia, 33*, 1359–1371.

De Beni, R., Pazzaglia, F., & Gardini, S. (2005). *Generation and maintenance of visual mental images: Evidence from types of image and aging.* Submitted for pubblication.

Denis, M. (1991). *Image and cognition*. New York: Harvester Wheatsheaf.

Di Vesta, F. J., Ingersoll, G., & Sunshine, P. (1971). A factor analysis of imagery tests. *Journal of Verbal Learning and Verbal Behavior*, *10*, 471–479.

Dirkx, E., & Craik, F. I. M. (1992). Age-related differences in memory as a function of imagery processing. *Psychology and Aging*, *7*, 352–358.

Dror, I. E., & Kosslyn, S. M. (1994). Mental imagery and aging. *Psychology and Aging*, *9*, 90–102.

Einstein, G. O., & McDaniell, M. A. (1987). Distinctiveness and the memory benefits of bizarre imagery. In M. A. McDaniell & M. Pressley (Eds.), *Imagery and related mnemonic processes* (pp. 78–102). New York: Springer-Verlag.

Floyd, M. & Scogin, F. (1998). Effects of memory training on the subjective memory functioning and mental health of older adults: A meta-analysis. *Psychology and Aging*, *12*, 150–161.

Galton, F. (1883). *Mental imagery.* London.

Gardini, S., Cornoldi, C., De Beni, R., Bromiley, A., & Venneri, A. (2004). *Behavioural and neuroanatomical correlates of general and specific mental image generation*. Poster Presented at the 10th Annual Meeting of the Organization for Human Brain Mapping, June 14–17, 2004, Budapest, Hungary.

Gardini, S., De Beni, R., Cornoldi, C., & Venneri, A. (2005). *Left mediotemporal structures mediate retrieval of episodic autobiographical mental images.* Poster presented at the XXIII European Workshop on Cognitive Neuropsychology, 23–28 January, Bressanone.

Hartmann, M., & Hasher, L. (1991). Aging and suppression: Memory for previously relevant information. *Psychology and Aging, 6*, 587–594.

Hasher L., Quig, M. B., & May, C. P. (1997). Inhibitory control over no-longer-relevant information: Adult age differences. *Memory and Cognition*, *25*, 286–295.

Hasher, L., & Zacks, R. (1988). Working memory, comprehension, and aging: A review and a new view. In G. H. Bower (Ed.), *The Psychology of Learning and Motivation* (Vol. 22, pp. 193–225). San Diego, CA: Academic Press.

Isingrini, M., Fontaine, R., Metras, F., Bonneau, D., & Rey, P. (1994). Imagery coding: The effects of stimulus type and explicit imagery instruction on free recall. *Année Psychologique*, *94*, 369–384.

Johnson S. H., & Rybash, J. M. (1993). A cognitive neuroscience perspective on age-related slowing: Developmental changes in the functional architecture. In J. Cerella, J. Rybash, W Hoyer, & M. L. Commons (Eds.), *Adult information processing: Limits on loss* (pp. 143–173). New York: Academic Press.

Kosslyn, S. M. (1980). *Image and mind*. Cambridge, MA: Harvard University Press.

Kosslyn, S. M. (1994). *Image and brain: The resolution of the imagery debate*. Cambridge, MA, US, MIT Press.

Kosslyn, S. M., & Koenig, O. (1992). *Wet mind: The new cognitive neuroscience*. New York: Free Press.

Kosslyn, S. M., Malijkovic, V., Hamilton, S., Horowitz, G., & Thompson, W. (1995). Two types of image generation: Evidence for left and right hemisphere processes. *Neuropsychologia*, 33, 1485–1510.

Kosslyn, S. M., Margolis, J. A., Barrett, A. M., Goldknopf, E. J. & Daly, P. F. (1990). Age differences in imagery abilities. *Child Development*, 61, 995–1010.

LaBerge, D. (2000). Networks of Attention. In Gazzaniga, M. S. (Ed.), *The New Cognitive Neurosciences – II Edition* (pp. 711–724). Bradford Book, Cambridge Massachusetts.

Lee, T. S., Mumford, D., Romero, R., & Lamme, V. A. F. (1998). The role of the primary visual cortex in higher level vision. *Vision Research, 38*, 2429–2454.

Mason, S. E., & Smith, A. D. (1977). Imagery in the aged. *Experimental Aging Research*, *3*, 17–32.

Paivio, A. (1971). *Imagery and verbal processes*. New York: Holt, Rinehart & Winston.

Paivio, A. (1986). *Mental representations: A dual coding approach*. Oxford: Oxford University Press.

Palladino, P., & De Beni, R. (1999). Working memory in aging: Maintenance and suppression. *Aging: Clinical and Experimental Research*, *11*, 301–306.

Palladino, P. & De Beni, R. (2003). When mental images are very detailed: Effects of aging on memory of mental images. *Acta Psychologica, 113*, 297–314.

Palladino, P., & De Beni, R. (2005). Effects of aging on memory for specific and self-referred mental images, EWIC Conference, St. Andrew, UK, 28–30 June.

Raz, N., Briggs, S. D., Marks, W., & Acker, J. D. (1999). Age-related deficits in generation and manipulation of mental images: II. The role of dorsolateral prefrontal cortex. *Psychology and Aging, 14*, 436–444.

Richardson, J. T. E (1980). *Mental Imagery and Human Memory*. London: The Macmillan Press.

Richardson, J. T. E., & Rossan, S. (1994). Age limitations on the efficacy of imagery mnemonic instructions, *Journal of Mental Imagery*, *18*, 151–164.

Rubin, D. C., & Schulkind, M. D. (1997). Distribution of important and word-cued autobiographical memories in 20-, 35-, and 70-years old adults. *Psychology and Aging*, *12*, 524–535.

Sharps, M. J., & Gollin, E. S. (1987). Speed and accuracy of mental image rotation in young and elderly adults. *Journal of Gerontology*, *42*, 342–343.

Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, 171, 701–703.

Verhaeghen P., Marcoen A., & Goossens, L. (1993). Facts and fiction about memory aging: A quantitative integration of research findings. *Journal of Gerontology*, *48*, 157–171.

Witte, K. L., & Freund, J. S. (1976). Paired-associate learning in young and old adults as related to stimulus concreteness and presentation method. *Journal of Gerontology*, *31*, 186–192.

CHAPTER 3.3

# Object-location memory in ageing and dementia

Roy P. C. Kessels and Albert Postma

## Introduction

There is abundant evidence that memory declines as a result of normal ageing. More specifically, various studies have shown that especially episodic memory is susceptible to age-related deterioration, while semantic memory is generally preserved (Allen, Sliwinski, Bowie, & Madden 2002; Piolino, Desgranges, Benali, & Eustache 2002; Nilsson 2003). This impairment might be due to the inability to store and retrieve contextual information, such as *when* an event occurred or *where*, while memory for the target information (i.e. the core of the event itself) remains relatively intact. This theory is known as the context memory deficit hypothesis (Mayes 1988). One of the contextual features that has been consistently found to deteriorate with advancing age is related to the spatial aspects, i.e. *where* did the event occur. Typically, spatial memory concerns the ability to remember the spatial characteristics of our environment. As such, it allows us to learn how to get from A to B and to remember where we have stored our personal belongings. Hence, it is crucial for everyday functioning and impairments in spatial memory may result in severe limitations.

Centrally, spatial memory is not a unitary function, but can be subdivided into a number of sub-processes (see also Chapter Postma & Kessels, this book). Generally, a functional distinction can be made between route learning, spatial working memory and object location memory. Also, clinical neuropsychological studies have shown that selective impairments in different aspects of spatial memory can occur, often depending on the underlying neuropathology. For example, dysfunction of the prefrontal cortex has been consistently reported to affect spatial working memory (Kessels, Postma, Wijnalda, & De Haan 2000), the posterior parietal lobe has been found to be involved in route learning (Berthoz 1997), and the hippocampal formation is crucial for object-location memory (Milner, Johnsrude, & Crane 1997).

With respect to age-related decline, consistent impairments in older participants compared to young adults have been reported on spatial-location memory (Cooney & Arbuckle 1997). Denney, Dew and Kihlstrom (1992) found that older adults were

impaired when asked to recall the locations of words, although an impairment in target memory (i.e., memory for the words themselves) was also present. Furthermore, Cherry, Park and Donaldson (1993) demonstrated impaired memory for three-dimensional spatial information in older adults.

While the context memory deficit hypothesis states that memory impairments might be due to an inability to encode and store the contextual features in itself, others have suggested that it is specifically the integration or binding of target and contextual features (such as location) that is impaired in older adults, resulting in a poor episodic memory performance, rather than poor memory for contextual features themselves. Crucially, information that has been processed through separate, highly specialised channels within our cognitive system has to be integrated eventually in memory, since we do not remember the world around us in terms of separate features (e.g., location, time, semantics). Chalfonte and Johnson (1996) found evidence for a specific impairment in the binding of item information to contextual features (colour and spatial location) in a group of healthy older adults compared to young participants. Memory binding has also been studied from a neuropsychological perspective. For example, Chalfonte, Verfaellie, Johnson and Reis (1996) investigated the binding of object information, such as colour, to spatial locations in amnesic participants and hypothesised the existence of a hippocampal-diencephalic "binding circuit" involved in the storage of complex memories which might be impaired in patients suffering from anterograde amnesia. Also, Mitchell, Johnson, Raye, Mather, & D'Esposito (2000a) and Mitchell, Johnson, Raye and D'Esposito (2000b) demonstrated that object-location binding declined in ageing, whereas memory for locations or objects in isolation was unimpaired, a finding which was related to diminished activation of the hippocampus in the older participants.

Although these results clearly show a decline in spatial memory in healthy older people, this deterioration appears to be most profound in explicit recall of spatial information, i.e. the conscious recollection of spatial information. In turn, implicit forms of memory (unconscious knowledge and skills) are presumed to be relatively spared in patients with neurological diseases affecting the cerebral cortex or in subjects of older age (Light & Singh 1987). However, implicit aspect of spatial memory are relatively unexamined. The purpose of the chapter is to present an overview of empirical studies focusing on object-location memory in older participants and patients with pathological ageing, i.e. dementia. First, we will focus on the assessment of object-location memory in these groups, both using clinical tests and using experimental paradigms. Second, we will systematically compare the context-memory deficit hypothesis and the binding-deficit hypothesis to investigate which theory can explain the decline in object-location memory in older people and in dementia. Third, we will study whether it is object-location as a whole which deteriorates, or whether some aspects, specifically implicit forms of object-location memory, are spared in older age or dementia.

## Assessment of object-location memory in older participants

While neuropsychological research shows marked deterioration of object-location memory in older age and dementia, the assessment of impairments in object-location memory in general clinical practice has been largely neglected. That is, only a few standardized tests exist which can be effectively applied to detect object-location memory deficits. For example, the Spatial Location Test was developed by Grober (1984) and adapted by Sanchez, Grober and Birkett (1997) for use in clinical settings. Here, four or eight pictures of common objects are presented on different locations on a large card, which have to be studied by the subject. Subsequently, the pictures have to be relocated to their correct positions, which are pre-marked in the relocation phase by empty rectangles (in a grid-like manner, i.e. top left, bottom right). This test correlated strongly with the Mental Status Questionnaire (MSQ) in a group of elderly patients with severe mental disorder (Sanchez et al. 1997). The authors suggest that this test may be useful for the assessment of object-location memory in absence of dementia. However, the impairments in this patient group were due to a mixed aetiology. Also, data from healthy control subjects are not available.

Alternatively, the The Brief Visuospatial Memory Test – Revised (BVMT-R) was developed by Benedict and Groninger (1995). Six geometric figures are presented in a $2 \times 3$ grid for a brief period (10 s). Next, these have to be reproduced and placed in the correct position, immediately and after a 25-minute delay. This pen-and-paper test comes with 6 alternate forms. Also, a yes-no delayed recognition test has been added recently (Benedict, Schretlen, Groninger, Dobraski, & Shpritz 1996). The BVMT-R has been studied in various age groups (between 18 and 88), but data on clinical populations are not available. However, a number of problems exist with these clinical tests for object-location memory. Most object-location memory tests rely heavily on visuoperceptual and visuo-constructional abilities, which cannot be measured in isolation with these spatial-memory tests. Moreover, most tests have been developed for the assessment of dementia, and may be less applicable for other neurological conditions or healthy participants.

More recently, the Location Learning Test (LLT) has been introduced, which overcomes some of these shortcomings. Here, ten everyday pictures are presented in a large grid (see Figure 1) and participants have to relocate them to the correct position immediately and after a delay period (Bucks & Willison 1997). This test was used to investigate in more detail the effect of age on object-location memory (Kessels, Nys, Brands, & Van Zandvoort 2004). A group of 97 healthy participants was examined, aged between 21 and 87, without cognitive impairments, neurological diseases or psychiatric disorders, using a modified administration procedure (i.e., with a short presentation duration and a long delay period to maximize the sensitivity of the test). Figure 2 shows the results, indicating a clear age-related decline of the performance on the LLT as measured with the learning index (i.e., the learning curve computed on the basis of the displacement scores over five consecutive trials using an identical display).

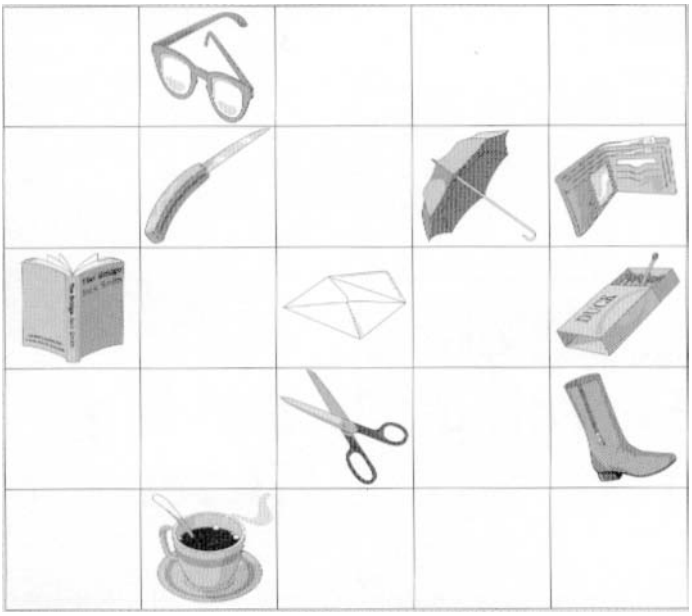


**Figure 1.** Stimulus of the Location Learning Test (actual size 42×38 cm). © 2000 Bucks, Willison & Byrne; published by Thames Valley Test Company. Reprinted with permission of the Publisher and authors.

Although both experimental task paradigms and clinical tests provide evidence of an age-related decline in object-location memory, they do not shed light upon the underlying cognitive mechanisms. Therefore, a new paradigm, *Object Relocation,* was developed to scrutinize in detail the underlying cognitive processes of object-location memory (Kessels, Postma, & De Haan 1999). This computer task employs a set up with a touch-sensitive screen to measure the responses. On the computer monitor, pictures of common objects are presented on different locations in a frame. The participant has to remember the locations as accurately as possible and subsequently relocate these to their correct locations. This paradigm makes it possible to study several aspects of object-location memory in isolation, such as positional encoding (only positions have to be remembered, regardless of the item content), object-location binding (objects have to be placed on pre-marked positions), and temporal-order memory (objects are presented sequentially on different locations). This paradigm was used to examine object-location memory in relation to the context-memory deficit hypothesis and the binding-deficit hypothesis in older participants as well as patients suffering from dementia.

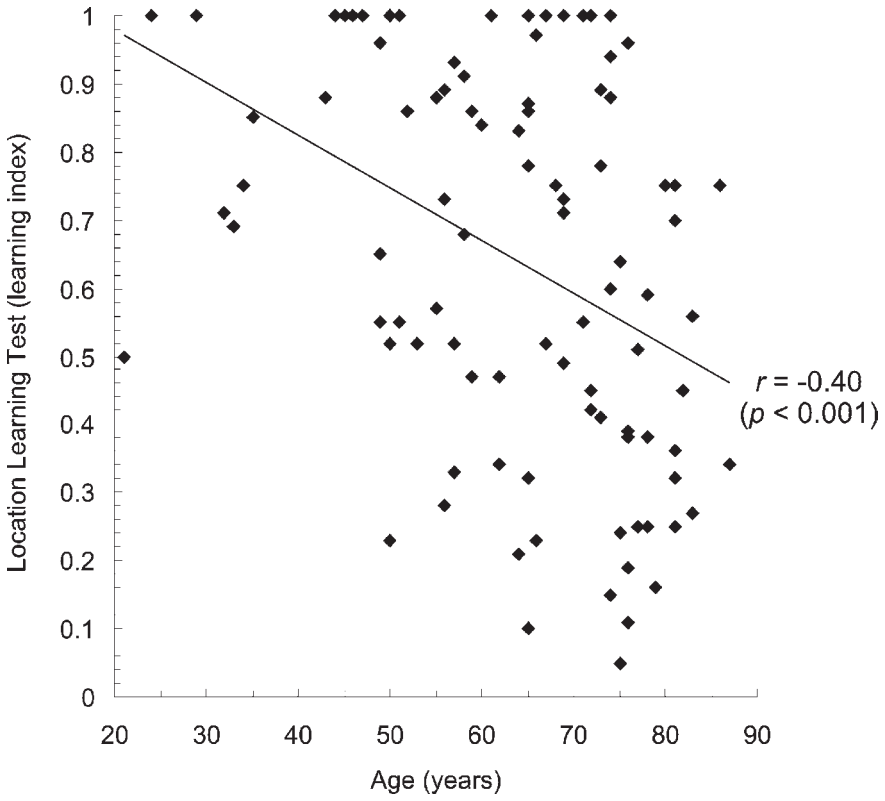



**Figure 2.** Correlation (Pearson's r) between age and object-location memory as measured with the learning index (an estimate of the learning curve based on five subsequent trials) of the Location Learning Test (data from Kessels, Nys, Brands, & Van Zandvoort 2004).

### Object-location memory in ageing: binding problem or context deficit?

Recently, Van Asselen (2005) examined memory for contextual features and binding in more detail in a group of young and older adults. Apart from spatial location, temporal-order memory was examined as well. That is, patients had to remember common objects, the locations of these objects, the order of presentation of these objects, or a combination of these. The results showed an impaired performance on memory for object location as well as memory for temporal order. Also, an additional deficit was found on trials requiring the integration of three features, that is, temporal order, spatial location and object identity. This might suggest a specific binding deficit next to a general impairment in context memory. However, the design has some methodological shortcomings. That is, the binding condition was generally regarded as highly difficult. Also, this study did not include a condition assessing target memory. Thus, it is possible that studies showing additional age effects on memory binding are the result of the increased complexity rather than the integration aspect itself. Hence,

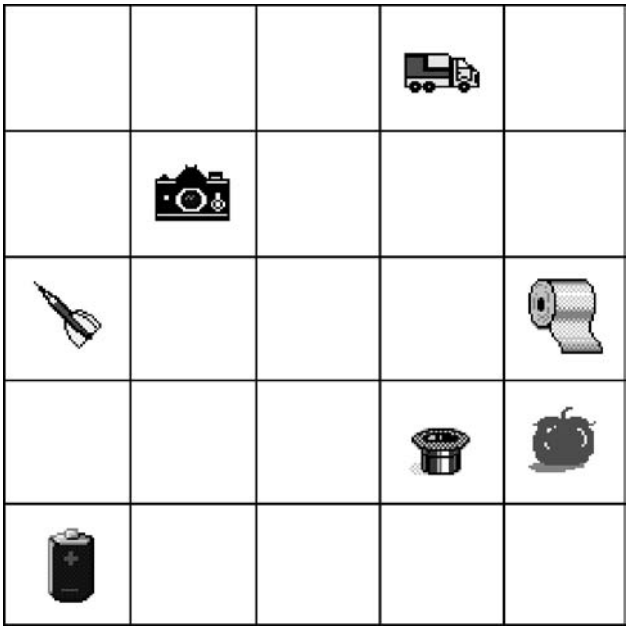


**Figure 3.** Example of a stimulus display in the Kessels, Hobbel and Postma (submitted) study. In this condition, participants had to remember as accurately as possible the location of each object. In the test phase, an empty grid was shown with the 7 objects placed on top of it.

a similar experiment was performed in a study in a large group of young ($N$ = 40) and older ($N$ = 40) adults (Kessels, Hobbel, & Postma, submitted). In this study, target and context memory were systematically compared, as well as conditions requiring the binding of information in memory in comparison to conditions that do not require integration. Different contextual features were examined, that is, memory for temporal order and spatial location (see Figure 3 for a stimulus display). Target memory was assessed by instructing the participants to remember the identities of the objects themselves, without spatial or temporal information. As expected, the results clearly showed age-related memory decline on all conditions (see Figure 4 for the results). However, some memory aspects were susceptible for age-related decline to a greater extent. First, spatial memory was impaired more compared to target memory in the older group. This finding corroborates the results of previous studies on ageing and spatial memory. For example, Lemay and Proteau (2003) demonstrated that older participants made more errors in pointing at a previously learned location than younger participants. Furthermore, Chalfonte and Johnson (1996) showed a disproportional decline in memory for locations compared to memory for the items themselves. These results refute the idea that spatial memory is a fully automatic memory process which is resistant for age-related cognitive deterioration (Hasher & Zacks 1979). For example, Ellis, Katz and Williams (1987) compared the memory performance of children, young

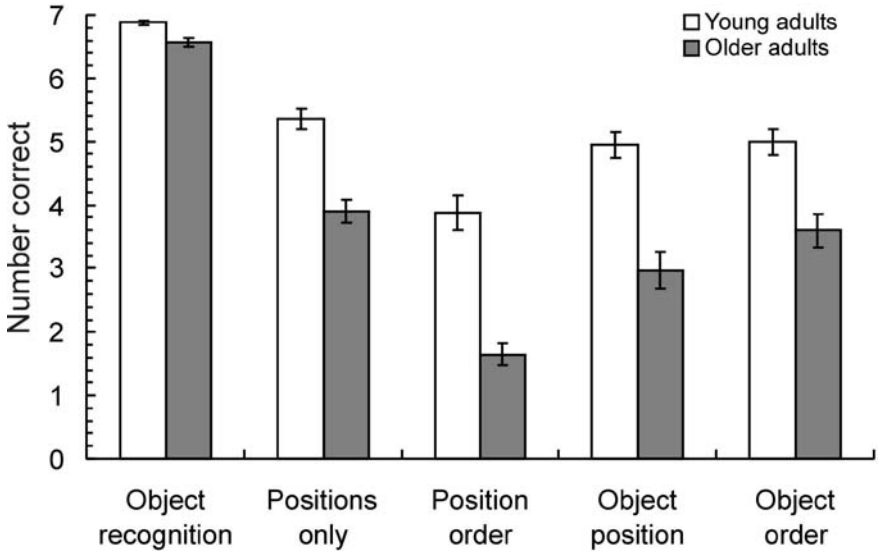



**Figure 4.** Performance of the young and older adults on the different types of memory (maximum score = 7) (data from Kessels, Hobbel, & Postma, submitted).

adults and older participants and did not report age differences in location memory. However, this latter null finding might have been due (at least in part) to a ceiling performance in the children and young adults, since some older participants showed clear age-related memory impairment.

While these results clearly showed spatial-memory decline as a result of ageing, other forms of memory deteriorated as well. That is, memory for temporal order declined to a similar extent as spatial memory, in line with previous studies in which temporal and spatial memory were compared directly (cf. Vakil, Weise, & Enbar 1997). Interestingly, memory for multiple features, i.e. binding, was affected to a greater degree than memory for single items. This extends the results of Chalfonte and Johnson (1996). It has been suggested that studies showing a binding deficit in older participants did not take into account the increased task load. That is, memory for multiple, bound items typically involves a higher test load than memory for single items. Consequently, memory binding impairments in older participants might be partly due to the increased amount of information that has to be remembered (Mitchell et al. 2000a). In all, these findings are in agreement with the context-deficit hypothesis of Mayes (1988) in that contextual memory (i.e., spatial and temporal order memory) deteriorates with advancing age. They also support the binding-deficit hypothesis; there was evidence for a specific memory binding dysfunction in the healthy older group.

## Implicit and explicit memory for object locations in healthy older adults

While age-related memory decline is reported in many studies, most have only focused on explicit forms of spatial memory. Explicit spatial memory refers to the ability to consciously store and retrieve information about the spatial layout of our environment. Implicit forms of spatial learning, that is, unconscious and possible automatic forms of spatial learning, however, are only scarcely examined. Since there is abundant evidence that implicit memory in general is less susceptible to the effects of ageing, it is interesting to focus in detail on the distinction between implicit and explicit forms of spatial memory in relation to ageing. One key study which examined the role of implicit and explicit processing in spatial memory has been performed by Caldwell and Masson (2001), comparing young and older adults. Participants had to study the locations of line drawings of everyday objects in five rooms presented on a computer screen. In the retrieval phase of the study, the process dissociation procedure by Jacoby, Toth and Yonelinas (1993) was applied, in which two different response instructions were given, i.e. an include and an exclude condition. In the include condition, participants were instructed to relocate the objects at their previously occupied (i.e., target) locations. In case the target location could not be explicitly remembered, the participant had to relocate the object at the first location that came to mind. It is assumed that both explicit memory (knowing) and implicit memory (guessing) produces the target response. In the exclude condition, participants were instructed to first recall the target location of the object, but subsequently had to relocate the object at a different (new) location than the previously occupied target location. Again, if the target location could not be remembered, the object had to be relocated at the first location that came to mind. Using this instruction, implicit memory generates the target response, while explicit memory generates an opposite and incorrect (new) response. The results showed that ageing affected explicit spatial memory but not implicit spatial memory.

Recently, the procedure of Caldwell and Masson (2001) was extended into a more ecologically valid version in that photographs of real rooms and objects were used (the *Rooms Task*; see Postma and Kessels, this book). This version of the paradigm was subsequently applied to investigate implicit and explicit memory for object locations specifically. This is clinically relevant as well in the light of possible interventions aimed at overcoming problems in spatial memory. That is, it has been suggested that intact implicit processing might interfere with the memory performance of people with explicit memory decline due to ageing or more severe neuropathologies such as dementia. Normally, explicit memory acts as a "supervisory monitor" which corrects possible errors that are made during learning. In the case of an explicit memory decline, it is thought that these errors are no longer corrected, but even might be implicitly stored. Hence, rather than correct responses, patients with explicit memory problems are more likely to produce erroneous responses which had been stored previously at an implicit level. To overcome this, it has been suggested that the prevention of errors during learning in people with explicit memory problems might enhance the

memory performance. This method of errorless learning has indeed yielded positive results in amnesia (see Kessels & De Haan 2003, for an overview).

However, no research has been performed to study whether errorless learning extends to the spatial domain. Also, recent papers suggest that the effects of errorless learning might not be related to the impairments in implicit memory. To examine this, the Rooms Task was performed by a large group of young ($N = 40$) and healthy older ($N = 40$) participants (Kessels, Te Boekhorst, & Postma 2005). In the learning phase, the participants had to learn the correct locations of objects in the rooms in either an errorless or a trial-and-error (i.e., errorful) manner. Half of the subjects performed the errorless condition, in which in each trial during the learning phase only the to be remembered location was shown in the room. The object had to be subsequently relocated to that position and its location had to be remembered. The other half of the participants performed the errorful learning condition, in which three locations were shown to which the object could be relocated, but only one was correct. Here, the participants had to guess the correct location until the correct location was found, which had to be remembered (see Figure 5 for an example of a stimulus display). In the test phase, the previously learned objects had to be related to their previously occupied positions. During the test phase, the process dissociation procedure was applied according to Caldwell and Masson (2001). The results clearly showed an overall worse memory performance in the older adults compared to the young group, in agreement with previous studies on age-related deterioration of episodic memory in general (Haaland, Price & Larue 2003) and allocentric spatial memory in particular (Desrocher & Smith 1998). In addition, the results of Caldwell and Masson (2001) were replicated. Young adults overall performed better than older adults in the Include condition and make less target responses in the Exclude condition. As expected, the contribution of explicit memory was smaller in older adults compared to the young group, and the estimate of implicit memory did not differ between the groups. This is in agreement with the notion that implicit memory function is relatively spared in ageing, while explicit memory function deteriorates.

With respect to the effects of the learning conditions, it was found that the young groups displayed a better overall performance in the errorless learning condition compared to the errorful learning condition in the include condition. Furthermore, the proportion of explicit memory processes in the young group is higher in the errorless learning than in the errorful learning condition. However, the older group did not benefit from the errorless learning method compared to errorful learning, and the proportion of explicit memory processes did not differ between the two learning conditions. Thus, this results counter previous findings in errorless learning of verbal memory, which has been found effective in amnesic patients. However, it is possible that the beneficial effects of errorless learning do not fully extend to the spatial domain. For example, it might be that explicit memory for spatial information has declined as a results of ageing to such an extent that learning without errors does not result in an improved performance anymore. However, the overall performance of the older group was above chance, thus excluding possible confounding results due to a floor



**Figure 5.** Example of a test stimulus in the Rooms Task; the participant had to relocate the object at the correct location (in Kessels, Feijen, & Postma 2005).

effect. Nevertheless, it could be that the amount of error introduced during learning was too small, since it was possible to guess the target location in the first attempt.

### Object-location memory in dementia

Of further interest is the question whether the object-location memory decline that is observed in healthy older people resembles the impairments in object-location memory in pathological ageing, i.e. dementia, albeit to a lesser extent, or whether quantitative differences exist in the object-location memory performance between normal ageing and dementia. Basically, dementia can be defined as a disorder which is characterized by a memory disorder in conjunction with a deficit in at least one other cognitive domain (e.g., executive function, language, attention) which has profound effects on everyday functioning (Knopman & Selnes 2003). Dementia as a syndrome can be the result of different underlying pathologies, such as Alzheimer's disease (AD), Huntington's disease or cerebrovascular diseases. In most cases, dementia is caused by a progressive neuropathological process. Since the memory dysfunction is one of

the most apparent symptoms of dementia, much research has focused on the early detection of memory impairment in relation to the differential diagnosis and in order to determine the disease's progression aimed at possible therapeutic intervention. Since spatial memory function is one of the crucial aspects of forming and remembering episodic information (e.g., to remember where events took place and where objects are stored in our environment), it is evident that assessment of spatial memory function is highly important in dementia. However, spatial memory is one of the less investigated memory processes in dementia. Only a few studies have been performed, demonstrating that AD patients are impaired on memory for spatial locations. For example, Adelstein, Kesner, and Strassberg (1992) studied memory for spatial location and temporal order in a group of Alzheimer patients in the mild-to-moderate stages of the disease. They presented subsequent trials consisting of a $4 \times 4$ grid with an X present in one of the cells. The participants had to remember the locations of these Xs, as well as the order in which the trials were presented. The results showed that memory for the last three presented trials was relatively preserved in the mild AD group, but that memory was poor for the trials at the beginning of the test. Furthermore, both spatial memory and order memory in the moderate group was severely impaired. Later, Bucks and Willison (1997) showed that the performance on the LLT was clearly impaired in AD already in the early stages of the disease. Others have demonstrated impaired memory for spatial patterns (Sahakian, Morris, Evenden, Heald, Levy, Philpot, & Robbins 1998) and spatial paired-associate learning (Swainson, Hodges, Galton, Semple, Michael, Dunn, Iddon, Robbins, & Sahakian 2004). Conversely, as is the case in many neuropsychological test procedures, the ecological validity of these assessment methods is limited. Only a few authors have investigated spatial memory functions that are related to everyday life, i.e. route learning, showing clear impairments as well (Cherrier, Mendez, & Perryman 2001). The difficulty in interpreting these results, however, lies in the fact that the observed route-learning problems could also be related to other cognitive deficits in these patients, such as spatial disorientation.

The abovementioned findings imply that specifically the assessment of object-location memory may be valuable for the differential diagnosis of dementia type and its early detection (Bucks & Willison 1997). Indeed, the performance on a test of spatial associative learning has been shown to be useful in discriminating AD patients and patients with depressive symptoms (Swainson et al. 2004), two groups which are often highly similar in clinical presentation. Furthermore, there is evidence that the performance on a spatial span task is poorer in AD compared to other different types of dementia, such as Lewy-body dementia, and might thus also be useful in discriminating between dementia types (Simard, Van Reekum, Myram, Panisset, Cohen, Freedman, Black, & Suvajac 2002). Since object-location memory is one of the forms of spatial memory that seems highly susceptible to cognitive deterioration, we set out to investigate object-location memory in patients suffering from dementia in more detail, The Rooms Task was used, since this task has the advantage of providing additional contextual support from which the (generally poor) memory performance of AD pa-

tients might benefit. Moreover, this task can be applied to estimate the differential contribution of both explicit and implicit mnemonic processes.

Eighteen AD patients participated in the study (Kessels, Feijen, & Postma 2005), the results of whom were compared to a no-dementia control group of approximately the same age. The overall results indicate that spatial memory is severely impaired in AD patients compared to controls. This is in agreement with previous findings showing impaired spatial memory in AD, which deteriorates further as the disease progresses. Most importantly, however, subdividing the memory performance into an explicit and an implicit memory component shows that explicit spatial memory is strongly suppressed in AD, whereas implicit memory seems unaffected. This is in line with neuropsychological studies in AD patients showing intact priming (Fleishman & Gabrieli 1997) and normal procedural memory (Braak & Braak 1991). Furthermore, intact implicit learning has also been demonstrated using event related potentials (ERP), showing positive ERPs after repeated presentation of verbal information, although this repetition-priming effect was less profound than in age-matched control participants (Friedman, Hamberger, Stern, & Marder 1992). Finally, we also demonstrated a significant correlation between the stage of the disease and the extent of the memory disorder as measured with the Mini-Mental State Examination and the explicit memory estimate, but not with the implicit memory estimate. This further supports the notion that especially explicit spatial memory deteriorates as the disease progresses, while implicit spatial memory remains intact.

## Neural processes related to (pathological) aging and spatial memory

While the foregoing clearly shows impairments in object-location memory in patients with dementia as well as in older healthy participants, the findings do not provide direct information about the underlying neural processes that are involved in object-location memory. However, previous neuropathological studies related to ageing and dementia show that there might be differential involvement of brain areas in dementia and ageing. Generally, there is clear evidence for both structural and functional changes in the prefrontal cortex related to cognitive ageing (for a review see Tisserand & Jolles 2003). To a lesser extent, mild hippocampal dysfunction has been demonstrated (Maguire & Frith 2003). In dementia, however, particularly the Alzheimer type, profound atrophy of the medial temporal lobe has been demonstrated, including the hippocampal formation (Van der Flier, Van den Heuvel, Waverling-Rijnsburger, Bollen, Westendorp, Van Buchem, Middelkoop 2002). In the later stages of the disease, other cortical areas deteriorate as well. Neuropsychologically, this is in agreement with the notion that in ageing, especially working memory and mental flexibility declines, resulting in suboptimal encoding of information. These are typical functions that are subserved by the prefrontal cortex. In turn, Alzheimer patients show "rapid forgetting", i.e. an inability to store information into long-term memory, a process which is commonly related to the hippocampal area.

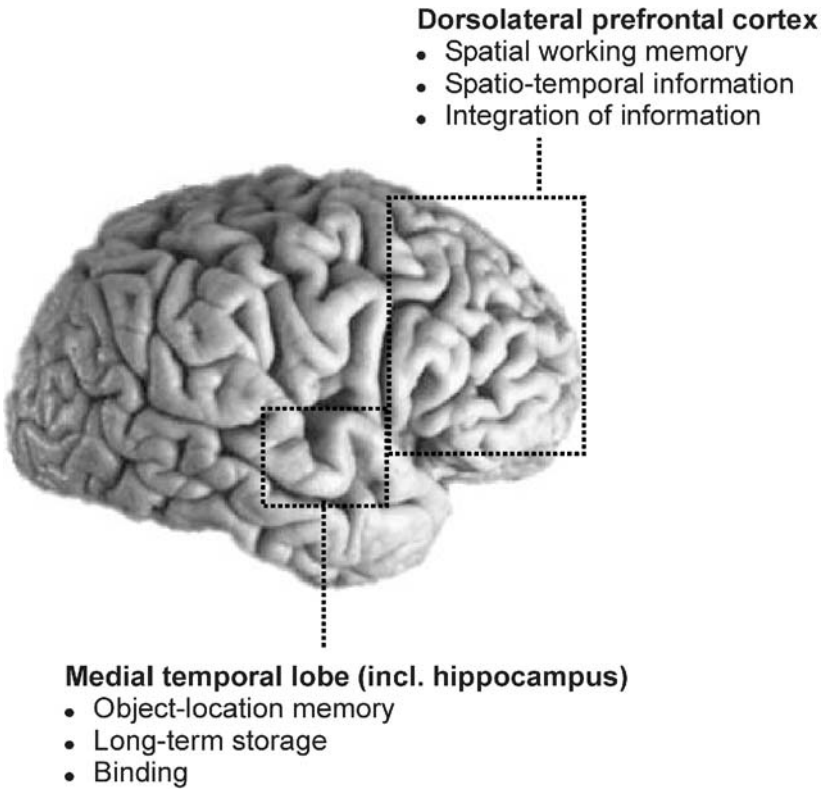



**Figure 6.** Schematic overview of the brain areas that are involved in different aspects of memory for object locations.

With respect to spatial memory function, a clear dissociation exists as well. More specifically, the dorsolateral part of the prefrontal cortex is involved in the online manipulation and short-term storage of spatial information and is implicated in the integration of spatial location and temporal order (Kessels et al. 2000). The medial temporal lobe including the hippocampal formation is involved in the binding of objects to locations and the long-term storage (Kessels, Hendriks, Schouten, Van Asselen, & Postma 2004). Furthermore, the role of the hippocampus in spatial memory has been extensively studied in rodents as well, resulting in the theory that the hippocampus probably serves as an allocentric "cognitive map" which enables us to store locations of objects in our environment, independent from our own position in space (O'Keefe & Nadel 1978). Smith and Milner (1981) were among the first to describe disordered memory for the location of common objects in human patients with focal lesions in the hippocampal area. While selective lesions in the hippocampus can be the result of surgery for the treatment of epilepsy (Kessels, De Haan, Kappelle, & Postma 2004), hippocampal atrophy has also been demonstrated in neurodegenerative disorders, such as Alzheimer's dementia (Van der Flier, et al. 2004). Furthermore, there

is evidence for both structural and functional changes in the hippocampus that are related to non-pathological age-related memory decline (Grady, McIntosh, & Craik 2003; Maguire & Frith 2003). Figure 6 displays a schematic overview of the neural processes involved in memory for object locations. With respect to spatial memory function, this distinction has not been studied extensively yet in relation to ageing and dementia.

## Conclusion

In all, neuropsychological data indicate that memory for object locations deteriorates as a result of ageing. Also, memory for temporal order deteriorates in older participants, while target memory is relatively preserved. This is in agreement with Mayes' (1988) context-deficit hypothesis, which suggests that the inability to encode the contextual features of episodic information might underlie organic amnesia or age-related memory problems. The previous results also show that memory for multiple items that have to be remembered in conjunction may decline to a greater extent than memory for single items. This counters the binding-deficit hypothesis which states that it is not context per se which is poorly encoded in people with memory dysfunction, but that the memory problems are the result of an inability to bind together multiple features of the to be remembered information. With respect to the neural basis, contextual encoding is probably subserved by prefrontal brain areas, which have been demonstrated to functionally decline as a result of normal ageing. In patients with severe memory problems due to dementia of the Alzheimer type, it was found that explicit object-location memory deteriorated as the disease progresses, but that implicit recall of spatial information remains relatively spared. Supposedly, the object-location memory deficits in dementia might be the result of the profound atrophy in the medial temporal lobe and the hippocampus, a brain region which is crucial for the binding of objects to locations and the storage of (spatial) information into long-term memory, possibly in the form of a "cognitive map".

## References

Adelstein, T. B., Kesner, K. P., & Strassberg, D. S. (1992). Spatial recognition and spatial order memory in patients with dementia of the Alzheimer's type. *Neuropsychologia*, *30*, 59–67.

Allen, P. A., Sliwinski, M., Bowie, T., & Madden, D. J. (2002). Differential age effects in semantic and episodic memory. *Journal of Gerontology, 57B*, P173–86.

Benedict, R. H., & Groninger, L. (1995). Preliminary standardization of a new visuospatial memory test with six alternative forms. *Clinical Neuropsychologist, 9*, 11–16.

Benedict, R. H., Schretlen, D., Groninger, L., Dobraski, M., & Shpritz, B. (1996). Revision of the Brief Visuospatial Memory Test: Studies of normal performance, reliability, and validity. *Psychological Assessment, 8*, 145–153.

Berthoz, A. (1997). Parietal and hippocampal contribution to topokinetic and topographic memory. *Philosophical Transactions of the Royal Society of London, 352B*, 1437–1448.

Braak H., & Braak E. (1991). Neuropathological stageing of Alzheimer-related changes. *Acta Neuropathologica, 82*, 239–259.

Bucks, R. S., & Willison, J. R. (1997). Development and validation of the Location Learning Test (LLT): A test of visuo-spatial learning designed for use with older adults and dementia. *Clinical Neuropsychologist, 11*, 273–286.

Bucks, R. S., Willison, J. R. & Byrne, L. M. T. (2000). *Location Learning Test: Manual*. Bury St. Edmunds, UK: Thames Valley Test Company.

Caldwell, J. I. & Masson, M. E. J. (2001). Conscious and unconscious influences of memory for object location. *Memory and Cognition, 29*, 285–295.

Chalfonte, B. L., & Johnson, M. K. (1996). Feature memory and binding in young and older adults. *Memory & Cognition, 24*, 403–416.

Chalfonte, B. L., Verfaellie, M., Johnson, M. K., & Reiss, L. (1996). Spatial location memory in amnesia: Binding item and location information under incidental and intentional encoding conditions. *Memory, 4*, 591–614.

Cherrier, M. M., Mendez, M., Perryman, K. (2001). Route learning performance in Alzheimer disease patients. *Neuropsychiatry, Neuropsychology, and Behavioral Neurology, 14*, 159–168.

Cherry, K. E., Park, D. C., & Donaldson, H. (1993). Adult age differences in spatial memory: Effects of structural context and practice. *Experimental Aging Research, 19*, 333–350.

Cooney, R., & Arbuckle, T. (1997). Age, context, and spatial memory: A neuropsychological approach. *Aging, Neuropsychology, and Cognition, 4*, 249–265.

Denney, N. W., Dew, J. R., & Kihlstrom, J. F. (1992). An adult developmental study of the encoding of spatial location. *Experimental Aging Research, 18*, 25–32.

Desrocher, M., & Smith, M. L. (1998). Relative preservation of egocentric but not allocentric spatial memory in aging. *Brain and Cognition, 37*, 91–93.

Ellis, N. R., Katz, E., & Williams, J. E. (1987). Developmental aspects of memory for spatial location. *Journal of Experimental Child Psychology, 44*, 401–412.

Fleishman, D. A., & Gabrieli, J. D. E. (1997). Repetition priming in normal aging and Alzheimer's disease: A review of findings and theories. *Psychology and Aging, 13*, 88–119.

Friedman, D., Hamberger, M., Stern, Y., & Marder, K. (1992). Event-related potentials (ERPs) during repetition priming in Alzheimer's patients and young and older controls. *Journal of Clinical and Experimental Neuropsychology, 14*, 448–462.

Grady, C. L., McIntosh, A. R., & Craik, F. I. (2003). Age-related differences in the functional connectivity of the hippocampus during memory encoding. *Hippocampus, 13*, 572–586.

Grober, E. (1984). Non-linguistic memory in aphasia. *Cortex, 20*, 67–73.

Haaland, K. Y., Price, L., & Larue, A. (2003). What does the WMS-III tell us about memory changes with normal aging? *Journal of the International Neuropsychological Society, 9*, 89–96.

Hasher, L., & Zacks, R. T. (1979). Automatic and Effortful Processes in Memory. *Journal of Experimental Psychology: General, 108*, 356–388.

Jacoby, L. L., Toth, J. P., & Yonelinas, A. P. (1993). Separating conscious and unconscious influences of memory: Measuring recollection. *Journal of Experimental Psychology: General, 122*, 139–154.

Kessels, R. P. C., & De Haan, E. H. F. (2003). Implicit learning in memory rehabilitation: A meta-analysis on errorless learning and vanishing cues methods. *Journal of Clinical and Experimental Neuropsychology, 25*, 805–814.

Kessels, R. P. C., De Haan, E. H. F., Kappelle, L. J., & Postma, A. (2001). Varieties of human spatial memory: A meta-analysis on the effects of hippocampal lesions. *Brain Research Reviews, 35*, 295–303.

Kessels, R. P. C., Feijen, J., & Postma, A. (2005). Implicit and explicit memory for spatial information in Alzheimer's dementia. *Dementia and Geriatric Cognitive Disorders, 20*, 184–191.

Kessels, R. P. C., Hendriks, M. P. H., Schouten, J., Van Asselen, M., & Postma, A. (2004). Spatial memory deficits in patients after unilateral amygdalohippocampectomy. *Journal of the International Neuropsychological Society, 10*, 907–912.

Kessels, R. P. C., Hobbel., D., & Postma, A. (submitted). Aging, context memory and binding: A comparison of "what, where and when" in young and older adults.

Kessels, R. P. C., Nys, G. M. S., Brands, A. M. A., & Van Zandvoort, M. J. E. (2004). De Location Learning Test als maat voor ruimtelijk geheugen: Bruikbaarheid van een nieuwe afnameprocedure en normgegevens [The Location Learning Test as a measure of spatial memory: Applicability of a modified administration procedure and normative data]. *Tijdschrift voor Gerontologie en Geriatrie, 35*, 147–152.

Kessels, R. P. C., Postma, A., & De Haan, E. H. F. (1999). Object Relocation: A program for setting up, running, and analyzing experiments on memory for object locations. *Behavior Research Methods, Instruments, and Computers, 31*, 423–428.

Kessels, R. P. C., Postma, A., Wijnalda, E. M., & De Haan, E. H. F. (2000). Frontal-lobe involvement in spatial memory: Evidence from PET, fMRI, and lesion studies. *Neuropsychology Review, 10*, 101–113.

Kessels, R. P. C., Te Boekhorst, S., & Postma, A. (2005). The contribution of implicit and explicit memory to the effects of errorless learning: A comparison between young and older adults. *Journal of the International Neuropsychological Society, 11*, 144–151.

Knopman, D., & Selnes, O. (2003). Neuropsychology of dementia. In K. M. Heilman & E. Valenstein (Eds.), *Clinical neuropsychology* (4th ed., pp. 574–616). Oxford: Oxford University Press.

Lemay, M., & Proteau, L. (2003). Aging affects pointing to unseen targets encoded in an allocentric frame of reference. *Experimental Aging Research, 29*, 319–333.

Light, L. L., & Singh, A. (1987). Implicit and explicit memory in young and older adults. *Journal of Experimental Psychology: Learning, Memory and Cognition, 4*, 531–41.

Maguire, E. A., & Frith, C. D. (2003). Aging affects the engagement of the hippocampus during autobiographical memory retrieval. *Brain, 126*, 1511–1523.

Mayes, A. R. (1988). *Human organic memory disorders*. Cambridge: Cambridge University Press.

Milner, B., Johnsrude, I., & Crane, J. (1997). Right medial temporal-lobe contribution to object-location memory. *Philosophical Transactions of the Royal Society of London, 352B*, 1469–1474.

Mitchell, K. J., Johnson, M. K., Raye, C. L., & D'Esposito, M. (2000b). fMRI evidence of age-realted hippocampal dysfunction in feature binding in working memory. *Cognitive Brain Research, 10*, 197–206.

Mitchell, K. J., Johnson, M. K., Raye, C. L., Mather, M., & D'Esposito, M. D. (2000a). Aging and reflective processes of working memory: Binding and test load deficits. *Psychology and Aging, 15*, 527–541.

Nilsson, L. G. (2003). Memory function in normal aging. *Acta Neurologica Scandinavica, 179* (Suppl.), 7–13.

O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford, UK: Oxford University Press.

Piolino, P., Desgranges, B., Benali, K., & Eustache, F. (2002). Episodic and semantic remote autobiographical memory in ageing. *Memory, 10*, 239–57.

Sahakian, B. J., Morris, R. G., Evenden, J. L., Heald, A., Levy, R., Philpot, M., & Robbins, T. W. (1988). A comparative study of visuospatial memory and learning in Alzheimer-type dementia and Parkinson's disease. *Brain, 111,* 695–718.

Sanchez, M., Grober, E., & Birkett, D. P. (1997). Dementia in left brain damage. *Clinical Gerontologist, 17* (4), 13–22.

Simard, M., Van Reekum, R., Myram, D., Panisset, M., Cohen, T., Freedman, M., Black, S., & Suvajac, B. (2002). Differential memory impairment in dementia with Lewy bodies and Alzheimer's disease. *Brain and Cognition, 49*, 244–249.

Smith, M. L., & Milner, B. (1981). The role of the right hippocampus in the recall of spatial location. *Neuropsychologia, 19*, 781–793.

Swainson, R., Hodges, J. R., Galton, C. J., Semple, J., Michael, A., Dunn, B. D., Iddon, J. L., Robbins, T. W., & Sahakian, B. J. (2004). Early detection and differential diagnosis of Alzheimer's disease and depression with neuropsychological tasks. *Dementia and Geriatric Cognitive Disorders, 12*, 265–280.

Tisserand, D. J., & Jolles, J. (2003). On the involvement of prefrontal networks in cognitive ageing. *Cortex, 39*, 1107–1128.

Vakil, E., Weise, M., & Enbar, S. (1997). Direct and indirect memory measures of temporal order: Younger versus older adults. *International Journal of Aging and Human Development, 45*, 195–206.

Van Asselen, M. (2005). *Neurocognition of spatial memory: Studies in patients with acquired brain damage and healthy participants*. Doctoral dissertation, Utrecht University, The Netherlands.

Van der Flier, W. M., Van den Heuvel, D. M. J., Weverling-Rijnsburger, A. W. E., Bollen, E. L. E. M., Westendorp, R. G. J., Van Buchem, M. A., & Middelkoop, H. A. M. (2002). Magnetization transfer imaging in normal aging, mild cognitive impairment, and Alzheimer's disease. *Annals of Neurology, 52*, 62–67.

CHAPTER 3.4

# Visuospatial and constructional impairments in mental deterioration

Dario Grossi, Massimiliano Conson, and Luigi Trojano

## Introduction

Visuospatial abilities can be intended as those high-order, non-verbal cognitive abilities which operate upon perceptual stimuli and mental images and allow individuals to interact with the environment. Although this definition is *prima facie* acceptable, it remains quite vague: it does not clarify what are elementary visuospatial processes and is not capable to identify what are "pure" visuospatial defects. From an operational point of view, De Renzi (1982) suggested using the term spatial perception in reference to elementary processing stages, while the term spatial cognition could designate more complex mental abilities requiring the use of mental ("internal") representations. Examples of spatial perception processes are those that allow location of points in space, and appreciation of dimensions, orientation or distance of an object, while examples of spatial cognition abilities are recognition of shapes, maze learning or mental rotation (De Renzi 1982).

## Visuospatial and visuoconstructional disorders

In clinical practice, only some aspects of visuospatial processing are usually assessed, often limited to the bidimensional space defined by a sheet of paper or a computer screen; however, even simple visuospatial tasks may require complex mental processes and be affected by age and educational level. The most used test to assess visuospatial abilities is the judgement of line orientation test (JLOT), in which subjects are required to identify, among several alternatives, the lines that have the same angulation as those presented as stimuli (Benton et al. 1975). Other visuospatial tasks are enclosed in the Visual Object and Space Perception Battery (VOSP; Warrington & James 1991): a dot counting task, to assess visual exploration abilities; tasks assessing position discrimination (to judge whether a dot in a square occupies the same position as in the target square, and to identify the location occupied by a digit in a square); and a task

assessing complex visuospatial skills (to count the number of cubes embedded in complex three-dimensional figures). These, and other similar tasks, have been included in a computerised assessment procedure of visuospatial performances (Kerkhoff & Marquardt 1998). A set of eight visuospatial tasks, adapted from several experimental paradigms, is enclosed in the Battery for Visuospatial Abilities (BVA, known in Italy as TERADIC; Angelini & Grossi 1993; Trojano et al. 2004), which taps both simple "perceptual" and complex "representational" visuospatial abilities. The four "perceptual" tasks enclosed in the battery are: line length and line orientation judgements, angle width judgement, point position discrimination; the four "representational" tasks are: mental rotation task, recognition of non-sense shapes, identification of geometric patterns embedded in complex figures, mental construction. All these tasks, but one, have the format of four-choice recognition, and subjects have to point the only item identical to the stimulus, without time constraints. The mental construction task has a different arrangement in that the display shows four subcomponents of the stimulus; subjects are required to identify with which side the four components are contiguous in the stimulus.

It is often maintained that the right hemisphere is specialised in visuospatial processing, but findings on traditional tasks in brain-lesioned patients are not so clear-cut as it might be expected. Systematic studies on focal brain damaged patients have demonstrated comparable defects on line orientation tasks (Treccani et al. 2005), or on position discrimination tasks (Postma et al. 2000) in right brain-damaged patients (RBD) and left brain-damaged patients (LBD), when subjects with visual exploration defects (unilateral spatial neglect) are not considered for the analysis. Analogous findings have been reported using a wider visuospatial assessment battery (BVA) (Trojano et al. 2004).

It appears, therefore, that elementary visuospatial processes are not strongly lateralised, although the right hemisphere could play a more prominent role depending on specific task requirements. Consistent with this consideration are findings from several functional neuroimaging studies. For instance, Ng et al. (2000) demonstrated a strong bilateral activation of the superior parietal lobes during a modified version of the JLOT, but the right parietal cortex appeared to be activated earlier than the left. Such findings confirm that visuospatial processes mainly rely on activation of the "dorsal", occipito-parietal visual pathway, while the "ventral" occipito-temporal pathway would mainly involved in visual object recognition (Ungerleider & Mishkin 1982). Moreover, Ng et al.'s data (2000) suggest a relative right specialisation for some aspects of visuospatial tasks.

Analogous considerations about the lack of strong hemispheric lateralisation may be applied to "constructional apraxia" (CA), identified as the specific inability to construct a complex object, arranging its component elements in their correct spatial relationships (Kleist 1934). According to Kleist's original definition CA derived from "an alteration in the connections between visual functions, that is visuospatial, and the kinetic engrams that control manual activity", thus distinguishing it from motor planning disorders (e.g., ideomotor apraxia) and elementary visuoperceptual deficits

(Kleist 1934). However, in subsequent years, because of divergent opinions about the nature of CA (see Gainotti 1985, for a full review of the literature), it gradually became customary to use the term to refer to any anomaly observed during the performance of a constructional task, i.e. in drawing, assembling and building complex models (Gainotti 1985).

In clinical practice, constructional abilities may be assessed by asking the patient to assemble a two-dimensional model by arranging component elements (e.g., sticks) in given spatial relationships (Benson & Barton 1970). The block design subtest of the WAIS (Wechsler 1981) – where the person has to reconstruct a two-dimensional pattern using multicoloured cube faces – is used for the same purpose, yet it is perhaps the clearest example of how a so-called constructional test taps different cognitive mechanisms, i.e. attentional, perceptual, planning, motor and visuospatial. Other tests investigate three-dimensional constructional abilities, beginning with simple shapes (Benton & Fogel 1962; Trojano et al. 1997). Drawing tasks are those most widely used to assess constructional abilities, but copying and free drawing (traditional constructional tasks) cannot be considered equivalent. Free drawing – in which the patient is asked to draw a named object (e.g., a clock, a face and so on) – reveals information about the patient's ability to draw complete shapes or a tendency to omit parts and his ability to organise the figure as a whole, with its component elements in their correct spatial relationships. However, free drawing relies also on non-constructional cognitive abilities (e.g., lexical-semantic mechanisms and imagery abilities; see Trojano & Grossi 1994), while copying tasks directly assess the patient's ability to reproduce a figure. Both simple shapes, e.g., circles and squares, and complex designs, e.g., the Rey-Osterreith Complex Figure (ROCF; Osterreith 1944), can be used for assessing copying abilities, but for diagnosis of CA it is crucial to adopt a standardised task, since performance on copying tasks is affected by age, educational level and even cultural background (see Rosselli & Ardila 2003 for a review).

Several early clinical studies on brain-damaged patients suggested a right hemisphere dominance for constructional abilities (see Gainotti 1985), but more recent studies demonstrated a similar prevalence of CA following focal lesions to the left or the right hemisphere (Villa et al. 1986; Kirk & Kertesz 1989; Carlesimo et al. 1993; Trojano et al. 2004), after controlling groups for severity of the lesion and neglect errors. With regards to the intrahemispheric locus of CA, it is generally accepted that CA is more frequently associated with parieto-occipital lesions (De Renzi 1982), although it can also be observed in patients with frontal lesions. Severity of constructional disturbances does not seem to differ in patients with anterior or posterior lesions (Black & Bernard 1984). Subcortical structures do contribute to the drawing process and it is possible to observe selective constructional defects after a single right subcortical lesion (Grossi et al. 1996). No distinctive features seem to characterise constructional disorders of subcortical origin (Kirk & Kertesz 1993).

It has been suggested that CA is subtended by different cognitive mechanisms in RBD and LBD: in RBD visuospatial defective mechanisms would predominate, whilst in LBD an ideational form of CA would be present (Duensing 1953). Several exper-

iments have tried to identify skills that correlate with constructional performance in one patient group but not in the other. The relationship between constructional disturbances and visuospatial disorders in RBD patients seems to be hardly demonstrated when one single test of visuospatial processing is used (Carlesimo et al. 1993), but can become evident when multiple visuospatial aspects are explored (Trojano et al. 2004). Cognitive mechanisms of CA in LBD remain to be clarified, but some studies suggest that a disorder at the elementary motor level could play a role (Kirk & Kertesz 1989; Carlesimo et al. 1993).

## Constructional disturbances in dementia

Some clinical and experimental studies attributed a causal role in the genesis of CA to general intellectual deterioration in patients with focal brain damage, because apraxic patients often show intellectual abilities which are inferior to those of non-apraxic patients (Arrigoni & De Renzi 1964). Adding weight to the argument, other studies have noted that constructional disorders represent an index for diffuse cognitive deterioration, both in left (Borod et al. 1982) and right (Benowitz et al. 1990) brain-damaged patients.

On the other hand, CA is considered one of the most common behavioural alterations in different forms of dementia. In the course of Alzheimer's disease (AD), CA has been described since early stages of the disease, with increasing severity as the illness progresses (Ajuraguerra et al. 1960). An attempt at a systematic description of AD patients' errors in a drawing to command task (Kirk & Kertesz 1991) has shown the frequent occurrence of simplifications, spatial alterations and lack of perspective; together, these characteristics would not constitute the type of drawing errors typically produced by left or right hemisphere patients. Patients' scores did not correlate with performance on language or memory tests, suggesting that constructional disabilities develop relatively independently during the course of the illness; in fact, individual patients may not show constructional disabilities even in the advanced stages of AD (Denes & Semenza 1982). However, free drawing poses a heavy load on semantic memory, and errors on this task (e.g., simplifications in drawing a house) may derive from impaired access to semantic knowledge or to impaired visuoperceptual processing (Grossman et al. 1996). For this reason, spontaneous drawing may show more impaired performance with respect to copying in the early stages of AD, while copying may deteriorate later (Figure 1; Rouleau et al. 1996). The reproduction of complex figures is particularly sensitive to the progression of the disease (Binetti et al. 1998). For instance, the ROCF may be reproduced in a simplified way, with single constitutive elements put one after the other, even in early AD (Figure 2). In these cases patients seem to be able to recognise and reproduce single well-known elements (as if they resorted to motor subroutines stored in a specialised long-term memory store – a sort of constructional lexicon) but are unable to reproduce complex spatial relationships correctly. Another "simplification" error may consist in the reproduction of more familiar

or simpler figures instead of more complex ones (e.g. a square instead of a diamond). As the disease progresses, patients usually become unable even to draw simple figures correctly, as they no longer had access to well-consolidated motor subroutines.

CA and visuospatial disorders are typically found in other degenerative dementias too. In particular, visuospatial difficulties are often early and prominent in dementia with diffuse Lewy bodies (DLB; Mc Keith et al. 1996); several studies have aimed to characterise these defects in order to implement more stringent differential diagnostic criteria. Visuospatial tasks, such as object size discrimination, form discrimination, overlapping figure identification, and visual counting tasks may reveal more impaired performances in DLB than in AD, and these defects likely contribute to the disproportionate impairment in constructional tasks in DLB patients (Mori et al. 2000). In line with these observations, it has been suggested that DLB patients may show parallel impairments in free drawing and in figure copying since early stages of the disease (Gnanalingham et al. 1996; Ala et al. 2001), at variance with AD patients, who would show relative sparing of figure copying (but see Swanwick et al. 1996; Della Sala et al. 2002). In the most recent paper on this issue, Cormack et al. (2004) have confirmed that DLB patients show significantly lower performance in copying geometrical figures with respect to AD; moreover, while in AD the impairment in copying figures was correlated with general cognitive deterioration, in DLB patients drawing was correlated only with visuospatial tasks, thus suggesting the existence of a specific defect in this disease.

A prominent visuospatial and constructional impairment is frequently observed also in less common degenerative dementias, such as cortico-basal degeneration (Graham & Bak 2003) and supranuclear progressive palsy (Aarsland et al. 2003), but definition of clinical features and of differential diagnostic value of CA in these disorders have not yet been studied in enough detail.

The relative preservation of visuospatial and constructional abilities, instead, is suggested to be among critical features capable to distinguish fronto-temporal dementia (FTD) from other degenerative dementias and, notably, from AD (Neary et al. 1998). These observations have been confirmed in recent clinical studies in which either patients with prominent behavioural disorders and frontal involvement (frontal variant of FTD; Perri et al. 2005), or patients with prominent language deficits (non-fluent progressive aphasia; Gorno-Tempini et al. 2004) have been examined by means of ROCF immediate reproduction. However, a specific study that compared frontal variant FTD and AD patients on a visuospatial battery (BVA), and on copying ROCF and simple geometrical drawings, failed to find significant differences between the two groups (Grossi et al. 2002). In particular, the groups did not differ on any visuospatial test and showed comparable constructional performances both on quantitative and qualitative evaluation. Since the study enrolled mild to moderate FTD and AD patients, Grossi et al. (2002) suggested that the relative preservation of visuospatial abilities in FTD may be found only in early stages of the disease. This hypothesis has found support in a recent meta-analysis suggesting that constructional abilities assessed on

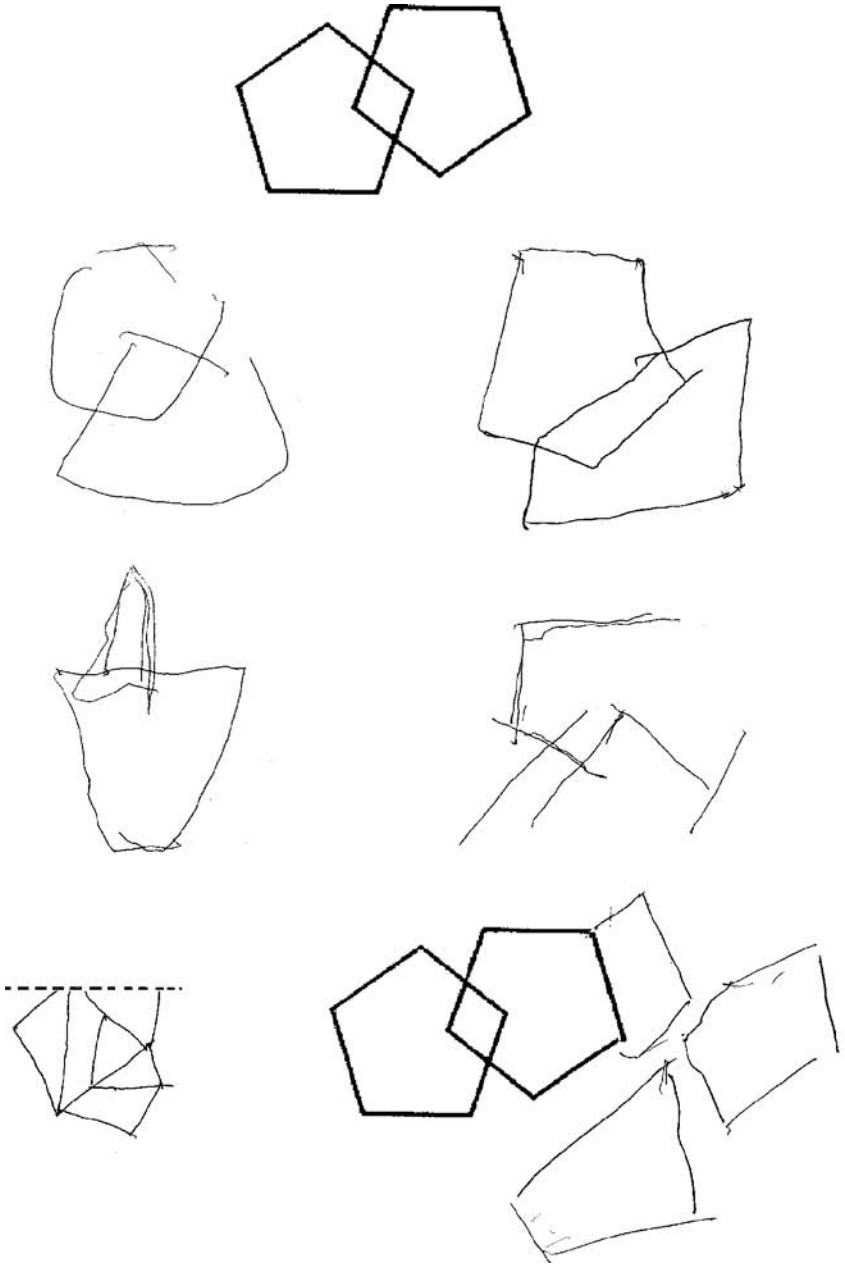


**Figure 1.** Copying of geometrical drawings: novel figure (model on the top). In the first row drawings by patients with mild to moderate AD, with relative sparing of copying accuracy. In the middle row drawings by patients with severe dementia, showing simplifications or gross spatial disorganisation. In the last row examples of closing-in: on the left, spatial disorganisation and tendency to overlap the figure to the edge of the sheet (represented by the dashed line), on the right closing-in and perseveration.

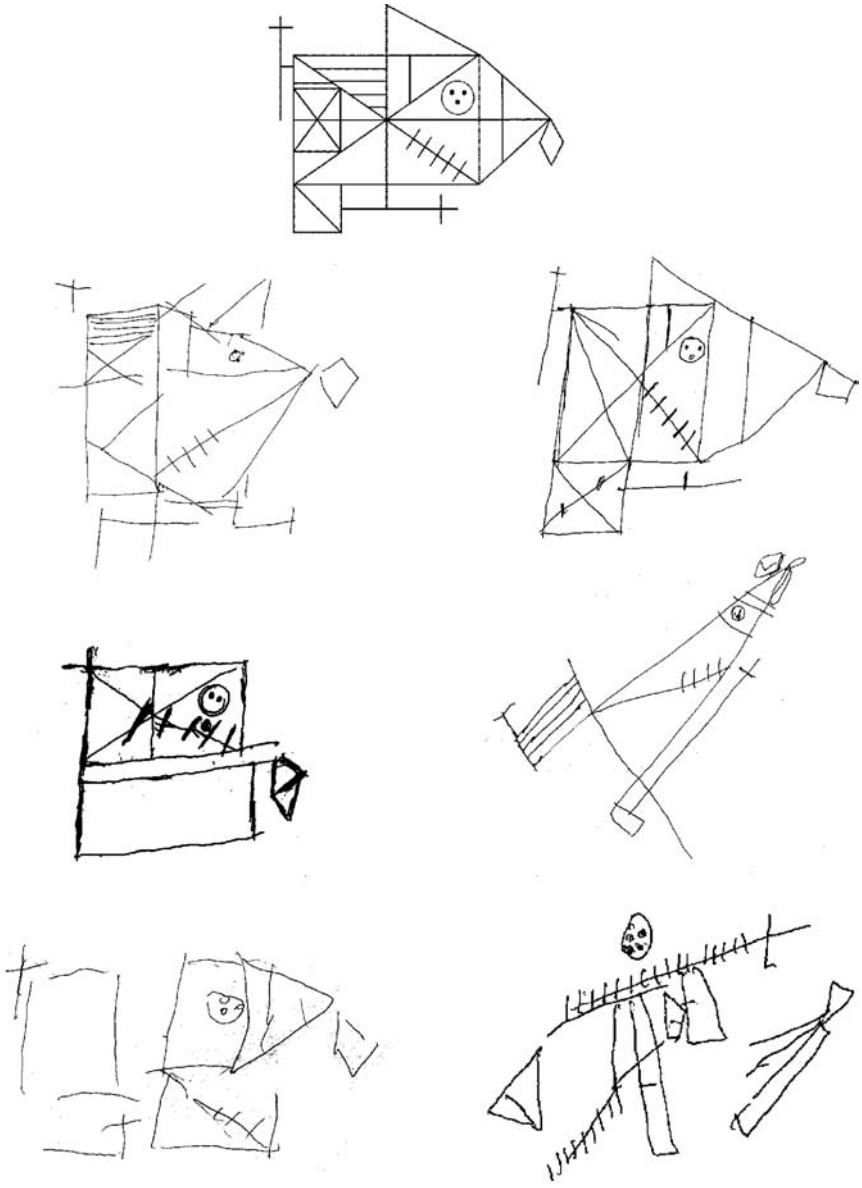


**Figure 2.** Copying of Rey figure (model on the top). In the first row drawings by patients with mild to moderate AD. In the middle row drawings by patients with severe dementia, showing simplifications or gross spatial disorganisation. In the last row, the reproduction of the single subcomponents of the figure is relatively spared, but spatial relationships among them are lost.

copying the ROCF quickly deteriorate as FTD progresses (Elderkin-Thompson et al. 2004).

Two peculiar constructional phenomena, perseverations and closing-in, deserve some brief comments, because of their frequency in demented patients. The observation of these drawing features may help to differentiate patients with AD from patients with non-AD degenerative pathologies or vascular dementia.

The former phenomenon, perseverations, can be considered among "productive" (or "positive") pathological signs, since they consist in iterative behavioural responses, not adequate to the current stimulus (Vallar 1998, 2001). Perseverations in drawing are of frequent observation in clinical practice (see Figures 1 and 2): for instance, patients may produce the same figure repeatedly, in response to only one stimulus, or replicate stimuli's elements (continuous perseveration, according to Sandson & Albert 1987); on other occasions, patients may inappropriately draw figures already drawn in previous trials, instead of reproducing the current stimulus (recurrent perseveration; Sandson & Albert 1987). Convergent findings from studies on perseverations on clock drawing task suggest that perseveration may be observed in a small proportion of AD patients, but would increase in moderate to severe stages of the disease (Cosentino et al. 2004; Rouleau et al. 1992, 1996).

These data would be consistent with a study reporting that perseverations are rare in typical AD patients on a cancellation task (Rusconi et al. 2002). At variance with AD patients, FTD patients would frequently show perseveration errors since early stages (Snowden et al. 1996; but see Grossi et al. 2002), while specific disturbances in reproducing spatial relationships would become evident later during the course of the disease. Perseverations, together with profound disorganisation of the copying procedures and frequent omissions, would characterise graphic productions by patients with Parkinson disease and subcortical vascular dementia (Freeman et al. 2000). These features, and particularly perseverations and omissions, would help in disentangling subcortical dementias from AD.

The latter constructional phenomenon is the tendency either to trace the pencil over the lines of the model, producing a scrawl, or to overlap the copy with the model or to draw starting from one or more model's elements (see Figures 1 and 2). Such a behaviour, termed "closing-in", has often been reported in demented patients (Mayer-Gross 1935; Ajuraguerra et al. 1960; Gainotti 1972), particularly in late stages of AD (Ober et al. 1991; Rouleau et al. 1996). The presence of closing-in seems consistent with a diagnosis of "primary degenerative dementia" (Gainotti et al. 1992), and could enhance sensitivity and specificity of diagnosis of AD versus subcortical vascular dementia (Kwak 2004). Closing-in has been described in patients with posterior cortical atrophy (Suzuki et al. 2003), but is rarely observed in patients with focal lesions (Gainotti 1972; Grossi et al. 1996).

Some authors consider this phenomenon as a primitive reflex in patients with diffuse cognitive deterioration (Gainotti 1972); patients might be strongly attracted by the model and be unable to detach from it. In some cases, however, a simple verbal instruction may suffice to avoid this constructional error. Other authors suggest

that closing-in occurs when patients who are unable to structure an empty space look for a reference point to solve difficult constructional dilemmas (De Renzi 1959). In these cases patients might be unable to generate a bidimensional frame in the copying paper (i.e., they cannot identify a "drawing space"), and try to use already existing frames, for example the border of the model or, in other cases, the edge of the paper ("margination" of the copy, seen also in children). However, the observation that the prevalence of closing-in may increase in copying complex rather than simple figures challenges an interpretation based on a pure visuospatial defect (Lee et al. 2004). Indeed, figure complexity increases demands on executive processes and, in case of a specific frontal impairment, the patient would be unable to inhibit attention and action towards salient stimuli. This hypothesis would tie in with observation on spatial transpositions generated by attentional mechanisms (Lepore et al. 2005), but further research is needed to understand cognitive and neural basis of closing-in (Kwak 2004).

## Mechanisms of constructional disturbances in dementia

As reported above, several dementing syndromes affect constructional performances. In some patients the impairment in constructional performance seems to be strictly related to a defect in visuospatial processes. One example of a "pure" visuospatial disorder has been reported in a patient with a bilateral parietal degenerative lesion (Stark et al. 1996). The patient failed at all spatial subtests of the VOSP, and in copying figures, but did not show disorders of low level visual perception, space exploration or spatially-guided reaching. The authors suggested that the visuospatial defect in their patient disrupted the elaboration of a three-dimensional supra-modal spatial representation in an egocentric coordinate system (Stark et al. 1996). Within this context, representation related to different spatial axis may dissociate. Actually, in another patient with primary degenerative dementia the ability to code spatial relationships along the horizontal axis was selectively impaired, with the appreciation of vertical and radial dimensions being spared (e.g., the patient was able to discriminate and copy vertical but not horizontal segments correctly), independently from visual exploration or eye movement disorders (Grossi et al. 1998).

However, conditions in which a specific visuospatial defect may be held responsible of a certain clinical picture have been rarely reported. Studies on groups of subjects have suggested that CA may stem from different cognitive mechanisms in AD patients. Binetti et al. (1998) found that whereas object perception was impaired since the early stages of the disease, a specific spatial impairment became evident only later, at a moderate level of severity. Moreover, the authors found a strict relation between the progression of visuoperceptual spatial impairment, measured on the spatial tasks of the VOSP, and the progressive deterioration of the performance on copying the ROCF. Rizzo et al. (2000) reported that mild AD usually spares basic visual sensory processes and affects all high-order visual processes, both occipito-temporal (ventral) and occipito-parietal (dorsal). A specific investigation of ventral and dorsal visual func-

tions has been conducted by Caine and Hodges (2001) in two separated studies. In the former, the authors assessed AD patients on JLOT, on object-based visuoperceptual tests and on semantic tests (picture naming). The authors found a great heterogeneity in the profile of patients' performance at the early stages of the disease, with only a few patients showing visuospatial deficits. In the latter study, Caine and Hodges (2001) further explored visuospatial processing by administrating AD patients with the entire VOSP battery. Again, only a small proportion of patients were impaired on visuospatial tasks. Taken together, Caine and Hodges' findings (2001) would demonstrate that in very early stages of AD a small group of patients may be identified with prominent visuospatial disorders; these patients could be regarded as forming a continuous spectrum at the other end of which are patients affected by a focal degenerative dementia involving occipito-parietal cortex, the so-called posterior cortical atrophy (Benson et al. 1988; Ross et al. 1996; Hof et al. 1997). In the moderate stage of AD, visuospatial impairment would become more evident, and play a relevant role in the development of constructional disorders (Binetti et al. 1998). More recently, Guerin et al. (2002) examined the cognitive mechanisms underlying the constructional performance of AD patients at different stages of the disease by means of a copying task and of visuospatial tasks measuring spatial exploration (visual search tasks), judgement of spatial relations and planning abilities. The results suggested that cognitive defects underlying constructional impairment in patients with AD involved the early phases of spatial-constructional processing, likely exploration and judgement of spatial relationships, rather than the late stage of planning.

A defect of planning processes could play a prominent role in the genesis of constructional apraxia in patients with Parkinson disease. Ogden et al. (1990) showed that, compared with controls, patients with Parkinson disease were impaired in copying the ROCF and on tasks that require sequencing but not in visuospatial tasks. These data support the view that in these patients constructional apraxia is strictly linked to frontal-subcortical defects.

A comparison among demented patients with different cortical and subcortical involvement has been made on a traditional constructional task, i.e. the clock drawing test (CDT). The CDT typically comprises two conditions: in the former, command condition, the patient is required to draw a clock face with all numbers, and then to set hands to a specified time (Figure 3); in the latter condition, the patient had to copy a model of a clock face (for a detailed analysis of the CDT, see Freedman et al. 1994). Different patterns of performance have been reported on the two conditions, and divergent interpretative approaches have been suggested. Some authors have observed similar accuracy in the two conditions in AD patients; these data would suggest that the main impairment in AD involves constructional abilities, and not executive control and planning abilities, tapped specifically by the command condition (Royall et al. 1998). On the contrary, other authors observed that AD patients show a disproportionate impairment in spontaneous drawing with respect to copying, at variance with patients with Huntington disease and vascular dementia (Libon et al. 1996; Rouleau et al. 1992) or with DLB (Gnanalingham et al. 1996; Ala et al. 2001; but see Swan-

wick et al. 1996; Della Sala et al. 2002), who would show comparable impairments in both conditions. Such findings could suggest that semantic memory defects in AD were the primary source of difficulty in the command condition, interfering with patients' ability to build an adequate representation of a clock, whereas the copying condition would more extensively rely on executive functions, and therefore would be more affected in frontal-subcortical dementias. Longitudinal studies would confirm that spontaneous drawing is impaired in the early stages of AD and that copying deteriorates only successively (Rouleau et al. 1996).

Recent functional neuroimaging investigations have tried to identify the anatomo-functional correlates of CDT in AD patients, by investigating the relationships between CDT impairment and regional cerebral blood flow (rCBF), as measured by SPECT or PET (Nagahama et al. 2005; Ueda et al. 2002). Although different scoring procedures were used to classify patients' performance on CDT, both studies showed a significant correlation between lower rCBF in the left posterolateral temporal cortex and a severe impairment on CDT. These findings suggest that, at least in AD, a dysfunction in the temporal cortex may play a critical role in representing and drawing a clock face correctly. Given that temporal cortex is specifically affected in progression of AD, such results could be confounded by disease severity, although Nagahama et al. (2005) carefully matched patients with impaired or normal scores on CDT with respect to MMSE score, age and educational level. Moreover, these data did not take into account the possible role of executive defects in the task. This issue has been addressed by a recent study on patients affected by AD or vascular dementia compared with patients affected by Parkinson disease (Cosentino et al. 2004). Errors in setting clock hands and in locating numbers in the command condition of the CDT, and perseverations and closing-in phenomena in the copying task correlated with impairments on executive frontal tasks. These errors, and an overall impairment in both conditions, were particularly frequent in demented patients with marked white matter alterations and in Parkinsonian patients, while demented patients with mild white matter alterations outperformed the other two groups. These findings suggested that the executive impairment associated with frontal-subcortical dysfunction may contribute to impairments on CDT in demented patients.

Neuroimaging data in demented patients underline the multi-componential nature of the drawing processes, and complement the use of neuroimaging methods in normal subjects to understand the neural correlates of cognitive processes involved in drawing. An fMRI study in which subjects had to trace clock hands with their fingers, compared with a control condition in which subjects had to trace horizontal and vertical lines, has demonstrated the activation of a bilateral fronto-parietal network (Ino et al. 2003). Such findings are consistent with clinical evidence showing defective performances on clock drawing tasks in patients with frontal or parietal focal lesions (Shulman 2000).

The involvement of frontal lobes in drawing has been demonstrated by means of intracortical recording in the monkey prefrontal cortex (Averbeck et al. 2002). Monkeys had been trained to copy simple geometrical drawings by drawing lines in a

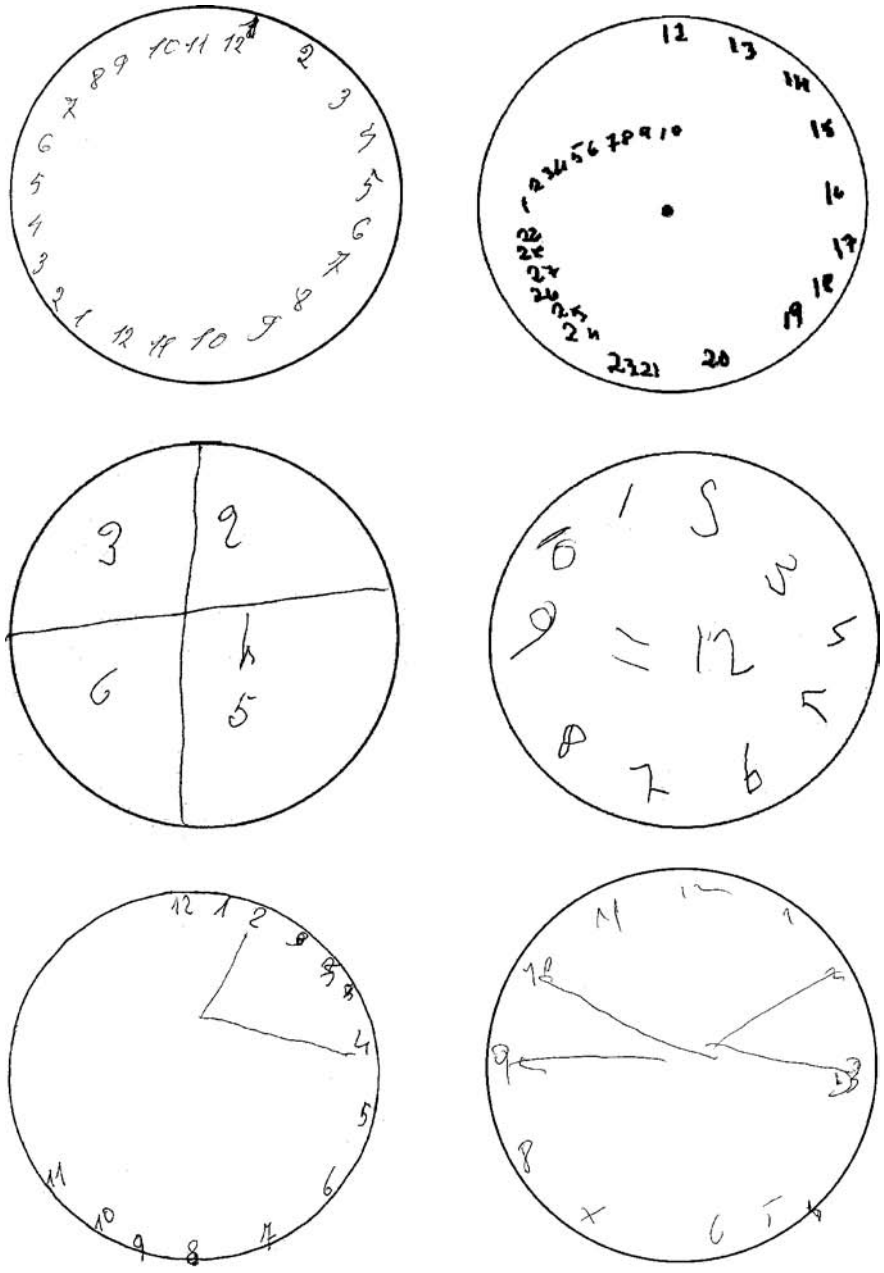


**Figure 3.** Clock drawing. In the first row, examples of perseveration and spatial disorganisation. In the middle row, examples of loss of semantic knowledge about hour position. In the last row, examples of errors in planning spatial disposition of hours, with digit drawn also upon the circle, and in setting clock hands.

sequential fashion. Intracortical recording showed activity of a specific neuronal assembly in relation to each segment to be drawn, particularly before execution of the first and the last segments. When the animal made an error in drawing, two neuronal assemblies reached the same activation level at the same time. Such data would demonstrate that the entire drawing plan is coded in terms of neuronal assemblies that specify the exact sequence of graphic movements. These observations are consistent with neuropsychological findings in brain damaged patients with focal frontal lesions, who show sequence errors in the execution of complex motor activities (Chevignard et al. 2000).

A further fMRI study on the copying of objects, compared with a condition in which subjects had to observe and name the same objects, has demonstrated that drawing relies on a wide network of cortical and subcortical structures (Makuuchi et al. 2003). Makuuchi et al. (2003) suggested that in copying a visually presented objects, information is mainly transferred to the parietal lobe via the visual dorsal pathway; the parietal lobe selects the drawing strokes to construct a representation of the object. This information is transmitted to the dorsal premotor area (BA 6) and the ventral premotor area (BA 44), and hence to motor areas, and to motor subcortical structures, i.e. basal ganglia and cerebellum. In parallel, the ventral stream processes properties of objects and this information may be implemented in the drawing plan.

This attempt at describing the neural basis of drawing cannot tackle issues regarding the cognitive processes which contribute to its execution. Several cognitive models of drawing abilities have been set forth so far (Roncato et al. 1987; van Sommers 1989; Grossi 1991). All of them distinguish some fundamental stages in the process of drawing and, although differentiated in terms of formal characteristics, depth of analysis and certain theoretical aspects, they share the idea that visuospatial processes, dedicated planning abilities and general control processes are all involved in drawing (for a review, see Grossi & Trojano 1999). None of these models have, at present, gained general acceptance, in the absence of adequate clinical and experimental evidence about their heuristic value. However, each model presents some interesting hints at a comprehension of different facets of drawing. It is worth mentioning that Grossi and Angelini (Grossi 1991) propose the existence of two copying procedures: a "lexical" route which predominantly involves activation of familiar constructional schemata (for example, in drawing a square or a face) and a "line-by-line" procedure, based on a spatial analysis which doesn't use constructional representations (activated when copying a doodle, for example). Both procedures may be adopted for copying complex pictures, but some patients might be constrained to use either one or the other. Here, the reader is reminded of the slow, slavish "line-by-line" copying procedure adopted by visual agnosic patients (Wapner et al. 1978; Trojano & Grossi 1992), who cannot access the lexical route for familiar objects. On the contrary, focal brain-damaged patients (Grossi et al. 1996; Trojano & Grossi 1998) or patients affected by degenerative dementia (see above), may show a defect in spatial analysis and in planning graphic reproductions so that they can draw successfully simple figures but are not able to integrate correctly-shaped simple elements in a coherent whole, when are

required to reproduce more complex stimuli. Such a clinical picture could be ascribed to planning or visuospatial defects in presence of a relatively spared ability to activate motor subroutines for drawing well-known figures. This kind of procedural memory might be conceived as a sort of "constructional lexicon", which develops as a result of formal education and personal aptitudes.

In a theoretical review, Guérin et al. (1999) argued that drawing relies on at least three cognitive systems: visual perception, visual imagery and graphic production. In general terms Guérin et al. (1999) cast some doubts about the specificity of the cognitive abilities thought to be necessary to draw, because they suggest that available models of visuospatial perceptual processes, mental imagery and planning abilities are sufficient to conceptualise drawing processes. However, Guérin et al. suggest that drawing unfamiliar objects requires visual imagery and planning abilities, while drawing familiar objects (which are strictly related to the drawer's premorbid abilities) may proceed through the activation of motor procedural memory, and this could correspond to what we have called a sort of constructional lexicon. Therefore, although drawing is strongly based on several skills not-specific for this constructional activity, several specific cognitive mechanisms are likely at work. The combination of cognitive and neuroimaging studies have begun to provide some clues about the multicomponential nature of the drawing processes, and to improve our comprehension of visuoconstructional disorders in dementia.

## References

Aarsland, D., I. Litvan, D. Salmon, D. Galasko, T. Wentzel-Larsen, & J. P. Larsen (2003). Performance on the dementia rating scale in Parkinson's disease with dementia and dementia with Lewy bodies: Comparison with progressive supranuclear palsy and Alzheimer's disease. *Journal of Neurology, Neurosurgery and Psychiatry*, *74*, 1215–1220.

Ala, T. A., L. F. Hughes, G. A. Kyrouac, M. W. Ghobrial, & R. J. Elble (2001). Pentagon copying is more impaired in dementia with Lewy bodies than in Alzheimer's disease. *Journal of Neurology, Neurosurgery and Psychiatry*, *70*, 483–488.

Ajuriaguerra, J., M. Muller, & R. Tissot (1960). A propos de quelques problèmes posés par l'apraxie dans les démences. *Encéphale*, *49*, 275–401.

Angelini, R., & D. Grossi (1993). *La Terapia Razionale dei Disordini Costruttivi.* Roma: Centro di Riabilitazione S. Lucia.

Arrigoni, C., & E. De Renzi (1964). Constructional apraxia and hemispheric locus of lesion. *Cortex*, *1*, 170–197.

Averbeck, B. B., M. V. Chafee, D. A. Crowe, & A. P. Georgopoulos (2002). Parallel processing of serial movements in prefrontal cortex. *Proceedings of the National Academy of Sciences of the USA*, *99*, 13172–13177.

Benowitz, L. I., K. L. Moya, & D. N. Levine (1990). Impaired verbal reasoning and constructional apraxia in subjects with right hemisphere damage. *Neuropsychologia*, *28*, 231–241.

Benson, D. F., & M. Barton (1970). Disturbances in constructional ability. *Cortex*, *6*, 19–46.

Benson, D. F., R. J. Davis, & B. D. Snyder (1988). Posterior cortical atrophy. *Archives of Neurology*, *45*, 789–793.

Benton, A. L., & M. L. Fogel (1962). Three-dimensional constructional praxis: A clinical test. *Archives of Neurology*, *7*, 347–354.

Benton, A., H. J. Hannay, & N. R. Varney (1975). Visual perception of line direction in patients with unilateral brain disease. *Neurology*, *25*, 907–910.

Binetti, G., S. Cappa, E. Magni, A. Padovani, A. Bianchetti, & M. Trabucchi (1998). Visual and spatial perception in the early phase of Alzheimer's disease. *Neuropsychology*, *12*, 29–33.

Black, F. W., & B. A. Bernard (1984). Constructional apraxia as a function of lesion locus and size in patients with focal brain damage. *Cortex*, *20*, 111–120.

Borod, J. C., M. Carper, & H. Goodglass (1982). WAIS performance IQ in aphasia as a function of auditory comprehension and constructional apraxia. *Cortex*, *18*, 212–220.

Caine, D., & J. R. Hodges (2001). Heterogeneity of semantic and visuospatial deficits in early Alzheimer's disease. *Neuropsychology*, *15*, 155–164.

Carlesimo, G. A., L. Fadda, & C. Caltagirone (1993). Basic mechanisms of constructional apraxia in unilateral brain-damaged patients: Role of visuo-perceptual and executive disorders. *Journal of Clinical and Experimental Neuropsychology*, *15*, 342–358.

Chevignard, M., B. Pillon, P. Pradat-Diehl, C. Taillefer, S. Rousseau, C. Le Bras, & B. Dubois (2000). An ecological approach to planning dysfunction: Script execution. *Cortex*, *36*, 649–669.

Cormack, F., D. Aarsland, C. Ballard, & M. J. Tovee (2004). Pentagon drawing and neuropsychological performance in Dementia with Lewy Bodies, Alzheimer's disease, Parkinson's disease and Parkinson's disease with dementia. *International Journal of Geriatric Psychiatry*, *19*, 371–377.

Cosentino, S., A. Jefferson, D. L. Chute, E. Kaplan, & D. J. Libon (2004). Clock drawing errors in dementia: Neuropsychological and neuroanatomical considerations. *Cognitive and Behavioral Neurology*, *17*, 74–84.

Della Sala, S., O. Turnbull, N. Beschin, N. Perini, & T. A. Ala (2002). Orientation agnosia in pentagon copying. *Journal of Neurology, Neurosurgery and Psychiatry*, *72*, 129–130.

Denes, G., & C. Semenza (1982). Sparing of constructional abilities in severe dementia. *European Neurology*, *21*, 161–164.

De Renzi, E. (1959). Osservazioni semeiogenetiche in tema di aprassia costruttiva. *Rivista Sperimentale di Freniatria*, *58*, 231–256.

De Renzi, E. (1982). *Disorders of Space Exploration and Cognition*. New York: Wiley and Sons.

Duensing, F. (1953). Raumagnostische und ideatorische-apraktische Storung des gestalten den Handelns. *Dtsch Z Nervenheink*, *170*, 191–204.

Elderkin-Thompson, V., K. B. Boone, S. Hwang, & A. Kumar (2004). Neurocognitive profiles in elderly patients with frontotemporal degeneration or major depressive disorder. *Journal of International Neuropsychological Society*, *10*, 753–771.

Freedman, M., L. Leach, E. Kaplan, G. Winocur, K. I. Shulman, & D. C. Delis (1994). *Clock Drawing: A Neuropsychological Analysis*. New York: Oxford.

Freeman, R. Q., T. Giovannetti, M. Lamar, B. S. Cloud, R. A. Stern, E. Kaplan, & D. J. Libon. (2000). Visuoconstructional problems in dementia: Contribution of executive systems functions. *Neuropsychology*, *14*, 415–26.

Gainotti, G. (1972). A quantitative study of the "closing-in" symptom in normal children and in brain-damaged patients. *Neuropsychologia*, *10*, 429–436.

Gainotti, G. (1985). Constructional apraxia. In J. A. M. Fredericks (Ed.), *Handbook of Clinical Neurology*, Vol. 45 (pp. 491–506). Amsterdam: Elsevier.

Gainotti, G., V. Parlato, D. Monteleone, & S. Carlomagno (1992). Neuropsychological markers of dementia on visuospatial tasks: A comparison between Alzheimer's type and vascular forms of dementia. *Journal of Clinical and Experimental Neuropsychology*, *14*, 239–252.

Gnanalingham, K. K., E. J. Byrne, & A. Thornton (1996). Clock-face drawing to differentiate Lewy body and Alzheimer type dementia. *Lancet*, *347*, 696–697.

Gorno-Tempini, M. L., N. F. Dronkers, K. P. Rankin, J. M. Ogar, L. Phengrasamy, H. J. Rosen, J. K. Johnson, M. W. Weiner, & B. L. Miller (2004). Cognition and anatomy in three variants of primary progressive aphasia. *Annals of Neurology*, *55*, 335–346.

Graham, N. L., T. H. Bak, & J. R. Hodges (2003). Corticobasal degeneration as a cognitive disorder. *Movement Disorders*, *18*, 1224–1232.

Grossi, D. (1991). *La riabilitazione dei disturbi della cognizione spaziale*. Milano: Masson.

Grossi, D., G. Correra, C. Calise, & L. Trojano (1996). Selective constructional disorders after right subcortical stroke. A neuropsychological premorbid and follow-up study. *Italian Journal of Neurological Sciences*, *14*, 23–33.

Grossi, D., N. A. Fragassi, E. Giani, & L. Trojano (1998). The selective inability to draw horizontal lines: On a peculiar constructional disorder. *Journal of Neurology, Neurosurgery and Psychiatry*, *64*, 795–798.

Grossi, D., N. A. Fragassi, L. Chiacchio, L. Valoroso, R. Tuccillo, C. Perrotta, P. Rapone, G. Conchiglia, & L. Trojano (2002). Do visuospatial and constructional disturbances differentiate frontal variant of frontotemporal dementia and Alzheimer's disease? An experimental study of a clinical belief. *International Journal of Geriatric Psychiatry*, *17*, 641–648.

Grossi, D., & L. Trojano (1999). Constructional apraxia. In G. Denes & L. Pizzamiglio (Eds.), *Handbook of Clinical and Experimental Neuropsychology* (pp. 441–450). Hove: Psychology Press.

Grossman, M., J. Mickanin, K. Onishi, K. M. Robinson, & M. D'Esposito (1996). Freehand drawing impairments in probable Alzheimer's disease. *Journal of International Neuropsychological Society*, *2*, 226–235.

Guerin, F., S. Belleville, & B. Ska (2002). Characterization of visuoconstructional disabilities in patients with probable dementia of Alzheimer's type. *Journal of Clinical and Experimental Neuropsychology*, *24*, 1–17.

Hof, P. R., B. A. Vogt, C. Bouras, & J. H. Morrison (1997). Atypical form of Alzheimer's disease with prominent posterior cortical atrophy: A review of lesion distribution and circuit disconnection in cortical visual pathways. *Vision Research*, *37*, 3609–3625.

Ino, T., T. Asada, J. Ito, H. Kimura, & H. Fukuyama (2003). Parieto-frontal networks for clock drawing revealed with fMRI. *Neuroscience Research*, *45*, 71–77.

Kerkhoff, G., & C. Marquardt (1998). Standardised Analysis of Visual-spatial Perception after Brain Damage. *Neuropsychological Rehabilitation*, *8*, 171–189.

Kirk, A., & A. Kertesz (1989). Hemispheric contributions to drawing. *Neuropsychologia*, *27*, 881–886.

Kirk, A., & A. Kertesz (1991). On drawing impairment in Alzheimer's disease. *Archives of Neurology*, *48*, 73–77.

Kirk, A., & A. Kertesz (1993). Subcortical contributions to drawing. *Brain and Cognition*, *21*, 57–70.

Kleist, K. (1934). *Gehirnpathologie*. Leipzig: Barth.

Kerkhoff, G. & C. Marquardt (1998). Standardised Analysis of Visual-spatial Perception after Brain Damage. *Neuropsychological Rehabilitation*, *8*, 171–189.

Kwak, Y. T. (2004). "Closing-in" phenomenon in Alzheimer's disease and subcortical vascular dementia. *BMC Neurology*, *4*, 3.

Lee, B. H., J. Chin, S. J. Kang, E. J. Kim, K. C. Park, & D. L. Na (2004). Mechanism of the closing-in phenomenon in a figure copying task in Alzheimer's disease patients. *Neurocase*, *10*, 393–397.

Lepore, M., M. Conson, D. Grossi, & L. Trojano (2005). Multidirectional transpositions suggesting pathologic approach behavior after frontal stroke. *Neurology*, *64*, 1615–1617.

Libon, D., B. Malamut, R. Swenson, L. P. Sands, & P. S. Cloud (1996). Further analysis of clock drawing among demented and nondemented older subjects. *Archives of Clinical Neuropsychology*, *11*, 193–205.

Makuuchi, M., T. Kaminaga, & M. Sugishita (2003). Both parietal lobes are involved in drawing: A functional MRI study and implications for constructional apraxia. *Cognitive Brain Research*, *16*, 338–347.

Mayer-Gross, W. (1935). Some observations on apraxia. *Proceedings of the Royal Society of Medicine*, *28*, 1203–1212.

McKeith, I. G., D. Galasko, K. Kosaka, E. K. Perry, D. W. Dickson, L. A. Hansen, D. P. Salmon, J. Lowe, S. S. Mirra, E. J. Byrne, G. Lennox, N. P. Quinn, J. A. Edwardson, P. G. Ince, C. Bergeron, A. Burns, B. L. Miller, S. Lovestone, D. Collerton, E. N. Jansen, C. Ballard, R. A. de Vos, G. K. Wilcock, K. A. Jellinger, & R. H. Perry (1996). Consensus guidelines for the clinical and pathologic diagnosis of dementia with Lewy bodies (DLB): Report of the consortium on DLB international workshop. *Neurology*, *47*, 1113–1124.

Mori, E., T. Shimomura, M. Fujimori, N. Hirono, T. Imamura, M. Hashimoto, S. Tanimukai, H. Kazui, & T. Hanihara (2000). Visuoperceptual impairment in dementia with Lewy bodies. *Archives of Neurology*, *57*, 489–493.

Nagahama, Y., T. Okina, N. Suzuki, H. Nabatame, & M. Matsuda (2005). Neural correlates of impaired performance on the clock drawing test in Alzheimer's disease. *Dementia and Geriatric Cognitive Disorders*, *19*, 390–396.

Neary, D., J. S. Snowden, L. Gustafson, U. Passant, D. Stuss, S. Black, M. Freedman, A. Kertesz, P. H. Robert, M. Albert, K. Boone, B. L. Miller, J. Cummings, & D. F. Benson (1998). Frontotemporal lobar degeneration: A consensus on clinical diagnostic criteria. *Neurology*, *51*, 1546–1554.

Ng, V. W., P. J. Eslinger, S. C. Williams, M. J. Brammer, E. T. Bullmore, C. M. Andrew, J. Suckling, R. G. Morris, & A. L. Benton (2000). Hemispheric preference in visuospatial processing: A complementary approach with fMRI and lesion studies. *Human Brain Mapping, 10*, 80–86.

Ober, B. A., W. J. Jagust, E. Koss, D. C. Delis, & R. P. Friedland (1991). Visuoconstructive performance and regional cerebral glucose metabolism in Alzheimer's disease. *Journal of Clinical and Experimental Neuropsychology*, *13*, 752–772.

Ogden, J. A., J. H. Growden, & S. Corkin (1990). Deficits on visuospatial tests involving forward planning in high-functioning Parkinson's. *Neuropsychiatry, Neuropsychology, and Behavioral Neurology*, *3*, 125–139.

Osterreith, P. (1944). Le test de copie d' une figure complexe. *Archives de Psychologie*, *30*, 206–356.

Perri, R., G. Koch, G. A. Carlesimo, L. Serra, L. Fadda, P. Pasqualetti, C. Pettenati, & C. Caltagirone (2005). Alzheimer's disease and frontal variant of frontotemporal dementia: A very brief battery for cognitive and behavioural distinction. *Journal of Neurology*, May 23.

Postma, A., Y. Sterken, L. de Vries, & E. H. F. de Haan (2000). Spatial localization in patients with unilateral posterior left or right hemisphere lesions. *Experimental Brain Research*, *134*, 220–227.

Rizzo, M., S. W. Anderson, J. Dawson, M. Nawrot (2000). Vision and cognition in Alzheimer's disease. *Neuropsychologia*, *38*, 1157–1169.

Roncato, S., G. Sartori, J. Masterson, & R. Rumiati (1987). Constructional apraxia: An information processing analysis. *Cognitive Neuropsychology*, *4*, 113–129.

Ross, S. J. M., N. Graham, L. Stuart-Green, M. Prins, J. Xuereb, K. Patterson, & J. R. Hodges (1996). Progressive biparietal atrophy: An atypical presentation of Alzheimer's disease. *Journal of Neurology, Neurosurgery and Psychiatry*, *9*, 191–224.

Rosselli M, & A. Ardila (2003). The impact of culture and education on non-verbal neuropsychological measurements: A critical review. *Brain and Cognition*, *52*, 326–333.

Rouleau, I., D. P. Salmon, N. Butters, C. Kennedy, & K. McGuire (1992). Quantitative and qualitative analyses of clock drawings in Alzheimer's and Huntington's disease. *Brain and Cognition*, *18*, 70–87.

Rouleau, I., D. P. Salmon, & N. Butters (1996). Longitudinal analysis of clock drawing in Alzheimer's disease patients. *Brain and Cognition*, *31*, 17–34.

Royall, D., J. Cordes, & M. Polk (1998). CLOX: An executive clock drawing task. *Journal of Neurology Neurosurgery and Psychiatry*, *64*, 588–594.

Rusconi, M. L., A. Maravita, G. Bottini, & G. Vallar (2002). Is the intact side really intact? Perseverative responses in patients with unilateral neglect: A productive manifestation. *Neuropsychologia*, *40*, 594–604.

Sandson, J., & M. L. Albert (1987). Perseveration in behavioural neurology. *Neurology*, *37*, 1736–1741.

Snowden, J. S., D. Neary, & D. M. Mann (1996). *Fronto-temporal Lobar Degeneration: Fronto-temporal Dementia, Progressive Aphasia, Semantic Dementia* (pp. 49–50). New York: Churcill Livingstone.

Stark, M. Coslett, & E. M. Saffran (1996). Impairment of an egocentric map of locations: Implications for perception and action. *Cognitive Neuropsychology*, *13*, 481–523.

Suzuki, K., Y. Otsuka, K. Endo, A. Ejima, H. Saito, T. Fujii, & A. Yamadori (2003). Visuospatial deficits due to impaired visual attention: Investigation of two cases of slowly progressive visuospatial impairment. *Cortex*, *39*, 327–341.

Swanwick, G. R. J., R. F. Coen, C. P. Maguire, D. Coakley, & B. A. Lawlor (1996). Clock-face drawing to differentiate dementia syndrome. *Lancet*, *347*, 1115.

Treccani, B., T. Torri, & R. Cubelli (2005). Is judgement of line orientation selectively impaired in right brain damaged patients? *Neuropsychologia*, *43*, 598–608.

Trojano, L., R. Angelini, P. Gallo, & D. Grossi (1997). An "ecological" constructional task. *Perceptual and Motor Skills*, *85*, 51–57.

Trojano, L., N. A. Fragassi, L. Chiacchio, O. Izzo, G. Izzo, G. Di Cesare, C. Cristinzio, & D. Grossi (2004). Relationships between constructional and visuospatial abilities in normal subjects and in focal brain-damaged patients. *Journal of Clinical and Experimental Neuropsychology*, *26*, 1103–1112.

Trojano, L., & D. Grossi (1992). Impaired drawing from memory in a patient with visual associative agnosia. *Brain and Cognition*, *20*, 327–344.

Trojano, L., & D. Grossi (1994). A critical review of mental imagery defects. *Brain and Cognition*, *24*, 213–243.

Trojano, L., & D. Grossi (1998). "Pure" constructional apraxia. A cognitive analysis of a single case. *Behavioral Neurology*, *11*, 43–49.

Ueda, H., Y. Kitabayashi, J. Narumoto, K. Nakamura, H. Kita, Y. Kishikawa, & K. Fukui (2002). Relationship between clock drawing test performance and regional cerebral blood flow in Alzheimer's disease: A single photon emission computed tomography study. *Psychiatry and Clinical Neuroscience*, *56*, 25–29.

Ungerleider, L. G., & M. Mishkin (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of Visual Behavior* (pp. 549–586). Cambridge: MIT Press.

van Sommers, P. (1989). A system for drawing-related neuropsychology. *Cognitive Neuropsychology*, *6*, 117–164.

Vallar, G. (1998). Spatial hemineglect in humans. *Trends in Cognitive Sciences*, *2*, 87–97.

Vallar, G. (2001). Extrapersonal visual unilateral spatial neglect and its neuroanatomy. *Neuroimage*, *14*, S52–S58.

Villa, G., G. Gainotti, & C. De Bonis (1986). Constructive disabilities in focal brain-damaged patients: Influence of hemispheric side, locus of lesion and coexistent mental deterioration. *Neuropsychologia*, *24*, 497–510.

Wapner, W., T. Judd, & T. Gardner (1978). Visual agnosia in an artist. *Cortex*, *14*, 343–364.

Warrington, E. K., & M. James (1991). *VOSP, The Visual Object and Space Perception Battery*. Bury St. Edmunds: Thames Valley Test Company.

Wechsler, D. (1981). *Wechsler Adult Intelligence Scale – Revised*. New York: Harcourt Brace Jovanovic.

CHAPTER 3.5

# Using visual imagery as a mnemonic for verbal associative learning

## Developmental and individual differences

Christopher Hertzog and John Dunlosky

### Introduction

Imagery has long been recognized as an important means of encoding materials for later remembering (e.g., Marschark & Hunt 1989; Paivio 1986; J. T. E. Richardson 1998). One venerable means of assessing learning and memory is the paired-associate (PA) task, in which individuals form new associations between elements, such as pairs of nouns. For example, individuals might be shown a list of items like CLOWN-SPOON and asked to associate the words, with recall later tested by cueing the individual with one element of the pair (e.g., CLOWN) and assessing recall for the remaining element (e.g., SPOON). PA tasks historically played an important role in studies of learning during the 20th century, and they continue to be used today to study phenomena like the accuracy of metacognitive monitoring (Nelson & Narens 1990) or associational deficits as a consequence of aging (e.g., Naveh-Benjamin 2000).

Paivio (e.g., Paivio 1971, 1986; Paivio & Yuille 1967) and his colleagues were among the first to study the use of imagery for learning PA items (see also Bower 1970). His dual-coding hypothesis stated that PA recall of words was enhanced by using imagery to mediate the new association, because it created dual codes – an imagistic code and a semantic code of the association. This hypothesis has proven to be controversial (e.g., Marschark & Hunt 1989), for reasons we shall not discuss here (see J. T. E. Richardson 1999, 2003). Nevertheless, the benefits of using imagery for mediating new associations has been firmly established by Bower, Paivio, Richardson, and many others. What is critically important in this regard is that imagery use in and of itself is not necessarily effective for learning new materials. Instead, an interactive image must be formed in which imaginal tokens of the concepts represented by the two words are actively engaging one another – in other words, the critical encoding activity is relational processing, in this case using imagery as the substrate. One realizes relatively little learning benefit from forming separate images of a clown and a spoon, but imag-

ing a clown interacting with a spoon (e.g., a clown balancing a bicycle-sized spoon on his red nose) results in greatly enhanced PA recall.

Our research program has studied imagery use for PA learning as part of larger effort to understand metacognition and its development across the adult life-span. Strategies, including imagery use, are critical in shaping memory development during childhood (e.g., Schneider & Pressley 1997). At issue in our research is whether strategic behavior remains intact during adulthood and into old age. A signature of this research is that we have used simple item-level self-reports of the types of mediators people generate for encoding PA items, either spontaneously or under experimenter instructions to use mediational strategies (e.g., Paivio & Yuille 1967; Yuille 1973; see J. T. E. Richardson 1998, 1999).

We have consistently found individual differences in the use of imagery as a mediational strategy (Hertzog & Dunlosky 2005). Some individuals spontaneously use imagery, others do not. Some use few strategies (if any at all), or rely on ineffective strategies like repeating the words over and over (rote repetition). Other individuals tend to use different, non-imagistic strategies, such as sentence generation. And, most important, people often use multiple strategies within a single list of PA items, indicating (perhaps) an adaptive selection of strategies as a function of the intersection of applying multiple cognitive resources and mechanisms to the affordances given items place on use of imagery, semantic, or other strategies (McDougall & Velmans 1993; Paivio 1971; see Schunn & Reder 2001, for a more recent discussion of the concept of strategic adaptivity). For example, PA items using abstract nouns are more likely to be encoded by using sentences rather than images, especially under conditions of limited presentation time. Although these individual differences are consistently large, aging per se does not explain them. We find little evidence for either age deficits in the production of interactive images or other effective strategies, or in adaptive strategic behavior, in terms of using multiple strategies (Hertzog & Dunlosky 2005).

A fairly large literature has also focused on self-report measures of imagery use in everyday life, in which scientists query people about whether they are able to use or actually do use imagery to accomplish cognitive goals (details are provided below). In contrast to experimental procedures designed to measure strategy use as it occurs in PA learning, these self-report measures rely on people's self-knowledge, or alternatively, their ability to remember and estimate how often they use imagery (and the vividness of such imagery use) in more naturalistic situations. Although these self-reports of everyday memory use likely demonstrate some validity by reflecting actual imagery use, they are also fallible because they can be influenced by an individual's (sometimes inaccurate) beliefs about his or her own cognition (Cavanaugh, Feldman, & Hertzog 1998; Ericsson & Simon 1993). Hence, they may be both (a) systematically biased and an inaccurate reflection of actual imagery use of imagery in general, and (b) of limited predictive validity for imagery use in a specific context. For this reason, comparing outcomes from self-report measures of imagery use in everyday life to actual use in controlled experimental studies provides valuable information about the construct validity of everyday measures of imagery use. We discuss such comparisons

from previous work and from our own work below. More specifically, the purposes of this chapter are to describe individual differences in imagery use during PA learning, and to evaluate self-reported use of imagery in everyday life as a predictor of individual differences in imagery use during PA learning.

## Individual differences in imagery use

That individual differences arise in the spontaneous use of imagery in cognition is well-accepted in field. Imagery is an effective medium for representing and solving problems, promoting navigation and way-finding, facilitating new learning, and so on (J. T. E. Richardson 1999). Indeed, recent writings on the embodiment problem in cognitive science emphasize imagery as a primary representational medium for internally simulating everyday activities and for representing the properties of common objects (e.g., Barsalou 1999; Kan et al. 2003). Imagery is phenomenally reported to accompany many kinds of retrieval of long-term memories (e.g., Brewer & Pani 1996). Despite the formidable epistemological issues associated with verifying the use of imagery (e.g., Anderson 1978), cognitive scientists have developed tasks that can measure the ability to form, maintain, and manipulate images (e.g., Finke 1989; Dror & Kosslyn 1994; Kosslyn 1980). Behavioral and neuroimaging data have converged to suggest that imagery is indeed evoked by such tasks (e.g., d'Esposito et al. 1997; Ganis, Thompson, & Kosslyn 2004).

Interest in the phenomenon of imagery use in everyday life prompted the development of questionnaires to assess self-reported imagery ability (see A. Richardson 1994 for a review and versions of several questionnaires). A detailed review of this literature is not possible in this chapter, but a few preliminary remarks are needed for our purposes. A major distinction between types of imagery questionnaire occurs between scales measuring the vividness of imagery formation and visual imagination, on the one hand, versus the self-reported (functional) use of imagery in everyday life to achieve cognitive goals, on the other. An example of the prior type of questionnaire is the Vividness of Visual Imagery Questionnaire (VVIQ, Marks 1973). In completing the VVIQ questionnaire, people are instructed to visualize objects (e.g., a friend's face, the rising sun) and then rate the vividness of the image in terms of clarity and detail. Other variants of this type ask individuals to control or manipulate imagery, including visualization of dynamic scenes or moving objects (A. Richardson 1994).

The second type of questionnaire involves personal ratings of the use of imagery in everyday life and often includes a dimension of cognitive style or preference to use or avoid imagery for certain purposes. For example, A. Richardson (1994) argued that persons can be classified along a verbalizer-visualizer dimension, indicating whether they habitually prefer to use linguistically based or imagery-based strategies to represent and solve problems. The hypothesis of a general cognitive style preference for imagery over sentences is not highly supported by empirical evidence (J. T. E. Richardson 1999). Nevertheless, it can be useful to determine whether self-reported

use of imagery in everyday life correlate with imagery use in experimental tasks such as associative learning.

There are several functionally oriented questionnaires, including Paivio and Harshman's (1983) Individual Differences Questionnaire (IDQ). An example item from the IDQ is, "I often use mental pictures to solve problems." The complete IDQ contains six scales measuring functional use of memory or a preference to use verbal-linguistic strategies in everyday life. In the data we report in this chapter, we used just two scales from the IDQ, which measure different aspects of imagery quality and use relevant to the distinction between imagery use and imagery vividness discussed earlier. The first, which we call *Imagery Use*, would involve the kind of item just listed. The second, which we call *Vivid Imagery*, differs from the VVIQ in that it does not instruct participants to image anything and rate the image's qualities. Rather, people indicate whether they have vivid images, dreams, and daydreams in everyday life. We describe the items on the IDQ in more detail below.

## Predictive validity of self-reported imagery

In this section, we further consider the validity of self-reported imagery measures, with a driving question being, why is the predictive validity of cognitive behavior by self-report imagery measures often so low? In response to this question, we argue for the importance of an approach based on construct validation involving multiple measures of relevant constructions. Partly stemming from this approach, we introduce the *behavioral specificity principle* of self-report validity, which identifies conditions that should support higher levels of predictive validity.

Although the VVIQ has correlated with a number of psychological tasks, in many cases correlations with cognitive performance involving manipulated imagery use have been disappointingly low, or even non-existent (e.g., McKelvie 1995; J. T. E. Richardson 1999). For example, the VVIQ does not correlate with performance on classic mental rotation tasks, which for most individuals involve the use of imagery as the medium to conduct the spatial transformations required (Shepard & Metzler 1971; Just & Carpenter 1986). As noted by Dean and Morris (2003), failures to predict visuospatial performance from self-reported vivid imagery could reflect mismatches between the types of imagery measured by the questionnaire and the types of imagery required by the cognitive task (see also Burton 2003; Burton & Fogarty 2003). In particular, failure of the VVIQ to correlate with tests of mental rotation and spatial visualization could indicate that vividness of retrieved memories or simulated objects do not capture the distinct nature of the transformations in visuospatial working memory that support mental rotation (e.g., Burton 2003; Farah et al. 1988; Poltrock & Agnoli 1986; Poltrock & Brown 1984). Dean and Morris (2003) showed that self-ratings of images of rotating two- and three-dimension objects, of the kind used in mental rotation tests, correlated reliably with mental rotation performance. Furthermore, these cor-

relations were consistently higher than corresponding correlations of mental rotation performance with the VVIQ.

Such findings highlight the importance of framing the problem of predictive validity for imagery self-reports in a larger context of construct validation (Cronbach & Meehl 1955). In this context, patterns of correlational and predictive relations are evaluated to demonstrate convergent and discriminant validity within the larger framework of a nomological net (i.e., a set of hypothesized patterns of relationships deriving from a specific theory about the phenomena and mechanisms involved). This approach stands in contrast to studies that seek to explore construct validity of imagery questionnaires by evaluating single correlations between questionnaire responses and a performance task. Moreover, studies that strive to evaluate construct validity of imagery self-reports must address the issue of the multidimensionality of imagery and self-reported imagery (as in the distinction between image vividness and functional use of imagery; Burton & Fogarty 2003). Finally, the results from Dean and Morris (2003) highlight the utility of seeking specific behavioral self-reports that are grounded in the phenomenon of interest (e.g., properties of imagery during mental rotation) rather than seeking more broadly defined styles of imagery use or characteristics of imagery summed over many behavioral domains.

The Dean and Morris (2003) findings are analogous to findings of Hertzog, Park, Morrell, and Martin (2000) in an entirely different domain – everyday prospective memory. Hertzog et al. (2000) found that self-reported memory complaints, measured by a widely-used questionnaire, correlated reliably with memory test performance but bore little relation to behaviorally observed medication adherence errors. Medication adherence was measured by the number of times pill bottles were opened over a one-month period, using a micro-electronic chip in the bottlecap. However, self-reports of difficulties in remembering to take the medications when one was actually prescribed (obtained in an interview using the pharmacist-labeled, original pill bottles to elicit valid self-reports) correlated more than .40 with the subsequent behavioral measures of forgetting to take medications. These correlations indicate prospective validity of the interview responses for medication adherence over the next month. However, the interview measure of problems remembering to take medications did not correlate with the memory complaints scales.

This pattern of dissociated discriminant validity supported the argument that predictive validity is enhanced by *behavioral specificity* in the self-reports. That is, obtaining self-reports of cognitive problems that are linked to a specific target behavior combined with specific measures of the target behavior in the natural ecology, produces the highest predictive validity of self-reports for cognitively-related behaviors. Apparently, the interviews about specific medications, and with the original pill bottles as cues, resulted in individuals being more able to access instances of forgetting and to assess their overall propensity to forget taking the medications (see Hertzog et al. 2000, for further discussion). As such, querying specific behaviors may represent the optimal means for assessing whether people have awareness and knowledge of their own cognitive functioning. In the case of mental imagery, querying the specific type of

imagery processes required by a task provides the best means for evaluating whether individuals are aware of their skills and use of imagery appropriate to the task.

One way to measure knowledge about effectiveness of imagery as a strategy to mediate learning new associations is to specifically ask people to rate the relative effectiveness of different possible mediational strategies, including imagery. In one of the studies we describe below, we contrasted effectiveness ratings for interactive imagery as a strategy for PA learning (arguably the specific, proximal belief that would influence strategic behavior) with the IDQ scales as predictors of self-reported imagery strategy use. Given that the IDQ scales assess imagery use across a broad range of cognitions, the behavioral specificity principle would predict stronger relations of imagery effectiveness ratings for PA learning to imagery use in the PA task, relative to the IDQ.

## Available data on self-reported imagery use during PA learning

As part of a larger research program on strategies and metacognition, we have collected data that are relevant to the issue of whether self-reported imagery skill and use in everyday life, as measured by the VVIQ and IDQ, predicts both PA imagery strategy production and PA recall. We report results from two different studies, one involving concurrent reports of PA learning strategies, and the other involving retrospective reports of strategies to reveal spontaneous imagery mediator use (see below).

The first study (Dunlosky & Hertzog 1998, Experiment 2) had young adults (students at two American universities) and older adults (community-dwelling volunteers who came to the same universities to participate) study pairs of unrelated noun-noun (dog-spoon) items under two conditions – one in which strategies were self-chosen, the other in which individuals were instructed to produce interactive imagery mediators for each PA item. The sample that completed the relevant questionnaires included 88 older adults (mean age = 71) and 61 younger adults (mean age = 19). We also collected data on two intellectual abilities, perceptual speed and vocabulary, along with two questionnaires measuring self-reported imagery in everyday life, the VVIQ and a short-form of the IDQ.

The second study (Hertzog, Dunlosky, & Robinson 2005) was designed to address issues about predictors of individual differences in PA learning and strategy use in a cross-sectional sample of approximately 300 adults, ages 25 to 80. A large set of ability tests, questionnaires, and memory tests were administered over 3 separate sessions. PA learning was measured with three different lists. The first and second lists were administered in an experimental manipulation of fast-paced study (2, 3 or 4 s. presentation rates per item) versus slow-paced study (10, 11, or 12 s. presentation rates), with persons randomly assigned to one of the two pacing conditions. At the end of the second PA list, retrospective strategy use data was collected, using the method validated by Dunlosky and Hertzog (2001). Then both groups were transferred to a slow-paced study on a third PA list, again with retrospective reports (see Hertzog, Dunlosky, & Robinson 2005, for more details). Mediator production for the second and third lists

correlated highly with each other, suggesting stability in strategic behavior. We focus primarily on performance on the transfer list, given that everyone received slow pacing during study. Fast pacing suppresses strategy use (including interactive imagery) and affects correlations of ability variables with strategy use (see Hertzog, Dunlosky, & Robinson 2005). Retrospective strategy reports for the transfer list correlated highly with mediator production for that list ($r = .70$). The short form of the IDQ was administered before the PA learning task, as was a questionnaire asking individuals to rate the effectiveness of different strategies for associative learning, called the Personal Encoding Preferences [PEP] questionnaire (see Hertzog & Dunlosky 2005, Appendix, for a copy of the questionnaire). Individuals rated the effectiveness of several strategies, including interactive imagery, sentence generation, and rote repetition on a 10-point Likert scale. The study also collected considerable data on beliefs about memory in adulthood that we do not consider in this chapter.

In both studies, the short form of the IDQ we administered consisted of the 19 items for Paivio and Harshman's (1983) Factors 2 and 6, described by these authors as measuring (a) "the habitual use of imagery" as well as imagery skill or ability, and (b) vividness of dreams and imagination. Table 1 lists the items from this short-form. We altered the response format from its original True-False binary choice to a 5-point Likert-rating (anchored by "strongly agree" versus "strongly disagree," in order to increase response variability). We computed three scales: an IDQ total scale score, and the two subscale scores, which we refer to as IDQ Imagery Use and IDQ Vivid Images. Scales were computed by unit-weighted summing of the relevant items after reversal of negatively worded items.

The scales displayed good internal consistency across items in both our samples. In the Dunlosky and Hertzog (1998, Experiment 2) sample, the estimated internal consistency reliability (coefficient alpha) for the four scales was .89 for the total IDQ scale, .87 for the IDQ Imagery Use scale, .72 for IDQ Vivid Images, and .92 for the VVIQ. In the Hertzog, Dunlosky, and Robinson (2005) sample, estimated internal consistency was .89 for the total IDQ scale, .86 for the Imagery Use subscale, and .70 for the Vivid Images subscale.

Given the relatively large sample size in the Hertzog, Dunlosky, and Robinson (2005) study, we also conducted a factor analysis of the 19 IDQ items in that data set. This analysis suggested that the IDQ item covariance structure was more influenced by positive versus negative item construction than by the distinction between functional imagery use and vivid everyday imagery. A confirmatory factor analysis achieved a reasonable fit ($\chi^2 = 369.38$, $df = 146$, Steiger's (1990) RMSEA = .069) by specifying four factors (separate factors for the positively and negatively worded items for the two target subscales). The factor correlations among the positively-worded Imagery Use factor and the positively-worded Vivid Images factor was .98, and the corresponding correlation among the two negatively-worded factors was .95. This suggests relatively poor discriminant validity between the two subscales. By contrast, the two different (positive and negative) Imagery Use factors correlated –.72, and the two different Vivid Images factors correlated –.89. These high factor correlations, along with their pattern,

**Table 1.** Individual differences questionnaire (short form)

| | |
|---|---|
| 1. | Listening to someone recount his experiences does not usually arouse mental pictures of the incidents being described. (Vivid Imagery, Reversed, .40, .17) |
| 2. | My daydreams are something so vivid I feel as though I actually experienced the scene. (Vivid Imagery, Standard, .41, .06) |
| 3. | I do not have a vivid imagination. (Vivid Imagery, Reversed, .45, .09) |
| 4. | I can easily picture moving objects in my mind. (Imagery Use, Standard, .59, .18) |
| 5. | I have only vague visual impressions of scenes I have experienced. (Vivid Imagery, Reversed, .46, .17) |
| 6. | I think that most people think in terms of mental pictures whether they are completely aware of it or not. (Imagery Use, Standard, .25, .07) |
| 7. | My powers of imagination are higher than average. (Imagery Use, Standard, .39, .09) |
| 8. | I can close my eyes and easily picture a scene I have experienced. (Imagery Use, Standard, .59, .10) |
| 9. | When someone describes something that happens to him, I sometimes find myself vividly imagining the events that happened. (Imagery Use, Standard, .59, .06) |
| 10. | I seldom dream. (Vivid Imagery, Reversed, .35, .12) |
| 11. | I never use mental pictures or images when trying to solve problems. (Imagery Use, Reversed, .59, .26) |
| 12. | I find it difficult to form a mental picture of anything. (Imagery Use, Reversed, 63, .20) |
| 13. | My dreams are extremely vivid. (Vivid Imagery, Standard, .52, .13) |
| 14. | My thinking often consists of mental pictures or images. (Imagery Use, Standard, .67, .13) |
| 15. | I do not form a mental picture of people or places when reading of them. (Imagery Use, Reversed, .53, .18) |
| 16. | My daydreams are rather indistinct and hazy. (Vivid Imagery, Reversed, .48, .09) |
| 17. | I often enjoy the use of mental pictures to reminisce. (Imagery Use, Standard, .62, .20) |
| 18. | I often use mental images or pictures to help me remember things. (Imagery Use, Standard, .68, .29) |
| 19. | When remembering a scene, I use verbal descriptions rather than mental pictures. (Imagery Use, Reversed, .30, .18) |

*Note*: All items rated on a 1–5 scale, from strongly agree to strongly disagree. Information in parentheses after item refers to (scale, direction, item-total correlation, correlation with reported PA imagery use), where scale is either the Imagery Use or the Vivid Imagery subscale; direction is the direction of scoring, either standard or reversed; item-total correlation is the corrected correlation of the item with its associated scale score, after reversal; and the correlation with reported PA imagery use is with the number of items participants reported using visual imagery on the PA learning task, after reversal of IDQ items.

would seem to support constructing a single total IDQ scale. Nevertheless, we decided to also retain the two subscales as recommended by Paivio and Harshman (1983). As we shall see, this distinction did produce differences in correlations of the two IDQ scales with strategic behavior and PA recall.

## Measurement of imagery mediator production

Students of learning since antiquity have heralded the benefits of imagery in memorizing and retaining associations (Yates 1997). Experimental evidence has been unequivocal. Memory performance is superior when individuals are instructed to use imagery to study items than when they are instructed to merely recite items repeatedly. Given the power of imagery, we have been investigating whether individual differences occur in the spontaneous use of imagery during study, and the degree to which imagery use can explain differences in criterion memory performance. Our approach to pursuing these issues has involved measuring the production of mediators at the level of individual items (e.g., Paivio & Yuille 1967; Yuille 1973). A participant would first study a given PA item, such as "apple – cat". After the item has been studied, the participant reports how he or she studied the item by selecting one of several responses, which include imagery, rote repetition, sentence generation, some other strategy, or no strategy. So, if the individual generated an image of a large apple in the shape of a cat, he or she should report using interactive imagery. By collecting these item-by-item reports of strategy use, individual differences in imagery generation can be assessed by simply computing the proportion of items that each participant reports using imagery.

The importance of obtaining item-by-item reports of strategy use cannot be understated. Without such measurement, the true effects of instructional manipulations cannot be accurately estimated (Eagle 1967; Paivio & Yuille 1967). Most relevant for our purposes in this chapter, individual differences in imagery use would be quite difficult to measure precisely (but see Hertzog, McGuire, & Lineweaver 1998; McNamara & Scott 2001). Moreover, item-by-item reports also enjoy several other qualities that make them quite ideal for investigating strategy use during associative learning (for evidence concerning the following conclusions, see Dunlosky & Hertzog 1998, 2001; J. T. E. Richardson 1998).

First, making strategy reports immediately after studying each item – termed *concurrent* reports – has a negligible effect on PA recall. Put differently, making the reports during study does not appear to have reactive effects on memory. Second, item-by-item reports can also be made retrospectively. For instance, after all items have been studied and tested, each one can be re-presented (e.g., apple – cat) with the query for a strategy report. Both kinds of report have strengths and possible weaknesses. In contrast to *retrospective* reports, the validity of concurrent reports cannot be undermined by forgetting which strategy had been used during study. And in contrast to *concurrent* reports which are intermingled with studying, *retrospective* reports cannot have any influence on the strategies individuals chose to use during study. If one wishes to study spontaneous strategy use uncontaminated by awareness of the existence of strategies induced by the experiment itself, then retrospective reports are required (even if their validity is constrained by forgetting the strategies actually used; Rowe & Schnore 1971). Reassuringly, Dunlosky and Hertzog (2001) demonstrated that retrospective reports suffer minimally from forgetting and concurrent reports have minor reactive effects on strategy use.

Third, and perhaps most important, item-be-item reports of strategy use have demonstrated construct validity in numerous investigations. One compelling demonstration is that criterion memory performance is consistently superior when participants report using relatively effective strategies (e.g., imagery) than when they report using less effective ones (e.g., rote repetition). Also, individual differences in the use of relatively effective strategies (e.g., imagery and sentence generation) are correlated with actual test performance (PA recall). For instance, in the sample from Dunlosky and Hertzog (1998) discussed here, the correlation between the proportion of effective strategy use (defined by use of imagery, sentences, predominantly) and PA recall was .32, $p < .001$. Individuals who more often reported using imagery and sentence generation also performed better overall, which again supports the validity of the item-by-item reports of strategy use. By virtue of its expanded measurement of abilities, memory, and other constructs, the study by Hertzog, Dunlosky, and Robinson (2005) provided even more impressive and wide-ranging evidence supporting the construct validity of the strategy self-reports. For example, self-reported strategy use mediated (in the statistical sense) the relationship between personal control beliefs about memory (e.g., Lachman, Bandura, Weaver, & Elliott 1995) and PA recall, supporting the construct validity of both the reports and the beliefs measures.

## Age and gender differences in IDQ scales

*Dunlosky & Hertzog (1998) Sample*. We conducted a correlation analysis on the IDQ scales, using age as an independent variable. Age was dummy coded (0 = younger adults, 1 = older adults) given that we used an extreme age-groups design for this sample. Given the small sample size, we held analysis of gender for the larger sample from Hertzog, Dunlosky, and Robinson (2005). The correlations between age and the three IDQ scales were all reliably different than 0: –.44 with IDQ total, –.42 with the Imagery Use Scale, and –.33 with the Vivid Images scale. Thus, compared to younger adults (university students), older adults showed lower reported use of imagery and the vividness of imagery.

*Hertzog, Dunlosky, & Robinson (2005) Sample*. We conducted a regression analysis on the IDQ scales, using linear and quadratic age terms and gender as independent variables. For the total IDQ scale, there was no gender difference, $\beta = .08$, $t = 1.40$, $df = 293$, $p > .10$, but there was a reliable age difference, $\beta = –.16$, $t = 2.70$, $df = 293$, $p < .05$. Increasing age was associated with a modest reduction in self-reported imagery. However, this difference was entirely attributable to age differences in the Vivid Images scale. Age differences were not reliable for the Imagery Use scale, $\beta = –.08$, $t = 1.41$, $df = 293$, $p > .10$, but were robust for the Vivid Images scale, $\beta = –.27$, $t = 4.75$, $df = 293$, $p < .001$. Older adults reported less vivid imagery. The differences between the results on age correlations may in part reflect the fact that the majority of students in the Dunlosky and Hertzog (1998) sample were students at a technical

university selected for high levels of intellectual ability and proficiency in spatial and mathematical thinking.

Harshman and Paivio (1987) reported "paradoxical" gender differences in their validation samples, with women reporting greater imagery use than men. The finding was deemed paradoxical given the fact that men are known to perform better on tests of spatial rotation than women (e.g., Voyer, Voyer, & Bryden 1995). Our sample revealed large gender differences favoring men in spatial ability, consistent with the psychometric literature. However, we did not replicate Harshman and Paivio's (1987) finding of greater self-reported imagery use by women. In our data, the gender difference trended toward higher self-reported imagery use in men, but the difference was not reliable (for Imagery Use, $\beta = .08$, $t = 1.40$, $df = 293$, $p > .10$). Likewise, there were no gender differences in rated effectiveness of the interactive imagery strategy from the PEP questionnaire (for men, $M = 6.40$, $SD = 2.90$; for women, $M = 6.38$, $SD = 3.13$; $t < 1$). On average, both men and women rated imagery as an effective strategy (ratings over 6 on a 10-point scale).

### Correlations of imagery questionnaires with PA mediator production

*Dunlosky & Hertzog (1998) Sample.* In this section, we first describe relevant outcomes concerning imagery production that are mainly available from our original report. Afterwards, we return to our focal issues by exploring the degree to which self-reports of imagery use and vividness from the imagery questionnaires are related to imagery production.

As noted earlier, a major feature of this study was that some people were encouraged to use any strategy they wished for any time, whereas others were instructed to use interactive imagery (even though strategy reports were collected). In the spontaneous (or self-chosen) condition, individuals reported, on average, using interactive imagery on 37% of the items, and an effective strategy on 64% of the items. After imagery instructions, reported imagery use rose to 57% of the items, with a total of 71% of the items reported to have been studied with an effective strategy. Thus, imagery use accounted for a little over half of effective strategy use in the self-chosen condition, but about 80% of the effective strategy use after interactive imagery instructions. Instructions boosted the use of imagery, relative to sentence production, and resulted in a small increase in the proportion of overall effective strategy use.

There were no reliable age differences in reported effective strategy use, and older adults in the self-chosen condition actually had slighter higher probability of reported imagery use (see Dunlosky & Hertzog 1998, for more details). In another study, however, small age differences were observed in the spontaneous use of mediators, as measured by retrospective reports (see Dunlosky & Hertzog 2001). From these studies, it is apparent that informing older adults of the existence of interactive imagery eliminates age differences in mediator production, which contradicts the hypothesis that age-related declines in visuospatial abilities (Hertzog 1989; Johnson & Rybash

**Table 2.** Correlations among self-reported strategy production and IDQ and VVIQ scales

| Measure | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| | Self-chosen group / Imagery group | | | | | |
| 1 PA imagery use | 1 | .03 | .27* | .33* | .16 | .24 |
| 2 PA imagery recall | .15 | 1 | .42* | .41* | .30* | .29* |
| 3 IDQ total | .04 | .41* | 1 | .96* | .83* | .61* |
| 4 IDQ Imagery use | .11 | .42* | .95* | 1 | .68* | .64* |
| 5 IDQ Vividness | .09 | .28* | .81* | .62* | 1 | .50* |
| 6 VVIQ | .02 | .08 | .28* | .26* | .39* | 1 |

*Note*. Correlations in lower-left quadrant of the table were based on scores from participants who were instructed to use any strategy they wanted (self-chosen group), whereas correlations in the upper-right quadrant were based on scores from participants who were instructed to use imagery during study. *$p < .05$. PA imagery use = proportion of items that a participant reported using imagery during study. PA imagery recall = proportion correct recall computed for items in which imagery was used during study.

1993; Salthouse 1992) render older adults less capable of using imagery as an encoding strategy (but see Dirkx & Craik 1992; Palladino & de Beni 2003).

Most relevant to our current goal of exploring the imagery questionnaires, we turn to new information from Dunlosky and Hertzog (1998) that pertain specifically to the correlations of self-reported imagery use and PA recall (conditionalized on imagery production) with the IDQ scales and with the VVIQ total score. We computed these correlations separately for individuals who were instructed to produce imagery during study (imagery group) versus those who were not instructed to use any particular strategy for study (spontaneous group). These correlations are presented in Table 2. Several outcomes are noteworthy.

First, the VVIQ and the IDQ scales are correlated, but not highly so relative to the magnitude of internal consistency, even for the IDQ Vivid Images subscale. By contrast, the two IDQ scales correlated substantially, suggesting either shared method variance, higher commonality of aspects of everyday imagery use, or both. Clearly, the rating of vivid imagery under instruction, as measured by the VVIQ, is not isomorphic with reports of vivid imagery in everyday life, even in an older sample.

Second, imagery mediator production in the PA learning task by participants who were not instructed to use a particular strategy (the self-chosen group), was not reliably correlated with the four imagery scales. By contrast, for participants who were instructed to use imagery (imagery group), the IDQ Imagery Use scale was correlated with how often individuals reported using imagery during associative learning. Thus, individuals who report using imagery in everyday life are more able (or likely) to use imagery when instructed to do so, although they did not prefer to use imagery when they were free to use any strategy. This result was surprising to us, but it is consistent with other studies suggesting that the IDQ does not measure a stable dimension of cognitive style in preferring imagery over verbal strategies (J. T. E. Richardson 1999).

One aspect to consider in evaluating the pattern of correlations in Table 2 is the correlation of imagery questionnaires with production of sentence mediators. In the self-chosen condition, use of both images and sentences did correlate weakly with IDQ Imagery Use, such that the correlation of overall effective strategy use (combining use of interactive imagery, sentence production, and other strategies) with the IDQ scale was reliable, $r = .37$, $p < .01$. Conversely, in the instructed condition, sentence use was negatively correlated with IDQ Imagery Use; hence, overall use of effective strategies did not correlate with IDQ Imagery Use. Sentence generation under instructions to produce images probably reflected an adjustment to an initial attempt to use the imagery strategy as instructed, and imagery may have been used even when it was the less effective strategy for a given item. Sentence generation in the self-chosen condition may have been more a function of item affordances for use of sentences versus images. Thus, the correlations of imagery use and imagery recall in the self-chosen condition may be attenuated by the fact that sentence production, when used, was an equally effective strategy in this study (see Dunlosky & Hertzog 1998).

Third, regardless of instructions, when participants reported using imagery, the imagery use and vividness scales were reliably correlated with PA recall when reporting imagery mediators. These results suggest that a propensity to use imagery in everyday life is associated with the effectiveness of imagery mediators produced during study. However, the relationship was largest for the IDQ Imagery Use scale and lowest for the VVIQ, consistent with earlier literature.

*Hertzog, Dunlosky, & Robinson (2005) Sample*. Table 3 reports the correlations of self-reported imagery use and sentence generation use with the IDQ scales and the PEP imagery and sentence mediator effectiveness ratings. There are several notable findings.

First, IDQ Imagery Use correlated more highly with imagery strategy production during PA learning than IDQ Vivid Images. This was also the case for correlations with PA recall. This outcome again supports the argument that self-reported functional imagery skill and use is more highly associated with the use of the imagery strategy than is the vividness of images in everyday life. To further evaluate this finding we also examined correlations of individual IDQ items with imagery use in the PA learning task. The highest correlation, $r = .29$, was produced by Item 18 (see Table 1).

Second, the PEP rating of imagery mnemonic effectiveness was significantly correlated with both PA imagery mediator use and PA recall. Moreover, the correlation was higher than the correlation of the IDQ Imagery Use scale with the PA strategy and recall measures. Hence, it appears that the most reliable predictor of spontaneous imagery use in the PA learning task is the belief that imagery is an effective strategy for forming new associations, rather than self-reported imagery use in everyday life. This finding supports the behavioral specificity principle discussed earlier (Hertzog, Dunlosky, & Robinson 2000).

It was the case (not shown in Table 3) that the IDQ scales correlated with the PEP imagery effectiveness rating ($r = .28$ for IDQ Total, $r = .31$ for IDQ Imagery Use, and $r = .16$ for IDQ Vivid Images). This pattern suggests that self-reported imagery use in

**Table 3.** Correlations of IDQ scales and PEP imagery effectiveness rating with PA learning, PA strategy use, and intellectual abilities

| Variable | IDQ – Total | IDQ – Imagery use | IDQ – Vivid images | PEP – Imagery |
|---|---|---|---|---|
| CES-D | –.01 | –.05 | .07 | –.11 |
| SE | .25* | .23* | .20* | .10 |
| PA PC | .26* | .29* | .17* | .39* |
| PA Imagery | .24* | .27* | .14 | .37* |
| PA Rote | .02 | .01 | .05 | –.17* |
| PA Sentence | –.01 | –.02 | .05 | .07 |
| PA PC\|I | .08 | .09 | .02 | .04 |
| PA PC\|R | .01 | –.01 | .05 | .07 |
| PA PC\|S | .05 | .02 | .07 | .19* |
| Per. Speed | .19* | .18* | .16* | .22* |
| Reasoning | .14 | .16* | .06 | .28* |
| Spatial | .22* | .22* | .18* | .24* |
| Asc. Fluency | .22* | .21* | .16* | .35* |
| Verbal | .20* | .24* | .04 | .33* |

Abbreviations: CES-D Center for Epidemiological Studies – Depression scale; SE – Self-Efficacy scale; PA PC – Paired-associate Learning, Percent Correct Recall; PA Imagery – Paired-associate Learning, Imagery Use; PA Rote – Paired-associate Learning, Rote Repetition Use; PA Sentence – Paired-associate Learning, Sentence Generation Use; PA PC|I – Paired-associate Learning Recall when using Imagery; PA PC|R – Paired-associate Learning Recall when using Rote Repetition; PA PC|S – Paired-associate Learning Recall when using Sentence Generation; Per. Speed – Perceptual Speed composite; Reasoning – Inductive Reasoning composite; Spatial – Spatial Visualization composite; Asc. Fluency – Associational Fluency composite; Verbal – Verbal Comprehension composite.
* $p < .01$

everyday life does predict the knowledge that imagery is an effective strategy for PA learning. To gain additional insight into this phenomenon, we examined individual IDQ item correlations with the PEP imagery effectiveness rating. These correlations ranged from .03 to .30, with the highest correlation associated with IDQ Item 18. Again, this pattern supported the idea of behavioral specificity in self-report. Be that as it may, the PEP strategy effectiveness rating cannot, by itself, account for IDQ-PA learning correlations. Partialling for the PEP imagery effectiveness rating did not eliminate the correlations of the IDQ Imagery Use scale with PA imagery mediator production (partial $r = .17$, $p < .01$) or PA recall (partial $r = .19$, $p < .01$). We return to this issue in a multiple regression analysis reported below.

Third, a general measure of self-efficacy (belief in one's own capacity to achieve desired goals) correlated reliably with the IDQ scales, suggesting that self-efficacy is involved in people claiming to have the ability to use imagery in everyday life. The self-efficacy measure was not reliably associated with the PEP imagery effectiveness rating.

Fourth, a widely-used depression screening measure, the Center for Epidemiological Studies – Depression scale (Radloff 1977), was unrelated to responses on the IDQ or the PEP. This finding suggests that negative affect (or its absence) cannot account for any relations of IDQ scales with strategy use reports or PA learning.

Fifth, both the IDQ and the PEP imagery rating correlated reliably with the intellectual ability composites, with the PEP imagery rating having somewhat higher correlations than the IDQ Imagery Use scale. Note that the pattern of correlations did not support the hypothesis that self-reported imagery use is more highly correlated with spatial ability or perceptual speed than with verbal ability and ideational fluency. This finding is consistent with negative findings in the literature regarding differential relations of self-reported imagery to spatial ability. As noted earlier, the kind of imagery needed for spatial rotation is quite different than the kind of imagery needed to support verbal learning. More important, correlations of self-reported imagery use with spatial ability are not specific to spatial ability, but seem to reflect a general relationship between high intellectual ability and imagery use. In general, people of high fluid and crystallized ability report higher use of imagery in everyday life, and rate imagery as an effective strategy for PA learning. In fact, Hertzog, Dunlosky, and Robinson (2005) found that crystallized intelligence, as measured by vocabulary and world knowledge, was the strongest predictor of effective strategy use and recall in the PA task, contrary to any expectation that image-based abilities would best predict recall performance. Associational fluency ability, which is highly related to crystallized intelligence, concerns the ability to make rapid and frequent use of semantic concepts (e.g., identify multiple conceptual associates to specific words). Hertzog, Dunlosky, and Robinson (2005) conjectured that verbal ability and fluency are important for efficient identification of possible mediational links between normatively unrelated words. This link to knowledge may be critical for identifying possible interactive imagery representations, after which imagery mechanisms are deployed to visualize the representation.

## Prediction of PA imagery production

*Dunlosky & Hertzog (1998) Sample*. We already know that intellectual abilities, such as processing speed and vocabulary, are predictive of individual differences in many cognitive tasks. A question arises as to whether IDQ imagery use will still be related to imagery production during PA learning (Table 2) when measures of intellectual abilities are statistically controlled. To address these issues, we ran a regression analysis on the data, focusing on imagery use and incorporating the IDQ Imagery Use scale as well as standard measures of intellectual abilities. In this regression analyses, we included IDQ Imagery Use, a perceptual speed composite score, vocabulary, age group (younger = 0, older = 1), and Instructional group (1 = imagery instructions, 2 = no imagery instructions) as predictors of imagery strategy production during PA learning

(for details on these measures and a path model for strategy production for all effective strategies in the aggregate, see Dunlosky & Hertzog 1998).

The regression model revealed that only two variables – instructional group and IDQ Imagery Use – were reliable predictors of imagery strategy production. The model produced an $R^2$ of .16, $F$ (5, 134) = 5.15, $p < .001$, with corresponding standardized regression weights of .40 and –.23 for instructional group and IDQ Imagery Use, respectively. Thus, for this sample, IDQ Imagery Use predicts imagery production during PA learning independently of verbal ability and processing speed.

When we analyzed the data separately by instructional group, the regression analysis revealed no significant effect for IDQ Imagery Use on imagery mediator production in the self-chosen condition ($\beta = .18$, $p > .10$) but there was a reliable effect for individuals instructed to use imagery ($\beta = .29$, $p < .05$). This result parallels the correlations reported in Table 2, but suggests the lack of relationship may be due in part to low statistical power.

We also conducted a regression analysis using recall, conditional on reporting imagery mediator use, as the dependent variable. In this regression analysis, we included IDQ Imagery Use, reported imagery production, perceptual speed, vocabulary, age group, and instructional group as predictors. This analysis resulted in an $R^2$ of .47, and yielded a reliable effect of age ($\beta = –.59$) and IDQ Imagery Use ($\beta = .14$, $t = 1.97$, $p = .05$). However, given the evidence that imagery production might imply different things in instructed versus self-chosen conditions, we analyzed the result with a moderated regression, adding the product variable of imagery product X Instruction group. Adding the interaction term increased $R^2$ to .49, $F$ (1, 131) = 4.88, $p < .05$. The regression coefficient for imagery production was reliable when analyzed separately for the self-chosen group ($\beta = .20$, $p < .05$) but not for the instructed group ($\beta = –.09$, $p > .25$). With the interaction term in the model, the effect of IDQ Imagery Use on recall when using imagery was still reliable, $\beta = .15$ $p < .05$.

Older adults received far less benefit from using imagery as a strategy than did younger adults. Dunlosky, Hertzog, & Powell-Moman (2005) have reported this effect in an independent sample, and more important, they demonstrated that this age deficit is is related to older adults' difficulties in retrieving the image mediators during the cued recall test. Thus, the effect may reflect retrieval difficulties rather than the production of ineffective images (see Dunlosky et al. 2005, for more details and discussion of this point).

IDQ Imagery Use was also a reliable predictor of recall when using imagery, even controlling on age, vocabulary, and perceptual speed. The effect size was quite modest, but the results showed that the correlations in Table 2 cannot be attributed to the influence of age or abilities.

Finally, although it is not obvious from the correlations in Table 2, there was a differential relationship of level of imagery production to the conditional probability of recall, given imagery production in the self-chosen condition. Controlling for age and abilities, people who produced more imagery recalled more items studied with im-

**Table 4.** Multiple regression predicting imagery strategy use in the PA learning task from the IDQ imagery use scale, spatial ability, verbal ability, and the PEP imagery effectiveness rating

| *Model without PEP Imagery Rating* | | |
|---|---|---|
| **Predictor** | **β** | **t** |
| IDQ Imagery Use | .14 | 2.71* |
| Spatial | .25 | 4.53* |
| Verbal | .33 | 5.79* |
| *Model with PEP Imagery Rating* | | |
| **Predictor** | **β** | **t** |
| IDQ Imagery Use | .09 | 1.69 |
| Spatial | .23 | 4.13* |
| Verbal | .28 | 5.01* |
| PEP | .22 | 4.03* |

Abbreviations: PEP – PEP Imagery effectiveness rating; Spatial – Spatial Visualization composite; Verbal – Verbal Comprehension composite.
* $p < .01$

agery afterward. Statistical control on age, which produced sizeable effects on imagery recall, enabled this relationship to emerge.

*Hertzog, Dunlosky, & Robinson (2005) Sample.* We have already reported that fluid intelligence and crystallized intelligence predict effective mediator use in this sample (Hertzog, Dunlosky, & Robinson 2005). To focus on imagery use, we ran new multiple regression analyses. In the first regression analysis, we included IDQ Imagery Use, Spatial composite, and the Verbal composite as predictors of PA interactive imagery strategy production. The regression model (based on 277 persons with complete data on these variables) showed that all three variables were reliable predictors of imagery strategy use in the learning task (see Table 4). The model produced an $R^2$ of .335, $F$ (3, 273) = 38.20, $p < .001$. Adding the PEP Imagery effectiveness rating resulted in a reliable increment to $R^2$ ($R^2$ change = .039, $F$ (1, 272) = 11.04, $p < .01$). When the PEP rating in the model, the IDQ Imagery Use scale was no longer a reliable predictor of PA imagery strategy use. Hence, the IDQ Imagery Use scale predicts imagery production independent of intellectual abilities, but not independently from the set of PEP strategy rating and abilities. See Hertzog, Dunlosky, and Robinson (2005) for further discussion and analysis of the relation of abilities to strategic behavior in episodic memory tasks.

## Conclusions

Taken together, the results from our studies are informative about self-reported imagery use in PA learning and in everyday life. Self-reports of functional use of imagery,

as in the IDQ, correlate more highly with imagery use for PA learning than the VVIQ, as would be expected from previous research. However, the pattern of reliable IDQ correlations varied across spontaneous, self-chosen, and instructed strategy conditions. Moreover, the correlations, when observed, were small in magnitude. Finally, the pattern of correlations with intellectual abilities did not support the argument that reported imagery use is a cognitive style dimension that is differentially associated with high spatial abilities (J. T. E. Richardson 1999). Instead, individuals with high fluid and crystallized intelligence are more likely to use imagery for PA learning and to report higher imagery use in everyday life.

Perhaps most telling, we found that a measure of strategy knowledge, an effectiveness rating for imagery as a strategy for PA learning, has a more robust relationship to imagery use for PA learning than the IDQ. These findings are broadly consistent with those reported in other studies (e.g., Dean & Morris 2003). They suggest that use of self-report questionnaires like the IDQ, while indicating some relationship between reported imagery use in everyday life and imagery use in cognitive tasks, is not a particularly fruitful direction for future research on individual differences in strategies and cognition (see Rabbitt et al. 1995, for similar concerns about self-reported memory questionnaires).

Certainly, if an investigator's goal is to predict future strategic behavior in an associative learning task, then the IDQ has little to recommend it. Instead, more specific measures of strategic behavior are more likely to predict future strategic behavior than questionnaires like the IDQ. Indeed, other research we have conducted on the acquisition of strategy knowledge through task experience supports this inference (Dunlosky & Hertzog 2000; Hertzog, Price et al. 2005). We find that individuals instructed to use either interactive imagery or rote repetition show a substantial shift in PA strategy effectiveness ratings, downgrading repetition ratings, and increasing imagery ratings. Measurement of beliefs at the level of specific behaviors yields the best predictive validity and affords an opportunity to study dynamic changes as a function of experience.

Nevertheless, the pattern of findings regarding IDQ correlations with imagery use and PA recall for the different experiments and conditions was fascinating. For spontaneous strategy use, the IDQ correlated reliably with imagery use but not with recall, conditional on having used imagery to encode the association. For instructed strategy use, the IDQ correlated reliably with recall when having used imagery, and this effect was not attributable to age or ability. Such findings hint at the hypothesis that adaptivity in spontaneous and self-chosen conditions was operating, such that people chose strategies best suited for their own processing of a given item (J. T. E. Richardson 1999). Within-individual switching of strategies across items to match item affordance with strategy could explain the elimination of correlations of reported imagery use with the conditional probability of recall, given strategy use. On the other hand, compliance with imagery strategy instructions increased imagery strategy production (even though compliance was far from perfect). This shift toward using imagery when instructed may be due to suppression of adaptive strategy choice. When strongly encouraged to use imagery, even when it is difficult to do so, individuals who routinely

use imagery in everyday life may achieve greater benefit from using the strategy than those who do not. We do not have enough data to draw firm conclusions about this phenomenon, either in terms of its replicability or our hypothetical interpretation of it. Given that adaptivity in strategy use is a hallmark of metacognitive theories about self-regulated learning and cognition (e.g., Metcalfe 2002; Schunn & Reder 2001), such findings merit further investigation focusing on direct measurement of adaptivity in this domain in combination with self-reported measures of strategy use in the specific task and in everyday life. Such findings could help build a nomological net validating both the concept of strategic adaptivity and methods of measuring it.

## References


Anderson, J. R. (1978). Arguments concerning mental representations for mental imagery. *Psychological Review*, *85*, 249–277.

Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences*, *22*, 577–660.

Bower, G. H. (1970). Imagery as a relational organizer in associative learning. *Journal of Verbal Learning and Verbal Behavior*, *9*, 529–533.

Brewer, W. F., & Pani, J. R. (1996). Reports of mental imagery in retrieval from long-term memory. *Consciousness and Cognition*, *5*, 265–287.

Burton, L. J. (2003). Examining the relation between visual imagery and spatial ability tests. *International Journal of Testing*, *3*, 277–290.

Burton, L. J., & Fogarty, G. J. (2003). The factor structure of visual imagery and spatial abilities. *Intelligence*, *31*, 289–318.

Cavanaugh, J. C., Feldman, J., & Hertzog, C. (1998). Memory beliefs as social cognition: A reconceptualization of what memory questionnaires assess. *Review of General Psychology*, *2*, 48–65.

Cronbach, L. J., & Meehl, P. E. (1955). Construct validity in psychological tests. *Psychological Bulletin, 52,* 281–302.

Dean, G. M., and Morris, P. E. (2003). The relationship between self-reports of imagery and spatial ability. *British Journal of Psychology*, *94*, 245–273.

d'Esposito, M., Detre, J. A., Aguirre, G. K., Stallcup, M., Alsop, D. C., Tippet, L. J., & Farah, M. J. (1997). A functional MRI study of mental image generation. *Neuropsychologia*, *35*, 725–730.

Dirkx, E. & Craik, F. I. M. (1992). Age-related differences in memory as a function of imagery processing. *Psychology and Aging*, *7*, 352–358.

Dror, I. E., & Kosslyn, S. M. (1994). Mental imagery and aging. *Psychology and Aging, 9,* 90–102.

Dunlosky, J., & Hertzog, C. (1998). Aging and deficits in associative memory: What is the role of strategy use? *Psychology and Aging*, *13*, 597–607.

Dunlosky, J., & Hertzog, C. (2000). Updating knowledge about encoding strategies: A componential analysis of learning about strategy effectiveness from task experience. *Psychology and Aging, 15,* 462–474.

Dunlosky, J., & Hertzog, C. (2001). Measuring strategy production during associative learning: The relative utility of concurrent versus retrospective reports. *Memory & Cognition*, *29*, 247–253.

Dunlosky, J., Hertzog, C., & Powell-Moman, A. (2005). The contribution of five mediator-based deficiencies to age-related differences in associative learning. *Developmental Psychology*, *41*, 389–400.

Eagle, M. N. (1967). The effect of learning strategies upon free recall. *American Journal of Psychology*, *80*, 421–425.

Ericsson, K. A., & Simon, H. A. (1993). *Protocol analysis: Verbal reports as data*. Cambridge, MA: M.I.T. Press.

Farah, M. J., Hammond, K. M., Levine, D. N., & Calvanio, R. (1988). Visual and spatial mental imagery: Dissociable systems of representation. *Cognitive Psychology*, *20*, 439–462.

Finke, R. A. (1989). *Principles of mental imagery*. Cambridge, MA: M.I.T. Press.

Ganis, G., Thompson, W. L., & Kosslyn, S. M. (2004). Neuroimaging of mental imagery: An introduction. *European Journal of Cognitive Psychology*, *16*, 625–630.

Harshman, R. A., & Paivio, A. (1987). "Paradoxical" sex differences in self-reported imagery. *Canadian Journal of Psychology*, *41*, 287–302.

Hertzog, C. (1989). The influence of cognitive slowing on age differences in intelligence. *Developmental Psychology*, *25*, 636–651.

Hertzog, C., & Dunlosky, J. (2005). Aging, metacognition, and cognitive control. In B. H. Ross (Ed.), *Psychology of Learning and Motivation* (pp. 215–251). San Diego: CA: Academic Press.

Hertzog, C., Dunlosky, J., & Robinson, A. E. (2005). *Intellectual abilities and metacognitive beliefs influence spontaneous use of effective encoding strategies*. Unpublished manuscript.

Hertzog, C., McGuire, C. L., & Lineweaver, T. T. (1998). Aging, attributions, perceived control, and strategy use in a free recall task. *Aging, Neuropsychology, and Cognition*, *5*, 85–106.

Hertzog, C., Park, D. C., Morrell, R. W., & Martin, M. (2000). Ask and ye shall receive: Behavioral specificity in the accuracy of subjective memory complaints. *Applied Cognitive Psychology*, *14*, 257–275.

Hertzog, C., Price, J., Burpee, A., Frentzel, W. J., Feldstein, S., & Dunlosky, J. (2005). *How is knowledge generated about memory encoding strategy effectiveness?* Unpublished manuscript.

Lachman, M. E., Bandura, M., Weaver, S. L., & Elliott, E. (1995). Assessing memory control beliefs: The Memory Controllability Inventory. *Aging and Cognition*, *2*, 67–84.

Johnson, S. H., & Rybash, J. M. (1993). A cognitive neuroscience perspective on age-related slowing: Developmental changes in the functional architecture. In J. R. Cerella, J. M. Rybash, W. J. Hoyer, & M. L. Commons (Eds.), *Adult information processing: Limits on loss* (pp. 143–173). San Diego, CA: Academic Press.

Just, M. A., & Carpenter, P. A. (1985). Cognitive coordinate systems: Accounts of mental rotation and individual differences in spatial ability. *Psychological Review*, *92*, 137–171.

Kan, I. P., Barsalou, L. W., Solomon, K. O., Minor, J. K., & Thompson-Schill, S. L. (2003). Role of mental imagery in a property verification task: fMRI evidence for perceptual representations of conceptual knowledge. *Cognitive Neuropsychology*, *20*, 525–540.

Kosslyn, S. M. *Image and mind*. (1980). Cambridge, MA: Harvard University Press.

McDougall, S., & Velmans, M. (1993). Encoding strategy dynamics: When relationships between words determine strategy use. *British Journal of Psychology*, *84*, 227–248.

McKelvie, S. J. (1995). The VVIQ as a psychometric test of individual differences in visual imagery vividness: A critical quantitative review and a plea for direction. *Journal of Mental Imagery*, *3 & 4*, 1–106.

McNamara, D. S., & Scott, J. L. (2001). Working memory capacity and strategy use. *Memory and Cognition, 29*, 10–17.

Marks, D. F. (1973). Visual imagery differences in the recall of pictures. *British Journal of Psychology*, *64*, 17–24.

Marschark, M., & Hunt, R. R. (1989). A reexamination of the role of imagery in learning and memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *15*, 710–720.

Metcalfe, J. (2002). Is study time allocated selectively to a region of proximal learning? *Journal of Experimental Psychology: General*, *131*, 530–542.

Naveh-Benjamin, M. (2000). Adult age differences in memory performance: Tests of an associative deficit hypothesis. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *26*, 1170–1187.

Nelson, T. O., & Narens, L. (1990). Metamemory: A theoretical framework and new findings. In G. H. Bower (Ed.), *The psychology of learning and motivation* (Vol. 26, pp. 125–173). New York, NY: Academic Press.

Paivio, A. (1971). *Imagery and verbal processes*. NY, NY: Holt, Rinehart, & Winston.

Paivio, A. (1986). *Mental representations: A dual coding approach*. NY, NY: Oxford University Press.

Paivio, A., & Harshman, R. A. (1983). Factor analysis of a questionnaire on imagery and verbal habits and skills. *Canadian Journal of Psychology*, *37*, 461–483.

Paivio, A., & Yuille, J. C. (1967). Mediation instructions and word attributes in paired-associate learning. *Psychonomic Science*, *8*, 65–66.

Palladino, P., & De Beni, R. (2003). When mental images are very detailed: Image generation and memory performance as a function of age. *Acta Psychologica*, *113*, 297–314.

Poltrock, S. E., & Agnoli, E. (1986). Are spatial visualization ability and visual imagery ability equivalent? In R. J. Sternberg (Ed.), *Advances in the psychology of human intelligence* (Vol. 3). Hillsdale, NJ: Erlbaum.

Poltrock, S. E., & Brown, P. (1984). Individual differences in visual imagery and spatial ability. *Intelligence*, *8*, 93–138.

Rabbitt, P., Maylor, E., McInnes, L., Bent, N., & Moore, B. (1995). What goods can self–assessment questionnaires deliver for cognitive gerontology? *Applied Cognitive Psychology, 9,* S127–S152.

Radloff, L. S. (1977). The CES-D scale: A self-report depression scale for research in the general population. *Applied Psychological Measurement*, *1*, 385–401.

Richardson, A. (1994). *Individual differences in imaging: Their measurement, origins, and consequences*. Amityville, NY: Baywood.

Richardson, J. T. E. (1998). The availability and effectiveness of reported mediators in associative learning: A historical review and an experimental investigation. *Psychonomic Bulletin & Review, 5*, 597–614.

Richardson, J. T. E. (1999). *Imagery*. Hove, UK: Psychology Press.

Richardson, J. T. E. (2003). Dual coding versus relational processing in memory for concrete and abstract words. *European Journal of Cognitive Psychology*, *15*, 481–509.

Rowe, E. J., & Schnore, M. M. (1971). Item concreteness and reported strategies in paired-associate learning as a function of age. *Journal of Gerontology, 26*, 470–475.

Salthouse, T. A. (1992). Reasoning and spatial abilities. In F. I. M. Craik & T. A. Salthouse (Eds.), *The handbook of aging and cognition* (pp. 167–211). Hillsdale, NJ: Lawrence Erlbaum Associates.

Schneider, W., & Pressley, M. (1997). *Memory development between two and twenty* (2nd ed). Mahwah, NJ: Erlbaum.

Schunn, C. D., & Reder, L. M. (2001). Another source of individual differences: Strategy adaptivity to changing rates of success. *Journal of Experimental Psychology: General, 130,* 59–76.

Shepard & Metzler 1971 Voyer, D., Voyer, S., & Bryden, M. P. (1995). Magnitude of sex differences in spatial abilities: A meta-analysis and consideration of critical variables. *Psychological Bulletin*, *117*, 250–270.

Voyer, D., Voyer, S., & Bryden, N. P. (1995). Magnitude of sex differences in spatial abilities: A meta-analysis and consideration of critical variables. *Psychological Bulletin*, *117*, 250–270.

Yates, F. A. (1997). *The art of memory*. Pimlico: London, England.

Yuille, J. C. (1973). A detailed examination of mediation in PA learning. *Memory & Cognition, 1,* 333–342.

SECTION IV

# Neuropsychological aspects of space representation

CHAPTER 4.1

# Spatial navigation

## Cognitive and neuropsychological aspects

Cecilia Guariglia and Luigi Pizzamiglio

### Introduction

Environmental spatial navigation is an ability shared by almost all animal species, from the lowest evolutionary level to the primates. In humans, navigation is sub-served by a complex system which includes processes partly common to lower order species as well as higher order processes such as language and graphical representation.

In recent years, considerable development has taken place in the study of navigational processing in humans. This field of investigation aims to define the mechanisms underlying the encoding, representation and storage of environmental information. The inability to navigate in familiar and novel environments (called topographical disorientation) has also received increasing attention, and several cases have been described to identify the relationship or the independence of topographical deficits and other neuropsychological disorders.

In the present chapter, we discuss some recent cognitive models of human environmental navigation and some neuropsychological data regarding selective impairments in brain damaged patients to support the hypothesis that multiple navigational systems exist in humans providing evidence for their functional and anatomical independence.

### Spatial navigation: Cognitive and neuropsychological aspects

Most cognitive studies on humans are based on navigation models developed in experimental and ecological studies on animals. It is well known that different species use different navigational strategies to process different types of information. A great contribution has been made by studies on rodents, particularly the discovery of specific cells that code different aspects of environmental information. These include the place cells in the hippocampus and in the superficial layers of the enthorinal cortex, which are active when the animal is in a specific location in the environment (O'Keefe

& Nadel 1978), and head direction cells in the thalamus and limbic cortex, which encode the direction of the head with respect to extrinsic spatial coordinates and which are independent from the animal's location in the environment (Taube et al. 1990; Taube 1995; Knierim et al. 2000). These cells contribute in different ways to develop the cognitive maps navigation is based on (Redish & Touretzky 1997).

Another important conceptualization concerns the way animals and humans encode spatial information. A first code (ideothetic) relays endogenous information such as vestibular and proprioceptive information derived from self motion in the environment. The second code (allothetic) is based on external inputs such as visual, acoustic, tactile, olfactive ones, which carry information relative to the position of near and distal landmarks.

Redish and Touresky (1997) proposed that navigation depends on the interaction of four different spatial representations: local view, path integrator, place code and head direction. The local view subsystem is essentially based on visual information and represents the animal's relationship with visible landmarks. The path integrator processes vestibular and proprioceptive inputs as well as the efferent copies of motor commands; it allows tracking the path from a starting location to a target point (i.e., the nest) without using any landmarks or environmental cues (Mc Naughton et al. 1996). The place code (processed by the hippocampal place cells) accurately represents the subject's location in a given environment (Wilson & McNaughton 1993). Finally, the head direction subsystem provides the representation of the animal's direction of motion, used like an internal compass to orient cognitive maps in the hippocampus (Knierim et al. 2000).

These processes are differently used in different types of navigation; each one can be defined by the relative importance of the idiothetic and allothetic information processing, the timing of decay in long term memory and the usefulness of the cognitive map.

At least three different systems are recognized based on the above described processes (Wang & Spelke 2002):

*Path integration.* This system continuously updates the animal's relation to one or more significant places; it is essentially based on idiothetic information. It also permits very complicated navigation in the environment. However, the spatial representation derived from path integration (Collett et al. 1998) is subject to relatively rapid decay from memory (Ziegler & Wehner 1997).

*View dependent place recognition*. This system is based on the recognition of environmental visual cues and their use in guiding navigation; it based on the processing of exogenous cues and has been described as a preferential system in insects such as bees and ants (Collett & Collett 2000; Collett et al. 1999); it is also used by rats (Sutherland et al. 1987).

*Reorientation*. This system restores the relationship between the animal and its environment when path integration is fully disrupted (Wang & Spelke 2002). It is primarily

based on geometric information about the shape of the environment, but may also process other non-geometric cues (Gouteaux et al. 2002).

Developmental studies show that humans can rely on multiple strategies. They also suggest that strategies may develop following different maturational rates. Very young children (18 months old) are able to process geometric information in order to reorient in a rectangular room, but they are unable to use visual cues as landmarks (Hermer & Spelke 1994; Hermer & Spelke 1996). Despite the relatively early age of acquisition of the ability to make subtle discriminations between visual properties of objects (colour, shape, texture, etc.), the ability to use even the easiest visual cues to reorient is not fully established until 3–4 (Gouteaux & Spelke 2001) or until 6 years of age (Hermer-Vasquez et al. 2001). Instead, Learmonth, Nadel and Newcombe (2002) state that in younger children the use of colour as a landmark depends on the dimensions of the environment. Five-year-old children tend to use only geometric features (i.e., the rectangular shape of the experimental room) to reorient when they are placed in a small experimental room (4x6ft), but successfully use colour in larger rooms (8x12ft). Older children (6 years of age) are able to use visual cues also to reorient in a small space (the 4x6 ft room). Although these data indicate differences in modular development of navigational skills (Hermer & Spelke 1994; Learmonth et al. 2001, 2002), it appears that in humans navigational skills are not fully acquired for many years.

Another still unresolved question is whether multiple systems are always available for navigation in humans and whether they can be activated depending upon the opportunity and economy of the navigation goal, or whether there is a preferential strategy, which can be possibly abandoned only when it is unsuccessful. Individual differences in preferential navigation strategies have been linked to sex (see for example Gron et al. 2000; MacFadden, Elias & Saucier 2003; Saucier, Bowman, & Elias 2003) or to differences in cognitive style (Iaria et al. 2003).

Neuropsychological studies on the navigational disorders have been conducted to verify the hypothesis of multiple navigational processes and to better understand their relationships and interactions. Particular interest has been shown in topographical disorientation, a disorder that severely impairs patients' ability to move into familiar environments and to learn to navigate in novel environments (Barrash 1998).

Since the seminal report by Paterson and Zangwill (1945), it is clear that being lost in one's home or town is not due to a single defect. In their accurate clinical study, Paterson and Zangwill described how the inability to follow a familiar route depended on two disturbances: the inability to recognize familiar landmarks, called topographical agnosia, and the inability to recall the direction to be taken from a given landmark or the route from one location to another, called topographical amnesia. Several single cases were studied to investigate the dissociation between these two distinct defects; however, as Farrel (1996) pointed out, the presence of agnosia in the absence of amnesia has been established, but there is still no evidence of isolated amnesia.

Topographical disorientation is quite diffuse in more pervasive deficits such as dementia, confusional states and global amnesia, but is not very frequent as an isolated

disorder. Consequently, many single case studies have been carried out to investigate the dissociation between topographical disorders and other possible neuropsychological impairments of visuo-spatial cognition that may affect the ability to discriminate or memorize topographical data. In this regard, Incisa della Rocchetta et al. (1996) submitted their disoriented patient to a set of tests to assess her ability to discriminate and memorize objects, faces, landmarks and landscapes. The results demonstrated that the inability to process environmental features is dissociated from those processing other types of visuo-spatial stimuli.

The independence of topographical agnosia from other forms of visual agnosia (especially prosopoagnosia, which is often co-present) was recently demonstrated by Takahashi and Kawamura (2002). The lesions of six patients, two with only topographical agnosia, two with only prosopoagnosia and two with a combination of topographical agnosia and prosopoagnosia, were analyzed. Results showed the involvement of the right posterior part of the parahippocampal gyrus in the inability to memorize novel information about buildings and landscapes. However, the anterior half of the lingual gyrus and the adjacent fusiform gyrus had to be involved in order for the ability to identify familiar buildings and landscapes to be affected. Instead, a lesion of the posterior half of the lingual and fusiform gyri is responsible for prosopagnosia, which frequently co-occurs with landmark agnosia.

In a recent review, Aguirre and D'Esposito (1999) proposed a detailed taxonomy for topographical orientation disorders. In accordance with anatomical and clinical data previously reported in the literature, the authors identified four different disorientation impairments. Specifically, patients with *heading disorientation* recognise landmarks available in the environment but are unable to recover directional information from them; this deficit is suggested to arise from lesions of the retrosplenial cortex (posterior cingulate) (Takahashi et al. 1997). *Landmark agnosia* involves more selective damage, i.e., the inability to recognise salient environmental landmarks; lesions to the medial occipito-temporal cortex (including the fusiform, lingual and parahippocampal gyri) are associated with this specific deficit (Pallis 1955). *Anterograde disorientation* is defined as the inability to learn pathways in novel environments; this deficit is associated with lesions to the parahippocampal cortex (Habib & Sirigu 1987). Finally, patients affected by *egocentric disorientation* are unable to use egocentric co-ordinates to localise environmental landmarks; namely, although they are able to recognise a landmark they cannot code its position relative to themselves (Stark, Coslett, & Saffran 1996); this topographical disorder results from lesions to the posterior parietal cortex. Recent cases demonstrate the co-existence of more than one deficit; for example, in the patient described by Hirayama et al. (2003) disorientation was attributed to the co-presence of landmark agnosia and heading disorientation.

Iaria et al. (2005) describe a patient with a congenital disease in which all of the impairment categories identified by Aguirre and D'Esposito seem to co-exist. The patient, MGC, suffered a foetal cerebral malformation involving middle occipito-temporal cortices. Despite this massive malformation, her development was quite normal and she successfully obtained a high school diploma. However, she never learned to navigate in

her environment. A detailed neuropsychological assessment showed normal IQ, normal verbal abilities, a slight long term memory impairment for visuo-spatial material and a mental rotation impairment. However, her visuo-spatial impairments were not sufficient to explain her severe inability to navigate. An assessment of MGC's navigational skills in ecological environments demonstrated that she was unable to select salient landmarks for navigation, she was occasionally able to recognize them, but did not detect perspective differences in recognized landmarks (i.e., she was unable to recognize that she had reached a landmark if she arrived from a different route). Furthermore, when a landmark was recognized or the experimenter suggested its identity, she was unable to use this information to orient her navigation. She was also unable to replicate short paths shown by the experimenter either when she was asked to go back to the starting point or when she was taken back to the starting point by the same or a different path. Despite her success in drawing the shortest path between two points on a map, she was completely unable to follow the path she had drawn using the map, even if she was allowed to rotate it. Thus, her impairment seems to be due to landmark agnosia and to heading disorientation, as well as to egocentric and anterograde disorientation. In an experimental environment using a human version of the Morris water maze, the basic navigational skills identified in Wang and Spelke's (2002) model were tested. MGC was severely impaired in path integration, reorientation and view-dependent navigation. At variance with almost all other cases of topographical disorientation described in the literature, MGC does not have an acquired deficit, but rather a developmental deficit in which a cortical malformation completely prevented the acquisition of navigational skills without affecting the acquisition of most, if not all, cognitive functions. Very interestingly, none of the cognitive navigational processes that have been identified in the human developmental literature (Wang & Spelke 2002) or have been described in selective topographical disorders seem to be spared in MGC.

Navigational impairments are often present in another neuropsychological syndrome, i.e., unilateral neglect. Patients with unilateral neglect are often described as unable to find their way in the hospital due to difficulty in identifying left-sided landmarks and to omission of left turnings (De Renzi 1982). A consistent number of neglect patients are also affected by a specific impairment in mentally representing the left side of familiar (Bisiach & Luzzatti 1978) as well as novel (Pizzamiglio et al. 1996) environments. Recent reports suggest that representational neglect has a specific relationship with navigation systems. Ortigue et al. (2003) described selective representational neglect for "far" imagined space. The patient, who had a right temporo-occipital junction lesion, was unable to describe the left side of Place Neuve in Geneva from memory or the left side of an imaged map of France. However, the patient made a detailed description of the left side of the inside of her car from memory as well as the left side of an array of objects on the table she had explored several minutes before. The authors interpreted these results as a further demonstration that perceptual and representational neglect are supported by independent cortical systems and that inferior temporal areas might be important for the mental representation of far space when a viewer-centred reference is imposed. Alternatively, in this case it

can be hypothesized that representational neglect affects a specific representational system devoted to constructing cognitive maps of the environmental space; these cognitive maps, which have an egocentric frame of reference, should be used to direct the subject's navigation.

Rode et al. (2004) also reported a patient who was unable to represent spatial information completely. The patient was unable to report the left-sided cities of France in a "spatialized" condition (he had to imagine the map of France) but was perfectly able to name them in a "no-spatialized" condition. Also in this case, the observation can be interpreted as demonstration of damage to a system that represents space in egocentric coordinates for navigation.

The role of the posterior parietal cortex (PPC), and more generally of retrosplenial areas, in egocentric representation of navigational space has already been discussed both in functional imaging studies and in lesioned animal studies (see Maguire 2001). However, the specific implications of this area in navigation, as well as the hemispheric lateralization of navigational processes in PPC, are still unclear.

To better understand the role of PPC in navigation and more specifically in updating egocentric spatial relationships, Farrell and Robertson (2000) tested patients with right and left dorsal parietal lesions and with right anterior parietal lesions. Patients were blindfolded and placed in the centre of a previously seen circular array of targets. In one condition, after being rotated they were asked to update their positions and to point to a named target from their new orientation. In another condition, they were rotated without vision and were asked to ignore the movement and to point to the named target as if they were still in their original position. Patients with right dorsal parietal lesions systematically underestimated the angle of rotation. They were not only impaired with respect to normal controls, but were more impaired than right anterior parietal and left and right parietal patients. A deficit in encoding angles of rotation should affect the ability to process idiothetic information and navigational processes, such as path integration, based on this information.

As a consequence, we should expect that patients with lesions of posterior areas, including the parietal cortex, will show some degree of impairment in path integration. In a study by Bisiach and co-workers (1997), a group of seven right brain damaged patients affected by unilateral neglect were tested using a classical path integration task. Since unilateral neglect is often due to a lesion involving the parietal cortex (see Vallar et al. 2003, for a recent review), blindfolded neglect patients should be impaired in indicating the starting point after two or three 90° leftward or rightward rotations. Instead, the performances of the seven patients did not differ from those of age, sex and education matched controls.

In this experiment, the patients were seated on a wheelchair and blindfolded. Thus, they had no visual or proprioceptive information from walking and they could rely only on vestibular input. The cortical and subcortical vestibular system, often unaffected in neglect patients, may have been responsible for their good performance on this task.

Instead, Pizzamiglio and co-workers (1998) used a reorientation task similar to the one used by Hermer and Spelke (1994) with children and found a specific impairment in right brain damaged patients with unilateral neglect. In a rectangular room without any environmental cues, a target object was shown in a corner; then the subjects were blindfolded, disoriented and the target was taken away; after the blindfold was removed, the subjects had to point to the target location (TL).

In this uniform environment, the TL corner and the diagonally opposed corner were indistinguishable. Normal controls and brain damaged patients without neglect pointed with equal frequency to the correct TL or to its homologue when the blindfold was removed; neglect patients performed the task in a completely random way, that is, they pointed to all four corners of the room. These results suggest the complete inability of neglect patients to use geometric information from the environment to guide their spatial exploration.

In a second condition, a red panel covered one wall of the room. The presence of a landmark facilitated the responses of controls and non-neglect brain damaged patients, who identified the TL at ceiling. The neglect patients' performances improved, but they still made a significant number of errors. The latter group was, therefore, impaired in processing geometric information as well as in integrating visual landmarks with the shape of the environment to reorient in this condition.

However, the deficit in processing geometric information was observed in a condition in which only visual inputs were available to construct the map of the environment, since the subjects never actively explored the environment by moving in it. In fact, the subjects performed the test while seated in a wheelchair and never actively moved in the environment.

It is possible that their impairment was basically due to a deficit in processing visual information and not to a specific deficit in navigation. If this were the case, consenting the neglect patients to actively move in the experimental room and therefore to process non-visual information (i.e. motor copying, vestibular and proprioceptive inputs) would have allowed them to process the configuration of the environment and to correctly identify the TL. Actually, Pizzamiglio and co-workers (2003) showed that in the absence of visual cues neglect patients were still able to process idiothetic information to construct a representation of space. The patients were passively displaced along a linear route and they replicated the same displacement in the same or in a different spatial direction without making more errors than the controls. This observation suggests that path integration is intact in neglect. Instead, in the same study the neglect group was unable to integrate idiothetic and visual information, suggesting a specific deficit in integrating visual and non-visual information for navigation.

In a successive study, a human analogue of the Morris water maze was developed to test path integration and reorientation in neglect (Guariglia et al. 2005a). In a rectangular room (5×6mt) the walls were completely covered by homogeneous grey curtains to eliminate all environmental cues; a photocell placed in the ceiling was directed toward a target location (TL) on the floor so that whenever a subject passed through the TL an acoustic signal was delivered. Subjects were brought into the room while blind-

folded and were placed in the centre the curtain covering the door was closed and the blindfold was removed. The subjects' task was to explore the room in order to find the TL. Soon after, they were required to memorize the TL; then they were blindfolded, disoriented and again placed in the centre of the room facing the same or a different wall. The blindfold was removed and the subjects had to reach the TL in the shortest and quickest way possible. After six trials, the blindfolded subjects were taken out of the experimental room and then reintroduced; then the blindfold was removed and they had to reach the TL again.

Three manipulations were introduced:

first, the subjects were placed in the centre of the room, facing the same wall as in the exploratory trial;
second, the subjects were placed in the centre, but facing a different wall;
third, the subjects were required to replicate the same task starting from the same position as in the exploration, but after a 30' delay.

Although in the first condition the task could be accomplished by relying on different processes, in the other conditions just one process could be successfully used. In fact, in the first condition the participants could rely on both path integration and a mental representation of the environment, but in the second condition, due to the change in the starting position, they could no longer use path integration and they had to reorient themselves in the environment using a mental map or the geometric module. In the third condition, the subjects had to organize their navigation based on a stored map of the environment because path integration was considered fully disrupted after this delay.

Five different groups of subjects took part to the experiment: control subjects with no history of psychiatric or neurological disease; right and left brain damaged patients without neglect; right brain damaged patients affected by perceptual neglect; right brain damaged patients affected by representational neglect. In the five groups of subjects, no differences were detected in path integration confirming that unilateral neglect does not affect the ability to process idiothetic information. Instead, re-orientation was severely damaged in representational neglect patients but not in perceptual one. This suggests that impairment in the representation of the contralesional side of space affects the ability to construct cognitive maps based on the geometric shape of the environment. This suggestion was confirmed by the fact that representational neglect patients (but not perceptual ones) were impaired in performing the delayed reaching of TL. In other words, the inability of representational neglect patients to construct a cognitive map of the experimental environment prevents them from storing the target position in long term memory.

The previous experiment showed that path integration is available in neglect patients but that they fail to reorient themselves for representational neglect. The next question is whether perceptual and representational neglect patients can integrate the relative position of various elements placed in the environment, that is, whether they can guide their navigation independently of the two above-mentioned processes.

In a very recent study (Guariglia et al. 2005b), this issue was studied in a modified version of the human analogue of the Morris water maze. Two distinct elements (a lamp and clothes-hook), similar for measures (size) and general aspect but not for colour and function, were introduced in the room. Procedures and task were identical to those of the reported study (Guariglia et al. 2005a). However, the presence of two landmarks allowed the participants to rely on the representation of the target position relative to the landmarks (that is, to use the view dependent place recognition process), without necessarily relying on path integration or representation of the geometric information. When perceptual neglect patients could direct navigation using landmarks, their performances did not differ from these of controls and right brain damaged patients without neglect.

Instead, representational neglect cannot benefit from the presence of landmarks, confirming that the impairment in mental representation affects the ability to construct cognitive maps of the environment and, therefore, to efficiently store the location of the target relative to the configuration of the room or to the position of the landmarks in long term memory.

The statement that representational neglect, but not perceptual neglect, specifically affects navigational processes because of an impaired ability to represent environmental information in a cognitive map is confirmed by a previous study. In reporting a double dissociation between perceptual and representational neglect, Pizzamiglio et al (1996) showed that the presence of severe perceptual neglect does not affect the ability to construct environmental cognitive maps. In this study, the ability of a patient affected by representational but not perceptual neglect (MC) to explore and mentally represent a novel environment was compared to that of a patient affected by perceptual but not representational neglect (BM). Each patient was brought into a previously unseen room and required to describe it in detail from the centre of each of the four walls. The number of elements reported on each side in each description was recorded. Soon after, the patient was brought into a different room where he spent one hour performing verbal neuropsychological tests that did not tax either memory or visuo-spatial abilities. At the end of this time, the patient was asked to imagine entering the room he had described before and standing at the door, recalling all the objects he saw; a description from memory from the opposite vantage point was also requested. The number of elements reported on each side of the mental image was recorded.

When required to describe the previously unknown room from four different vantage points, MC correctly reported all features (furniture, objects, windows, etc.) in detail. However, after the one-hour interval MC was unable to describe the contraleteral side of the room from memory, but he correctly described the ipsilesional one.

On the other hand, BM described only the ipsilesional side of the same room while visually inspecting it, but very surprisingly demonstrated having elaborated a full mental representation of the room when required to describe it from memory. In fact, after the one-hour interval, BM reported the elements on both contralesional and ipsilesional sides of the room. These observations suggest that representational neglect is due to damage of a system devoted to processing environmental information for con-

structing cognitive maps to be used for navigation; in the case of perceptual neglect, without representational neglect this system is unaffected. Therefore, the system guiding visual exploration and directing visuo-spatial manipulation does not prevent the partially perceived environmental elements from being included in a correct cognitive map by means of the system representing space for navigation.

## Concluding remarks

Our review of the neuropsychological contributions to understanding navigational skills in humans can be divided into two sections.

The first, thus far based on a single case, describes a condition in which none of the processes identifiable in individual adults (or in different animal species) are available.

The case of MGC presents a striking segregation between "normal" development of a variety of cognitive functions and the complete inability to organize an orientation strategy even in very familiar environments. MGC's successful completion of high school, which implies the mastery of a number of linguistic and non linguistic skills as well as normal I.Q. and other cognitive abilities, is very surprising in light of her total incapacity, at the age of 18, to walk outside her home without being accompanied by a relative.

We wish to stress that this abnormal behaviour has no psychiatric base such as agoraphobia, anxiety or any other kind of abnormal social behaviour.

The explanation of this dramatic, "isolated" and persistent behaviour must be connected to some basic mechanisms, which are incomprehensible given the lack (to the best of our knowledge) of any other similar cases of congenital topographical impairments. Further, the careful study of her profoundly dysmorphic brain does not help in interpreting this finding.

On the other side, all of the other rich documentation of human navigation impairments is based on descriptions of acquired disorders following strokes, tumours, traumatic brain injuries etc., which document selective impairment of one or more basic navigational processes occurring after the development of navigational abilities.

Particular attention has been given to studies on neglect patients whose navigational disorders are described in the literature.

More specifically, we have tried to outline what can be associated with extrapersonal, perceptual neglect and what must be interpreted as specific to representational neglect, the importance of which has recently been distinguished from the other disorders characterizing this complex syndrome.

Very generally, it can be suggested that what we need is a model capable of specifying the existence and the nature of a "core" mechanism operating in the developing individual (in both humans and animals) which may be blocked at a critical period of development. The consequence of this block is the complete inability to segregate more specialized subsystems capable of generating one or many ways to acquire the skill to navigate in novel or familiar environments.

If these skills are able to develop from the hypothetical "core" system and based on a biological program, the emergence of a number of subsystems or modules, each representing a separate spatial competence, can be observed in this as well as in other cognitive domains.

These considerations are compatible with the possibility of documenting selective deficits in cases of acquired disorders, e.g., deficits in reorienting or integrating multimodal information with the preservation of other unaffected abilities such as path integration.

## References


Aguirre, G. K., & D'Esposito, M. (1999). Topographical disorientation: A synthesis and taxonomy. *Brain, 122*, 1613–1628.

Barrash, J. (1998). An historical review of topographical disorientation and its neuroanatomical correlates. *Journal of Clinical and Experimental Neuropsychology, 20*, 820–836.

Bisiach, E., & Luzzatti, C. (1978). Unilateral neglect of representational space. *Cortex, 14*, 129–133.

Bisiach, E., Pattini, P., Rusconi, M. L., Ricci, R., & Bernardini, B. (1997). Unilateral neglect and space constancy during passive locomotion. *Cortex, 33*, 313–322.

Collett, M., Collett, T. S., Bisch, S., & Wehner, R. (1998). Local and global vectors in desert ant navigation. *Nature, 394*, 269–272.

Collett, M., Collett, T. S., & Wehner, R. (1999). Calibration of vector navigation in desert ants. *Current Biology, 9*, 1031–1034.

Collett, M., & Collett, T. S. (2000). How do insects use path integration for their navigation? *Biological Cybernetics, 83*, 245–259.

De Renzi, E. (1982). *Disorders of space exploration and cognition*. John Wiley, Chichester.

Farrel, M. J. (1996). Topographical disorientation. *Neurocase, 2*, 509–520.

Farrel, M. J., & Robertson, I. H. (2000). The automatic updating of egocentric spatial relationship and its impairment due to right posterior cortical lesions. *Neuropsychologia, 38*, 585–595.

Gouteaux, S., & Spelke, E. S. (2001). Children's use of geometry and landmarks to reorient in an open space. *Cognition, 81*, 119–148.

Gouteux, S., Thinsi-Blanc, C., & Vauclair, J. (2001). Rhesus monkeys use geometric and nongeometric information during a reorientation task. *Journal of Experimental Psychology. General, 130*, 505–519.

Gron, G., Wunderlich, A. P., Spitzer, M., Tomczak, R., & Riepe, M. W. (2000). Brain activation during human navigation: gender-different neural networks as substrate of performance. *Nature Neuroscience, 3*, 404–408.

Guariglia, C., Piccardi, L., Iaria, G., Nico, D., & Pizzamiglio, L. (2005a). Representational neglect and navigation in real space. *Neuropsychologia, 43*, 1138–1143.

Guariglia, C., Iaria, G., Piccardi, L., Nico, D., & Pizzamiglio, L. (Submitted 2005b). Landmark'use in representational and perceptual neglect during environmental navigation.

Habib, M., & Sirigu, A. (1987). Pure topographical disorientation: A definition and anatomical basis. *Cortex, 23*, 73–85.

Hermer, L., & Spelke, E. S. (1994). A geometric process for spatial reorientation in young children, *Nature, 370*, 57–59.

Hermer, L., & Spelke, E. S. (1996). Modularity and development: The case of spatial reorientation. *Cognition, 61*, 195–232.

Hermer-Vasquez, L., Moffet, A., & Munkholm, P. (2001). Language, space and the development of cognitive flexibility in humans: The case of two spatial memory tasks. *Cognition, 78*, 263–299.

Hirayama, K., Taguchi, Y., Sato, M., & Tsukamoto, T. (2003). Limbic encephalitis presenting with topographical disorientation and amnesia. *Journal of Neurology, Neurosurgery and Psychiatry, 74*, 110–112.

Iaria, G., Petrides, M., Dagher, A., Pike, B., & Bohbot, V. D. (2003). Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: Variability and change with practice. *The Journal of Neuroscience, 23*, 5945–5942.

Iaria, G., Incoccia, C., Piccardi, L., Nico, D., Sabatini, U., & Guariglia, C. (2005). Pure topographical disorientation due to congenital brain malformation: A case study. *Neurocase, 11*, 463–474.

Incisa, della Rocchetta A., Cipolotti, L., & Warrington, E. K. (1996). Topographical disorientation: Selective impairment of locomotor space? *Cortex, 32*, 727–735.

Knierim, J. J., Mcnaughton, B. L., & Poe, G. R. (2000). Three-dimensional space selectivity of hippocampal neurons during space flight. *Nature Neuroscience, 3*, 211–212.

Learmonth, A. E., Newcombe, N. S., & Huttenlocher, J. (2001). Toddlers' use of metric information and landmarks to reorient. *Journal of Experimental Child Psychology, 80*, 225–244.

Learmonth, A. E., Nadel, L., & Newcombe, N. S. (2002). Children's use of landmarks: Implications for modularity theory. *Psychological Sciences, 13*, 337–341.

Maguire, E. A. (2001). The retrosplenial contribution to human anvigation: A review of lesion and neuroimaging findings. *Scandinavian Journal of Psychology, 42*, 225–238.

MacFadden, A., Elias, L., & Saucier, D. (2003). Males and females scan maps similarly, but give directions differently. *Brain and Cognition, 53*, 297–300.

McNaughton, B. L., Barnes, C. A., Gerrard, J. L., Gothard, K., Jung, M. W., Knierim, J. J., Kudrimoti, H., Qin, Y., Skaggs, W. E., Suster, M., & Weaver, K. L. (1996). Deciphering the hippocampal polyglot: The hippocampus as a path integration system. *Journal of Experimental Biology, 199*, 173–186.

O'Keefe, J. & Nadel, L. (1978). *The Hippocampus as a Cognitive Map*. Clarendon, Oxford.

Ortigue, S., Viaud-Delmon, I., Michel, C. M., Blanke, O., Annoni, J. M., Pegna, A., Mayer, E., Spinelli, L., & Landis, T. (2003). Pure representational neglect for far space. *Neurology, 60*, 2000–2002.

Pallis, C. A. (1955). Impaired identification of faces and places with agnosia for colours. *Journal of Neurology, Neurosurgery and Psychiatry, 18*, 218–224.

Paterson, A., & Zangwill, O. L. (1945). A case of topographical disorientation associated with unilateral cerebral lesion. *Brain, 68*, 188–211.

Pizzamiglio, L., Guariglia, C., Nico, D., & Padovani, A. (1996). Two separate systems for space cognition. In W. J. M. Levelt (Ed.), *Advanced Psycholinguistics: A Bressanone Retrospective for Giovanni B. Flores D'Arcais* (pp. 157–162). Nijmengen, NL.

Pizzamiglio, L., Guariglia, C., & Cosentino, T. (1998). Evidence for separate egocentric and allocentric space processing in neglect patients. *Cortex, 34*, 719–730.

Pizzamiglio, L., Iaria, G., Berthoz, A., Galati, G., & Guariglia, C. (2003). Cortical modulation of whole body movements in brain-damaged patients. *Journal of Clinical and Experimental Neuropsychology, 25*, 769–782.

Redish, D. A., & Touretzky, D. S. (1997). Cognitive maps beyond the hippocampus. *Hippocampus, 7*, 15–35.

Rode, G., Rossetti, Y., Perenin, M. T., & Boisson, D. (2004). Geographic information has to be spatialised to be neglected: A representational neglect case. *Cortex, 40*, 391–397.

Saucier, D., Bowman, M., & Elias, L. (2003). Sex differences in the effect of articulatory or spatial dual-task interference during navigation. *Brain and Cognition, 53*, 346–350.

Sutherland, R. J., Chew, G. L., Baker, J. C., & Linggard, R. C. (1987). Some limitations on the use of distal cues in place navigation by rats. *Psychobiology 15*, 48–57.

Stark, M., Coslett, H. B., & Saffran, E. M. (1996). Impairment of an egocentric map of locations: Implications for perception and action. *Cognitive Neuropsychology, 13*, 481–532.

Takahashi, N., Kawamura, M., Shiota, J., Kasahata, N., & Hirayama, K. (1997). Pure topographic disorientation due to right retrosplenial lesion. *Neurology, 49*, 464–469.

Takahashi, N., & Kawamura, M. (2002). Pure topographical disorientation – The anatomical basis of landmark agnosia. *Cortex, 38*, 717–725.

Taube, J. S., Muller, R. U., & Ranck, J. B. (1990). Head direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. *The Journal of Neuroscience, 10*, 420–435.

Taube, J. S. (1995). Head direction cells recorded in the anterior thalamic nuclei of freely moving rats. *The Joutnal of Neurosciences, 15*, 1953–1971.

Vallar, G., Bottini, G., & Paulesu, E. (2003). Neglect syndromes: The role of the parietal cortex. *Advances in Neurology, 93*, 293–319.

Wang, R. F., & Spelke, E. S. (2002). Human spatial representation: Insights from animals. *Trends in Cognitive Sciences, 6*, 376–382.

Wilson, M. A., & McNaughton, B. L. (1993). Dynamics of the hippocampal ensemble code for space. *Science, 261*, 1055–1058.

Ziegler, P. E., & Wehner, R. (1997). Time-courses of memory decay in vector-based and landmark-based systems of navigation in desert ants, Cataglyphis fortis. *Journal of Comparative Physiology, 181*, 13–20.

CHAPTER 4.2

# Visuomotor control of spatially directed action

A. David Milner and Monika Harvey

## Introduction: Two functions served by vision

Visual systems first evolved to enable animals to provide distal sensory control of their movements, whereas vision as 'sight' is a relative newcomer on the evolutionary landscape (Milner & Goodale 1995). When we reach out for a particular object, we use a set of calibrated visuomotor responses that take into account the location and physical properties of the target object as well as the location and state of the body, arm and hand. This means that the role of vision in guiding manual prehension is not only to activate appropriate action plans and specify the configuration of the fingers but also to determine the relative positions of the hand and the object to be grasped.

There has been a huge expansion of research over the past 20 years in which investigators have sought to understand how the human brain uses visual information to program and control our movements. This expansion has in large part been driven by the discovery through primate neurophysiology during the 1970s and 1980s of the important role played in visuomotor control by systems within the posterior parietal cortex and associated structures in the premotor cortex and the cerebellum (Hyvärinen & Poranen 1974; Mountcastle et al. 1975; Glickstein & May 1982; Andersen 1987; Rizzolatti & Gentilucci 1988; Caminiti et al. 1998). An equally important development has been the parallel discovery of two separate "streams" of visual processing in the primate brain (Ungerleider & Mishkin 1982): a dorsal stream, passing from primary visual cortex to posterior parietal cortex, and a ventral stream passing from V1 to inferior temporal cortex. Although many new cortical visual areas have been discovered since that time (e.g. Van Essen & DeYoe 1995), their anatomical interconnections remain consistent with this broad ventral/dorsal division (see Morel & Bullier 1990, Baizer et al. 1991; Young 1992). These two areas of research converged when it was realised that the dorsal stream embodies precisely the visuomotor control systems that had been studied neurophysiologically, along with their input areas in prestriate cortex (Goodale & Milner 1992, 2004; Jeannerod & Rossetti 1993; Milner & Goodale 1995).

The consensus view that has emerged through this convergence of research is that the primate brain has at least two somewhat distinct visual systems operating in parallel within it, each with different functions and acordingly different output pathways.

The ventral stream provides the visual contents of our perceptual experience, and codes information in an abstract form suitable for storage and for deploying in cognitive processes like imagining, recognizing, and planning. The dorsal stream serves the much more immediate function of guiding our actions visually from moment to moment, and therefore needs to code information in a quick, ephemeral and view-specific form. Its contents are probably not normally accessible for cognitive elaboration or conscious monitoring (Milner & Goodale 1995; Goodale & Milner 2004). Both streams ultimately function to guide behaviour, but they have evolved to achieve this in different and complementary ways: the dorsal stream by mediating direct transformations of the visual input into effector-based coordinates, and the ventral stream through the construction of perceptual and mnemonic representations that can transcend the temporal limitations of the dorsal stream. It is important to note that both the direct and the indirect visual routes to action need to provide spatial as well as intrinsic information about objects in the environment, and we will review in this chapter some neuropsychological evidence in support of this contention.

Although physiology and neuroanatomy have provided the catalysts for leading the recent rapid development of these ideas, their seeds had already been sown by behavioural neuroscience and neuropsychology. It has been known for over 100 years that bilateral damage to the posterior parietal cortex in monkeys causes severe visuomotor difficulties in reaching for and grasping food objects (Ferrier and Yeo, 1884; see review by Milner & Dijkerman 1998), and it has been known for over 90 years that comparable damage in humans results in similar difficulties (Bálint 1909; translation by Harvey 1995). Bálint's patient had great difficulty in reaching out to take hold of objects under visual guidance: yet this was not due to a purely visual difficulty, since he only reached inaccurately when using his right hand. Presumably, therefore, the necessary visuospatial information must have been processed sufficiently well to be able to guide his skilful left hand. In addition, Bálint's patient could touch named parts of his own body quite accurately with either hand, showing that his difficulties were not simply motor. Bálint thus concluded that the disorder must be *visuomotor* rather than *visuospatial*, and he coined the term *optic ataxia* to capture this insight. Similar conclusions have been reached in studies of nonhuman primates. For example, unilateral parietal lesions cause misreaching only with the contralesional arm (Ettlinger & Kalsbeck 1962; Faugier-Grimaud et al. 1978); yet a visuospatial loss would have affected the ipsilesional arm as well.

We now know that the visuomotor mechanisms of the dorsal stream are located in homologous areas in both monkeys and humans. Furthermore, although some form of egocentric (effector-based) visuospatial coding has to be used to guide both manual reaching movements and saccadic eye movements, we know that separate maps are present in the dorsal stream to mediate these transformations both in the monkey (Snyder et al. 1997) and in the human (Culham & Kanwisher 2001). Yet although spatial information for immediate action clearly has to be processed in egocentric coordinates, spatial information for perception and subsequent cognitive processing would be of little use in this form. Object locations need to be coded in relation to

neighbouring items in the scene if we are to be able to retain them in a useful form over even quite short time intervals. The proposal that such coding would typically take place within the ventral stream and its adjoining medial-temporal areas is consistent with the association of deficits in scene perception and recognition with right ventromedial occipito-temporal damage (topographical agnosia: Landis et al. 1986; Habib & Sirigu 1987). Furthermore, a specific visual area identified through functional MRI in this same part of the brain is preferentially activated while looking at visual scenes (area PPA: Aguirre et al. 1998; Epstein & Kanwisher 1998). It is our purpose in this chapter to review some recent developments in the neuropsychology of visually-guided action, and in so doing to demonstrate how different forms of visuospatial processing depend upon information provided by different visual input systems.

## Reaching to a single target

*Patients with optic ataxia*

Surprisingly, although there are clearly complex mechanisms guiding manual prehension, clinical impairments of it are relatively rare. As described above, one of the first researchers to highlight a specific impairment as a result of bilateral posterior parietal lesions was Bálint (1909; Harvey 1995). His patient, when asked to grasp a presented object with his right hand, would miss it regularly, and would find it only when his hand knocked against it. Crucially, all movements performed defectively with the right hand were executed perfectly with the left hand. Bálint described the disorder as 'optic ataxia', a specific deficit of the visual control of movement unrelated to motor, somatosensory, visual acuity or visual field deficits. Later studies into the visuomotor behaviour of humans confirmed Bálint's observation: Perenin and Vighetto (1988) and Jeannerod (1986) reported patients with parietal lesions whose reaching movements proved inaccurate, often erring towards the visual midline, and also kinematically abnormal, with increased movement durations and lower peak velocities. During reaching to pick up objects the finger grip would also often open too widely, with either no or poor preshaping, the grasp closing only on making contact with the object (Jeannerod 1986; Jeannerod et al. 1994). In similar fashion, Jakobson et al. (1991) described a patient with a severe loss of anticipatory grip formation, who demonstrated great difficulty in sculpting the hand geometrically to match the shape of the object. Interestingly, many of these patients had no major difficulties in their perceptual reports concerning the location and orientation of the objects they were unable to grasp (Perenin & Vighetto 1988), and they rarely complained of any visual difficulty. Recent studies by Milner et al. (1999b), Pisella et al. (2000), Rossetti et al. (2005), and Khan et al. (2005a, b) have provided considerable insights into the nature of the visuomotor transformations that are impaired in optic ataxia patients, and some of these discoveries are reviewed in later sections of this chapter.

Although most of these studies have been conducted with patients whose optic ataxia is global, due to a bilateral parietal lesion, some interesting insights have come

from unilateral patients. For example, the pattern of impairment tends to be different between patients with left and right hemisphere damage, with the former being more likely to show the 'hand' pattern seen in Bálint's patient (who had a bilateral parietal lesion, but one sufficiently asymmetrical to cause only a unilateral optic ataxia), while patients with right hemisphere lesions tend to show a 'visual field' pattern, misreaching to targets throughout the contralesional hemifield, whichever hand is used (Perenin & Vighetto 1988). However, variations on these basic patterns also regularly occur.

*Patients with hemispatial neglect*

Patients suffering from hemispatial neglect after right hemisphere lesions, usually involving the temporo-parietal junction (Vallar & Perani 1987; Mort et al. 2003, 2004), also show characteristic disturbances of visually directed action. They typically demonstrate a deficient response to stimuli located contralaterally to the lesion and fail to explore the contralesional space with either eye or limb movements. A wide range of investigations into hemispatial neglect has looked at reaction times and movement times towards points and objects located in the contralesional hemispace, and has generally found these to be increased (see Mattingley & Driver 1997 for review, but also Mattingley et al. 1998). In line with these studies Goodale and colleagues (1990) investigated visually guided pointing in right hemisphere lesioned patients who had recovered from neglect. Patients were asked to point either midway between two lights or directly on top of a single light. It was found that all patients made large rightward directional errors at the outset of the reach. These initial errors were observed not only in bisection, but also in simple pointing; however they were more poorly corrected in the bisection task, so that the final rightward errors remained much larger than those seen in pointing. A related study on pointing and bisecting by Harvey et al. (1994), using a wider sample of right-and-left hemisphere lesioned patients, found rightward biases in the reach trajectory, as well as a larger terminal error for the right hemisphere lesioned patients, when such patients were reaching in the absence of visual feedback. Jackson et al. (2000) similarly reported rightwardly curved trajectories in the pointing movements of recovered left neglect patients.

However, whether visuomotor behaviour in neglect patients is necessarily subject to lateral spatial biases has become a matter of some debate. Perenin (1997) failed to observe any directional skewing of open-loop pointing in four neglect patients. Similarly, Karnath et al. (1997) who tested acute neglect patients and right hemisphere lesioned patients without neglect on a simple pointing task, found no evidence of a rightward bias in the reach trajectory either in a closed or an open-loop condition. In fact, neither patient group varied from the healthy controls in terms of either reach deviation or final accuracy. Additionally, although movement times were longer in the two patient groups compared to the healthy control group, the velocity profiles of the neglect patients to leftward targets did not differ from those to targets in right hemispace, giving no indication for a direction specific deficit in the control of hand velocity (Konczak & Karnath 1998; see also Konczak et al. 1999, for similar results). These findings seem surprising in the light of the severe visuospatial disturbance these patients

generally experience. However, a similar sparing was reported by Chieffi and colleagues (1993) in an earlier experiment in which a recovered neglect patient showed normal reaching and handgrip movements towards single objects. Only when her attention was diverted by distractor objects presented simultaneously to the right of the target, did she show a rightward deviation of the wrist trajectory. Her preparatory grip aperture was never affected. In a similar vein, Pritchard and colleagues (1997; Milner et al. 1998) described a neglect patient who was able to calibrate her finger-thumb grip aperture accurately when reaching to grasp different sized cylinders, with no asymmetry in grip size between target locations on the two sides of visual space. Only when asked to indicate manually the size of the cylinders, did she consistently underestimate them when they were located on her left (as compared with her right) side. Later studies with groups of neglect patients have replicated this symmetrical behaviour for grasping in open and closed loop conditions (Harvey et al. 2002) and towards objects of different sizes (McIntosh et al. 2002). Finally, using a pointing task, this time comparing acute as well as recovered neglect patients and right hemisphere damaged patients without neglect, Himmelbach and Karnath (2003) again failed to find any spatial bias in the neglect groups in either final accuracy or hand trajectory (even when applying all of the different measures of hand path curvature used in previous studies).

These recent findings provide clear evidence that patients with hemispatial neglect do not show the consistent misreaching for visual targets that is observed in patients with optic ataxia. As pointed out by Himmelbach and Karnath (2003), even patients with severe spatial neglect in the acute stage of their stroke can reach accurately to a target (with or without actual feedback about hand position), and they can do so in both left and right hemispace. It may be that the conflicting results of earlier studies can be explained by methodological differences, including the speed of the reaching response, the presence of potentially competing stimuli in the visual environment, and the task instructions. Of course, one cannot argue for a complete double dissociation between optic ataxia and hemispatial neglect, since one cannot generalize about all patients with optic ataxia, and certainly not about all patients with neglect. However, there are certainly some patients with optic ataxia who can still make accurate perceptual reports concerning the location and orientation of objects (Perenin & Vighetto 1988; Jakobson et al. 1992). In contrast there is, of course, extensive evidence for pervasively disordered spatial perception in neglect patients (Milner et al. 1992, 1993; Bisiach et al. 1998a, b; Kerkhoff 2000; Bisiach et al. 2002; Pitzalis et al. 2004; Ricci et al. 2004). And although large parietal lesions can cause both neglect and optic ataxia, there are many instances of patients who show optic ataxia but not neglect, and many more who show the converse (see also Perenin 1997). We have argued elsewhere (Milner 1997; Milner et al. 1998) that spatial neglect is primarily a failure to deal with *perceptual* information at a high (scene-based) level of representation, information initially received via the ventral stream. Neglect should therefore only affect action indirectly; for example where a choice of actions has to be made, or where an action is used to express a perceptual judgement (as in line bisection).

*The neuroanatomy of optic ataxia and neglect*

Perenin and Vighetto (1988) superimposed the scans of their optic ataxic patients and inferred that the common area of damage was located in the superior parietal lobe, within and dorsal to the intraparietal sulcus, sparing the human inferior parietal lobe. A range of further studies have confirmed the association of superior parietal lesions and the banks of the intraparietal sulcus with symptoms of optic ataxia (Garcin et al. 1967; Ratcliff & Davies-Jones 1972; Levine 1978; Jakobson et al. 1991; Jeannerod et al. 1994; Pisella et al. 2000). In agreement with these data, a recent fMRI study has revealed a region of the occipitoparietal cortex that seems to correspond to the 'parietal reach region' in the monkey, lying posteriorly and medially within the superior parietal lobule (Connolly et al. 2003). This, however, may be only one part of a wider network of parietal areas concerned with visually guided reaching, clustering on both sides of the intraparietal sulcus (see Culham & Kanwisher 2001).

The lesions that cause hemispatial neglect, although also generally including parietal lobe tissue, are very different from these areas around the intraparietal sulcus. The damaged areas held in common among most patients with neglect lie in the inferior parietal lobe (Vallar & Perani 1987; Mort et al. 2003, 2004), including the temporo-parieto-occipital junction (Leibovitch 1998), generally in the right hemisphere. While not disputing these findings, however, recent studies by Karnath and colleagues (2001, 2004) have shown that this may not be the *critical* area for causing neglect. By subtracting the lesions of patients who do *not* show neglect, they have implicated the right superior temporal cortex rather than the inferior parietal lobe as the critical area for neglect. These findings are still hotly debated (see Mort et al. 2003, 2004), and it is very likely that the outcomes of such subtractive analyses will be critically dependent on the particular tests used as criteria for the presence of neglect. Indeed in recent studies using transcranial magnetic stimulation in healthy subjects, posterior parietal and superior temporal areas of the right hemisphere have been differentially implicated not only in search as opposed to space-perception tasks, but also in different kinds of search tasks (Ellison et al. 2005; Schindler et al., submitted).

In any event, all researchers in the field are agreed that the critical areas where damage causes neglect lie much more inferiorly than those where damage causes optic ataxia, and of course that the left/right hemisphere incidence of such causative lesions is quite different, with optic ataxia being just as likely to be caused by left as right hemisphere lesions. Even though a recent study using subtraction methodology suggests that the most critical site for causing optic ataxia may lie at the occipito-parietal junction (Brodmann's area 39), i.e. more ventrally than the major lesion overlap region in the intraparietal sulcus (Karnath & Perenin 2005), this is still very distant from the lesion focus for neglect.

*Patients with visual form agnosia*

Unlike damage to the dorsal stream, damage that directly compromises the ventral stream, which is thought to be dedicated to perception rather than directly to guiding action (Milner & Goodale 1995), should not affect simple reaching or grasping

movements. The sparse evidence that is available bears out these expectations in two patients with severe visual form agnosia, D.F. (Goodale et al. 1991; Milner et al. 1999a) and S.B. (Lê et al. 2002; Dijkerman et al. 2004). In the case of D.F., there is now well-documented structural and functional MRI evidence for bilateral damage to the ventral stream area LO, an area known to be intimately concerned with object perception (James et al. 2003), and visual inspection of his MRI scans suggests a similar picture in S.B. (for a review of the neuropsychology and pathology of visual form agnosia, see Heider 2000). Simple pointing and grasping in both of these patients is essentially normal. In a more complex reaching task, D.F. was asked to point to sequences of coloured tokens set out in a quasi-random array (Murphy et al. 1998). Her performance still remained essentially flawless. In sharp contrast to this, however, when she was asked to reproduce the array using fresh tokens at an adjacent location on the table, D.F. was markedly impaired, in spite of unlimited free viewing of the model and unrestricted self-corrections. She retained some sensitivity to the categorical spatial structure of the arrays, tending to order the tokens correctly in crude left-to-right and top-to-bottom sequence, but her copy did not reproduce the correct coordinate information about the relative locations of the tokens (Murphy et al. 1998).

In a different approach to examining D.F.'s spatial-motor skills, we attempted to assess her ability to use allocentric information for the guidance of her grasping movements (Dijkerman et al. 1998). We examined D.F.'s ability to adjust her grasp to take hold of objects through two or three holes in them, rather than by grasping them at their edges. In the three-holed case in particular, D.F. was completely insensitive to orientation of the main thumb-finger axis as well as the spatial separation between thumb, index and middle fingers. D.F., however, did perform better when the disc only contained two holes. She now managed to adjust her hand orientation appropriately, although she still remained unable to adjust her grip aperture to the distance between the two holes. We suggested that D.F. was unable to use information about the distance between the two holes for guidance of her grasping movement, even though she could use information about the location of the individual holes. This distinction is consistent with the idea that her impairment was one of processing allocentric rather than egocentric space. In a re-examination of this idea, however, McIntosh and colleagues (2004c) point out that even control subjects note the effortful, conscious control necessary to direct three digits towards the three holes, unlike the effortless unconscious nature of everyday object grasping. They asked D.F. to grasp pairs of separated rectangular blocks that were mounted on a piece of card with a 3, 4 or 5 cm separation between them. Here D.F. scaled her maximum grip aperture to the overall width of object pairs in a manner that was indistinguishable from her grasping of solid objects of the same overall dimensions.

Given D.F.'s expert performance of goal-directed acts with respect to the location, orientation and physical dimensions of objects present in her visual field, we inferred some years ago that she must be using relatively intact structures in the dorsal stream to accomplish these skills (Milner & Goodale 1995). We now have direct functional imaging evidence to support this conjecture (James et al. 2003; Culham 2004): there

is dorsal-stream activation during reaching and grasping in patient D.F., qualitatively like that seen in healthy subjects (Culham et al. 2003), though less extensive, no doubt partly due to the clear presence of left posterior parietal damage. It is not yet known to what extent these observations may be replicable in patient S.B.: the picture may be complicated by the fact that he has more extensive unilateral dorsal stream damage than D.F. (Lê et al. 2002). But of course even if it were fully intact, a dorsal stream working alone would have limited visual resources at its disposal. When reaching for targets at different distances, for example, healthy subjects can calibrate their reaches using depth cues based on monocular 'pictorial' cues, such as perspective, shading and texture, as well as the known size of stimulus objects. In contrast, the isolated dorsal stream appears to gauge depth and distance purely through binocular cues, as shown by D.F.'s failure to correct retinal angle for distance and tilt when grasping objects viewed monocularly (Dijkerman et al. 1996; Marotta et al. 1997). When tested binocularly within a rich visual context, D.F.'s reaching to objects at different distances is good, and considerably better than her ability to report distances verbally (Carey et al. 1998). But as soon as these conditions change, her limitations become apparent.

In a series of studies, Mon-Williams et al. (2001a, b) found first that D.F. not only relied heavily on binocular vision when reaching in depth, but did so in a surprising way. Instead of using the disparity of the two retinal images to provide a 3-D visual representation that could guide her reaching, she evidently monitored her state of ocular convergence instead. This was discovered by artificially making her eyes converge too much or too little, using a wedge prism oriented inwards or outwards over one of her eyes. She made big errors in the extent of her reaches that could be almost entirely accounted for by the geometry of the prisms. In other words, her brain must have been relying almost completely on monitoring her eye convergence in computing how far to reach. Normal observers too are influenced by such prismatic manipulations, but only to a minor degree, indicating that they do not rely heavily on vergence information. It should be noted, however, that this evidence for D.F.'s reliance on vergence distance information was obtained in a task where the targets were viewed at eye height (Mon-Williams et al. 2001a). Under conditions where D.F. simply reached out to target objects on a table top, her performance remained reasonably accurate even despite large prismatic manipulations of her vergence angle (Mon-Williams et al. 2001b). The investigators showed that her behaviour only came under the complete control of vergence signals when the target objects were placed at eye height. They argue that D.F. uses vertical gaze angle to gauge target distance in normal prehension, and only secondarily, when nothing else is available, does she depend on vergence cues. These studies reveal the limited range of cues by which the dorsal stream can gauge distance – cues that are of course completely overshadowed in healthy observers by their ability to bring to bear pictorial cues that are processed within the ventral stream.

## On-line adjustments during reaching

The effects of target perturbation on reaching and grasping in healthy subjects have long been a topic of investigation in studies of visuomotor control. It is now well established that target jumps occuring at the outset of a reaching movement engage rapid automatic on-line control mechanisms which do not require visual awareness of the jump; and that healthy subjects make a seamless change of trajectory to take the perturbation into account. This has been consistently reported for pointing (Goodale et al. 1986; Pelisson et al. 1986; Prablanc et al. 1986; Pisella et al. 2000), as well as grasping (Desmurget et al. 1997; Gréa et al. 2000). Patients with optic ataxia, however, are severely impaired at changing track when the target of a reaching action is shifted unexpectedly after the onset of the reach (Pisella et al. 1999, 2000; Gréa et al. 2002). Patient I.G., for example, was severely impaired when objects were experimentally displaced at the onset of either her pointing or grasping movements. Although she could eventually reach the final target position this occurred only after she completed her initially programmed movement. She gave no evidence of the fast corrections which were produced by the control subjects. In line with this, in a further experiment where a target shift was cued by a colour change instead of a simple change in location, a task for which slower deliberate corrections always take place, she was unimpaired (Pisella et al. 2000).

Rossetti and his colleagues (Pisella et al. 2000; Rossetti et al. 2003) have argued that these impairments of on-line visuomotor control can explain the frequent findings that optic ataxia patients have much greater problems in reaching for peripheral as opposed to central targets (Jeannerod 1988; Perenin & Vighetto 1988; Carey et al. 1997; Buxbaum & Coslett 1998). When motor programming is based on foveal visual information, on-line corrections are needed during goal-directed actions only for minor final adjustments, and a lack of this would have only minor implications, possibly on deceleration (Jakobson et al. 1991). Conversely however, when an action is based on imprecise peripheral information, on-line control is essential to succeed in reaching or grasping, and indeed patients like I.G. are far more impaired under these conditions. Desmurget and colleagues (1999) found that transcranial magnetic stimulation of the posterior parietal lobe disrupted movement corrections made in response to a target jump, further demonstrating that the posterior parietal cortex is implicated in on-line visuomotor control. Despite these arguments, however, other research, including studies of patient I.G., shows clearly that the reach trajectories made by patients with optic ataxia are systematically inaccurate right from the start of the movements (Milner et al. 2003). As is clearly illustrated in the top right panels of Figures 1 and 2, these patients do not set off like healthy subjects, but then fail to correct themselves on-line: rather their reaches are directed incorrectly from the very outset. The failure of optic ataxia patients to correct their movement direction online, therefore, is not *sufficient* to explain the misreaching of these patients – there are also serious errors in the initial programming of the reaches. Other research, which has examined reaction times to initiate reaches to different target locations, also supports the conclusion that there is a

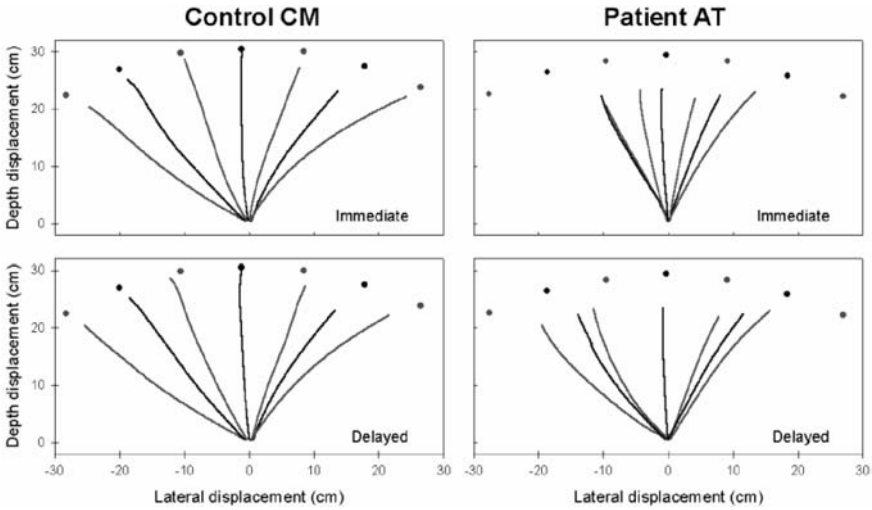



**Figure 1.** Immediate and delayed pointing trajectories in patient A.T. and the control subject C.M., averaged only over the depth points common to all reaches. A.T.'s medially biased errors are present throughout her reach. The improvements conferred by the delay condition are also evident throughout the trajectories. Reproducted from Milner et al. (2003) with permission from Elsevier.

programming deficit in optic ataxia for peripheral targets (Ishihara et al. 2004). Taken together, these results clearly support the idea that both the initiation *and* the control of immediate visually guided reaching are impaired in optic ataxia, in agreement with inferences based on evidence from parietal neurophysiology (Milner & Goodale 1995).

If our arguments of divergent behavioural patterns in patients with optic ataxia compared to those with hemispatial neglect are correct, then this impairment in making online corrections when a target object is shifted unexpectedly should not occur in neglect patients, even if the target shift occurs in a leftward direction. After all, patients with spatial neglect generally have a spared dorsal stream. To our knowledge, there is only one study so far that has tested patients with hemispatial neglect in a target-perturbation paradigm. Farnè et al. (2003) required seven right brain damaged patients (four with neglect) to grasp one of five possible objects spaced 10 deg apart (whichever was illuminated). On perturbed trials, the target shifted from the central location to one of the others (a shift of 10 or 20 deg). The authors found that on these trials the patients' movement times were longer to make a leftward adjustment than to make a rightward one, a difference not present in the controls. Various kinematic landmarks were likewise attained relatively late in the patients' reaches to leftwardly perturbed targets. Unfortunately, the X-Y trajectories were not analysed to examine whether these results reflected later turning points in the movements when leftward corrections were made, relative to rightward ones. However the illustrative plots of individual trials show that even the healthy controls made very late adjustments on

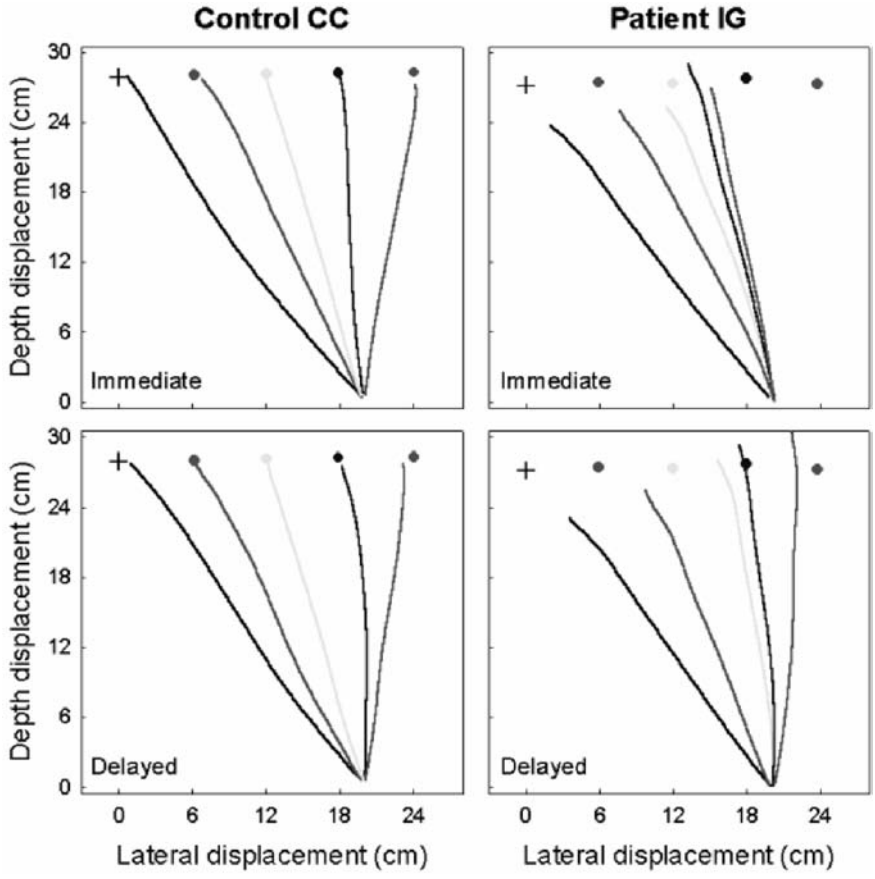



**Figure 2.** Immediate and delayed pointing trajectories in patient I.G. and the control subject C.C., averaged only over the depth points common to all reaches. I.G.'s medial (i.e. leftward) errors are clearly present throughout her reach, as are the changes induced by the delay condition. The point of fixation is indicated by a plus sign. Reproducted from Milner et al. (2003) with permission from Elsevier.

perturbed trials, reaching towards the initial (central) target and then making partial withdrawal movements of the hand while redirecting their reaches. It appears from the illustrated traces that the patients made even later corrections (evidently almost touching the initial target first), but this was true even on trials where the target shifted rightwards. A clear indication that even healthy subjects generally had to program two successive movements is that they typically opened and closed their handgrip twice *en route* to a displaced target. The reason for these late corrections even in the control subjects may have been partly that the target was shifted by a substantial distance (10 or 20 deg), coupled with the fact that the initial target did not disappear, but simply dimmed, necessitating a choice between an old and a new target. In any event, normal

behaviour in this task contrasts with that of the controls in the previously mentioned studies where failures to make on-line shifts were found in the optic ataxic patient I.G. (Pisella et al. 2000; Gréa et al. 2002). In those tasks the controls corrected their reach trajectories early, making seamless movements to the new location, even being drawn irresistibly to it against their own wishes and contrary to the experimenter's instructions (Pisella et al. 2000).

Our prediction would be that neglect patients would be unimpaired in making online corrections in tasks more like those used by Pisella et al. (2000) and Gréa et al. (2002). Indeed even in the study by Farnè et al. (2003), it should be noted that the impairments shown were very subtle: the patients were not functionally defective in that they still correctly grasped and lifted the perturbed leftward target objects, a behaviour in stark contrast to those of the optic ataxic patients described above, who typically completed their movements to the initial location of the target. Moreover, in line with the reaching studies reported earlier, the authors failed to find a specific impact of neglect *per se* on the patients' kinematics, even on perturbed trials. The perturbations influenced the behavioural kinematics similarly in both patients with and without neglect.

This prediction that neglect patients should be able to correct their reaches in a normal on-line fashion implies that their neglect relates primarily to perceptual awareness rather than to visual processing for action. A recent study by Schenk and colleagues (2005) casts an interesting light on this notion. They tested a patient (V.E.) who had recovered from neglect, but who still suffered from a persistent visual (and tactile) extinction. They designed the experiment in such a way that on a high proportion of the trials V.E. could not see an LED attached to his left index finger, due to extinction resulting from the presence of the target LED in front of him. The question they asked was whether visual feedback about the location of the hand during reaching would be beneficial for performance even when the patient was unaware of this information. The results showed that V.E.'s performance was significantly better when visual feedback from the hand was present than when it was not; but this was true quite regardless of whether or not the information was available for verbal report. They conclude that visual awareness is not required for the effective use of visual feedback from the hand during reaching.

Of course, we do not claim that the healthy individual is unaware of visual targets (or his/her hand) during reaching and grasping movements. One is normally very much aware both of the target itself and of one's actions towards it. What we are suggesting is that the visual processing that gives rise to our perceptual awareness is not the *same* as the processing that guides our actions. An everyday illustration of this is that we can often successfully catch an object that we inadvertently knock off the table before we have formed a conscious percept of the falling object. Experimental confirmation of the fact that our actions can precede our awareness of their visual determinants was provided several years ago by Castiello et al. (1991). In their experiment, subjects could respond manually to the shift of an object's location some 300 ms before they were able to report the shift. As a general rule, of course, processing

time is likely to be a much more critical constraint for visuomotor control than for the perceptual analysis supporting conscious awareness (Milner & Goodale 1995). For example when an animal has to catch a moving prey object, it needs to be able to make very rapid adjustments from moment to moment.

We have argued that neglect patients are not necessarily impaired in the visuomotor control of spatially directed action. Furthermore, evidence is now accruing that this relatively unimpaired system could be utilized to aid neglect rehabilitation. Robertson and colleagues (1995) were the first to demonstrate that reaches to bisect a metal rod were significantly more central when neglect patients were allowed to grasp the rod, as if to pick it up, than when asked to point to its centre. They went on to demonstrate that when neglect patients were asked to grasp and lift a rod at its centre over repeated trials, significant positive effects were found for twenty minutes after the intervention on two out of four *perceptual* tests (Robertson et al. 1997). More recently, Harvey et al. (2003) found that an extension of this visuomotor feedback training resulted in significant long-term improvements on various measures of neglect behaviour, in a group of chronic neglect patients. In a similar vein, Rossetti et al. (1998) showed that only a short period of visuomotor adaptation to a right prismatic shift of the visual field was enough to significantly ameliorate neglect, and related studies run since then have shown that the effect can last for a day (Farnè et al. 2002) or even for weeks (Frassinetti et al. 2002). Together, these recent discoveries suggest that the performance of visually guided actions may help to improve the distorted visuospatial perception of neglect patients via some form of dorsal-to-ventral recalibration.

## Delayed reaching

The evidence summarized in the last section indicates that spatial coding for immediate action is impaired in optic ataxia, but as far as we can see, not in visual form agnosia. Visual form agnosia involves ventral-stream damage, and is by its nature a deficit of perception rather than of visually guided action (Milner et al. 1991; Goodale et al. 1991). According to the model of Milner and Goodale (1995), the dorsal stream's control of action is designed for dealing with target stimuli in the 'here and now', while they are still visible, rather than days, minutes, or even seconds later. It is assumed that when time is allowed to pass and a reaction has to be made on the basis of a visual memory, then the ventral stream is required for successful performance. In other words, 'visuomotor control' in the sense of the guidance of an action by a visible target, is replaced by 'perceptual control' in which a percept of the object has to be held in, or retrieved from, memory and then used to guide behaviour. We would therefore expect that D.F.'s ventral stream damage would impair *delayed* visually-guided actions, since these must depend on some form of temporary perceptual coding in working memory. In agreement with this expectation, it was demonstrated some years ago by Goodale and colleagues (1994) that patient D.F. failed completely to scale her grip

aperture when pretending to reach out and grasp objects that she had seen but which were no longer present.

Similar though less severe impairments were observed when we asked D.F. to make manual pointing movements or saccadic eye movements, under conditions where a target was presented and then removed before she was allowed to respond (Milner et al. 1999a). D.F. made greatly increased errors of localization when asked to point to an LED target 10 seconds after it was switched off, and similarly made large errors when asked to move her eyes to such a target, in this case after a 5-sec delay. Yet in both tasks D.F. performed with normal accuracy when responding immediately. Of course in these tasks healthy subjects too tend to make slightly larger errors than when responding immediately (Berkinblit et al. 1995; McIntyre et al. 1997; Milner et al. 1999a); but the extent of this reduced accuracy is much less than that shown by D.F. Presumably a healthy person can cope to some degree with the delay by recoding the location of the target in relative visuospatial or verbal terms (e.g. '10 cm to the left of the fixation point'). This would be a strategy much less easy for D.F. to use, though given practice she might be able to 'imagine' herself making the requisite movement at the time of stimulus exposure, and re-code this motor imagery in a verbal form (see Dijkerman & Milner 1997). We have also tested D.F. on a 'pantomimed' version of the more complex pointing task described earlier, where she was faced with a quasi-random array of up to 5 differently coloured tokens. Instead of pointing directly to each of the tokens in a prescribed sequence, her task was to make an equivalent sequence of pointing movements on an adjacent blank sheet. Her performance resembled her efforts when asked to reproduce the array using fresh tokens (Murphy et al. 1998): that is, she was able to retain crude categorical information about individual local pairs of locations, but not to reproduce the overall gestalt of the stimulus array. (Carey et al. 2006).

We interpret these data as consistent with the idea that immediate visuomotor control relies on a rapid automatic transformation from vision to action, whilst delayed control is mediated by perceptual (or perceptually-derived) representations. These representations provide the healthy observer with more flexibility than the self-referenced visual information that determines immediate responding. Their availability allows action to become freed from the constraints of the proximal stimulus and instead to be guided by a general-purpose 'working memory' system. Of course, these more 'cognitive' control systems should be – at least partially – spared in patients with optic ataxia. This expectation leads to the counterintuitive prediction that unlike healthy subjects (and especially unlike D.F.), these patients should make *smaller* errors when making delayed 'pantomimed' responses than when responding immediately. By requiring them to delay before responding, we should cause them to switch from the damaged direct route to the indirect 'perceptual' route from vision to action. We found precisely this result (Milner et al. 1999b) in a patient with extensive bilateral parietal damage (A.T.: Jeannerod et al. 1994): that is, her pointing accuracy improved significantly after a 5 s delay as compared with her immediate pointing (see Figure 1, bottom). This surprising result has been confirmed in other patients (Milner et al. 2001, 2003; Revol et al. 2003), including I.G. (see Figure 2, bottom). I.G. also showed a

similar improvement in a task of indirect (displaced) pointing, in which pantomimed pointing was required but no delay imposed (Perenin et al. 1999), showing that delay is not essential for inducing this 'perceptual' guidance of reaching.

Even more surprisingly, recent data show that some optic ataxia patients can go still further, and switch to a perceptual strategy for guiding reaching even in what is ostensibly an *immediate* pointing task. Rossetti et al. (2005) used a task of 'delayed real pointing' (as opposed to delayed *pantomime* pointing) to investigate this possibility. In both the real and the pantomime tasks, the subject first views a stimulus, which is then hidden by a barrier, and after 5 s the barrier is removed and the subject asked to point. The difference is that in the real pointing task, the subject does not have to point to a *remembered* location, since the stimulus is still present after the delay. Indeed the task is presented as one of 'immediate' pointing to the target stimulus after the delay, and of course the reaches of healthy subjects are fully controlled by the stimulus facing them (presumably through the dorsal stream route). But patients with bilateral optic ataxia (I.G. and A.T.) did not treat the task this way; presumably because their dorsal streams cannot efficiently initiate an immediate action on the basis of the stimulus in front them. This fact became apparent on critical test trials, when the location of the target stimulus was covertly switched during the delay, either from the most to the least eccentric location, or vice-versa. Quite unlike controls, the patients initiated their reaches not to the target location ("T2"), but instead to the previewed location ("T1") on these trials. Although they usually ended up at the correct location, the first portions of their trajectories were guided entirely by the previewed location (see Figure 3, and Milner et al. 2003; Rossetti et al. 2005). We may infer then, that even on normal (unperturbed) trials, the patients were using this same mode of visual control of their reaches, that is that they were using a perceptual or 'cognitive' strategy throughout their performance on the delayed real pointing task.

What is the nature of the stored representations that intervene in this more indirect use of visual information to guide action? Presumably the patients must have been using visuospatial working memory to bridge the temporal gap between perception and action. A hint as to how they may do this is given by a report by Darling et al. (2001), in which a number of patients with focal brain damage were tested using a delayed pointing task. They found that all of their patients with damage to the *inferior* parietal lobule were impaired on this task. Also consistent with the idea that inferior parts of the parietal lobe may play an important role in visuospatial working memory is the discovery that many neglect patients show a deficit in tasks that tap this ability (Pisella et al. 2004; Malhotra et al. 2005). Yet of course the visual information first has to be coded as a perceptual representation in order to allow for the possibility of later flexible access to that information through working memory. The evidence from D.F. and from many other sources indicates that this initial perception of the object and its location in space depends on the occipito-temporal (ventral) stream of visual processing. Indeed there is preliminary evidence that the ventral stream is selectively activated during delayed pointing in patient I.G. (Himmelbach et al. 2003).

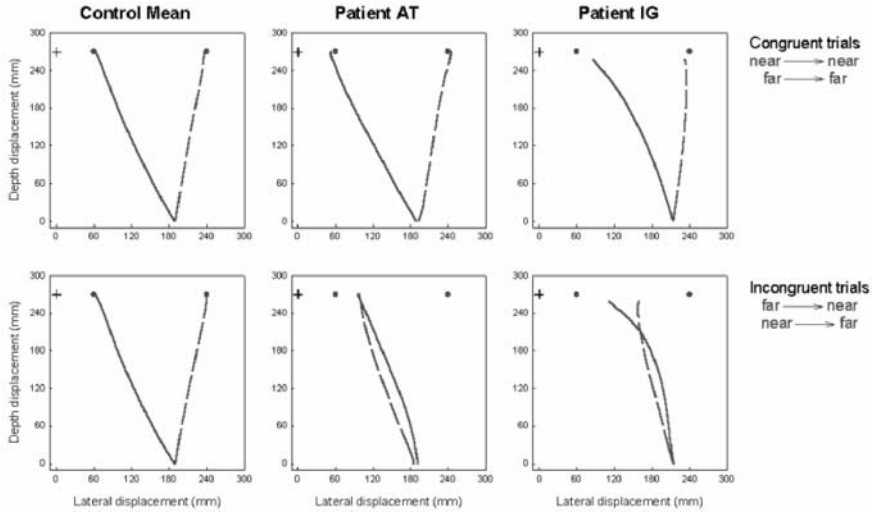



**Figure 3.** Reaching trajectories in 'delayed real pointing'. Congruent pointing trials are shown at the top, in which the target has been previewed 5 s earlier at the same location (near or far) as it is presented for pointing. In the incongruent trials (bottom), the target has been previewed at the opposite location. On the left are the mean trajectories of three healthy controls. Reaches with the near target present at the time of response are shown in red, and those to the far target in green.
Whether reaching for the most peripheral or the least peripheral target, the controls were unaffected by the previously viewed location of the target. The two patients, in contrast, set out in quite the wrong directions on the perturbed trials, and had to correct their trajectories en route. These corrections are particularly prominent when the patients were reaching toward the more central location. Reproducted from Milner et al. (2003) with permission from Elsevier.

## Reaching between obstacles

The evidence we have reviewed so far almost entirely concerns tasks where there is essentially only one relevant stimulus in the workspace. It is with such a minimalist task environment, with merely a target stimulus for action, that all of the animal neurophysiology, all of the human functional MRI studies, and almost all of the neuropsychological studies on manual prehension and reaching have been performed. But of course such impoverished environments are quite atypical of the everyday tasks faced by our visuomotor system: we often have to negotiate our reaching movements through a cluttered visual environment. It is clear from the data we have already reviewed that the dorsal stream plays a major role in governing our ability to take into account the location and physical properties of the *target* object, as well as the location and state of our body, arm, and hand. But our actions also need to take into account the location of any potential obstacles near to the intended route of the reaching move-

ment. In practice, the brain seems to insure against collisions by building into our movements a tendency to veer away from non-target objects, even when they are actually too far away to pose a serious threat of collision (Tresilian 1998; Mon-Williams et al. 2001c). The question therefore arises as to which brain mechanisms might mediate this implicit obstacle avoidance.

Some recent studies of neurological patients have helped to narrow down the search. Our first study was with patient D.F. In an early study, we asked her to reach out and grasp a target block in the presence of a secondary object placed in locations to the left or right of the target (McIntosh et al. 2000; Rice et al., in press). D.F. took good account of the obstacle's location relative to the target, systematically shifting her reach trajectories in the same manner as control subjects. Given D.F.'s bilateral damage to the ventral stream, we inferred that she might be dependent on her relatively intact dorsal stream to achieve this skilled navigation. In other words, we suggested that both target-related processing *and* obstacle-related processing might share a common parietal substrate.

In a subsequent group study of twelve patients with spatial neglect, we examined the trajectories of arm movements during two tasks, both of which required the patient to steer between two objects (McIntosh et al. 2004a). In one task the patient had to point to the midpoint between two objects, while in the other she simply had to reach between them to a more distant target area. In both tasks, the locations of the left and right object varied independently of each other from trial to trial. We found that all but two of our patients fully retained their ability to take appropriate account of both objects whilst reaching between them, though they predictably failed to take adequate account of the one on the left ('neglected') side when trying to bisect the space between them. A crucial distinction can be drawn between the demands of the two tasks used by McIntosh et al. (2004a). The bisection task requires a deliberate perceptual judgement, whereas the reaching task merely requires the programming of a route that will minimize the risk of collision as the hand passes between the objects. In short, the first task requires spatial cognition, the second spatially guided action. Phrased in these terms, the requirements of the bisection task would seem likely to tax the ventral stream, whereas those of the reaching task might only involve the dorsal stream. We have therefore recently tested both of our visual-form agnosia patients, D.F. and S.B., on a closely similar pair of tasks. We found that they both made normal adjustments to their movements while reaching between the potential obstacles, but failed to do so in the bisection task, on which they performed below the normal range (Rice et al., in press). These data point clearly to the idea that implicit obstacle avoidance behaviour may indeed be served by the dorsal stream, which of course is largely spared both in our agnosic patients and in our neglect patients.

These studies have provided *indirect* evidence for dorsal-stream involvement in obstacle navigation, by showing that the skill survives damage that mainly affects the perceptual processing systems of the ventral stream and its putatively associated representational system, while leaving dorsal-stream structures relatively intact. We next set out to test the dorsal-stream hypothesis more directly, by testing two patients with

bilateral optic ataxia (I.G. and A.T.). In full confirmation of our prediction, they took no account whatsoever of the varying obstacle positions during reaching (Schindler et al. 2004). As before, we also tested the same patients on a task of bisecting the space between the two objects, in order to exclude a purely attentional interpretation of their impairment on the reaching task. In accordance with our hypothesis, the patients took perfectly full account of the objects in this more explicit 'perceptual' task.

It should be emphasized that the obstacle avoidance we have been studying in these experiments is of one specific kind – an 'automatic' or 'implicit' modification of reaching movements that allows people to minimize the risk of collision with a non-target object without having to think about what they are doing. It is automatic in the sense of being quite unintentional – in fact the separations we used would pose very little risk of collision in healthy subjects. But this behaviour also appears to be implicit, in the stronger sense of operating independently of visually awareness. In a study of the visual extinction patient V.E., who was referred to earlier, we were able to show that conscious awareness of the obstacles during reaching is quite unnecessary for achieving successful obstacle avoidance (McIntosh et al. 2004b). His reach trajectories did not vary when reaching between two fixed poles in the workspace, irrespective of whether or not he reported seeing the left pole. In contrast, his trajectories when there really *was* only the right pole present (or just the left pole alone) were highly significantly shifted (leftwards or rightwards, respectively) from the reaches when both poles were present.

Of course in some circumstances we need to do rather more than just minimize the risk of collision; we need to remove the risk entirely, either to protect the object or ourselves – for example when the potential obstacle is fragile or noxious, respectively. In this case, we can assume that perceptual processing, vested in the ventral visual stream, must play a role – otherwise the fragile or noxious nature of the obstacle could not be identified. The result will typically be a far more cautious navigation around the obstacle than otherwise, giving it a wider berth and slowing down more than usual. This 'perceptual' form of obstacle avoidance will presumably often involve conscious monitoring of the hand as well as the obstacle during a reach, a scenario that thereby resembles our bisection task more than our reaching task. Such conscious control would be necessary also in situations where the clearance available to the hand is more limited than in our task, or where the obstacle lies directly in the path of the intended reaching movement.

## Conclusions

Milner and Goodale (1995; Goodale & Milner 2004) have argued that both the dorsal and ventral visual streams participate in the guidance of spatially directed behaviour, but that they have evolved to achieve this in different and complementary ways: the dorsal stream by mediating direct transformations of the visual input into effector-based coordinates, and the ventral stream through the construction of perceptual and mnemonic representations that can transcend the temporal limitations of the dorsal

stream. We have presented supporting evidence from studies of the syndromes of optic ataxia, hemispatial neglect, and visual form agnosia; in relation to direct reaching and delayed reaching, as well as reaching between obstacles; and conclude that the dorsal stream's control of action is designed for dealing with target stimuli in the 'here and now', while they are still visible, rather than days, minutes, or even seconds later. On the other hand when time is allowed to pass and an action has to be made on the basis of a visual memory, then the ventral stream is required for successful performance. The data point directly to a 'two cortical visuospatial systems' hypothesis: one for perception and cognition (and *ultimately* for action), the other for *direct* control of spatially directed action. Thus just as object processing occurs in both ventral and dorsal streams, so does spatial processing. The difference between the streams is not about their inputs (Ungerleider & Mishkin 1982), it is fundamentally about their outputs (Milner & Goodale 1995; Goodale & Milner 2004).

## References


Aguirre, G. K., Zarahn, E., & D'Esposito, M. (1998). Neural components of topographical representation. *Proceedings of the National Academy of Science, USA, 95*, 839–846.

Andersen, R. A. (1987). Inferior parietal lobule function in spatial perception and visuomotor integration. In V. B. Mountcastle, F. Plum & S. R. Geiger (Eds.), *Handbook of Physiology, Section 1: The nervous system, Volume V. Higher functions of the brain, Part 2* (pp. 483–518). Bethesda, MD: American Physiological Society.

Baizer, J. S., Ungerleider, L. G., & Desimone, R. (1991). Organization of visual inputs to the inferior temporal and posterior parietal cortex in macaques. *Journal of Neuroscience, 11*, 168–190.

Bálint, R. (1909). Seelenlähmung des 'Schauens', optische Ataxie, räumliche Störung der Aufmerksamkeit. *Monatsschrift fuer Psychiatrie und Neurologie, 25,* 51–81.

Berkinblit, M. B., Fookson, O. I., Smetanin, B., Adamovich, S. V., & Poizner, H. (1995). The interaction of visual and proprioceptive inputs in pointing to actual and remembered targets. *Experimental Brain Research, 107*, 326–330.

Bisiach, E., Ricci, R., & Mòdona, M. N. (1998a). Visual awareness and anisometry of space representation in unilateral neglect: A panoramic investigation by means of a line extension task. *Consciousness and Cognition, 7*, 327–355.

Bisiach, E., Ricci, R., Lualdi, M., & Colombo, M. R. (1998b). Perceptual and response bias in unilateral neglect: Two modified versions of the Milner landmark task. *Brain and Cognition, 37*, 369–386.

Bisiach, E., Neppi-Modona, M., & Ricci, R. (2002). Space anisometry in unilateral neglect. In H.-O. Karnath, A. D. Milner & G. Vallar (Eds.), *The cognitive and neural bases of spatial neglect* (pp. 145–152). Oxford: Oxford University Press.

Buxbaum, L. J., & Coslett, H. B. (1998). Spatio-motor representations in reaching: Evidence for subtypes of optic ataxia. *Cognitive Neuropsychology, 15*, 279–312.

Caminiti, R., Ferraina, S., & Mayer, A. B. (1998). Visuomotor transformations: Early cortical mechanisms of reaching. *Current Opinion in Neurobiology, 8*, 753–761.

Carey, D. P., Coleman, R. J., & Della Sala, S. (1997). Magnetic misreaching. *Cortex, 33*, 639–652.

Carey, D. P., Dijkerman, H. C., & Milner, A. D. (1998). Perception and action in depth. *Consciousness and Cognition, 7*, 438–453.

Carey, D. P., Dijkerman, H. C., Murphey, K. J., Coodale, M. A., & Milner, A. D. (2006). Poiting to places and spaces in a patient with visual form agnosie. *Neuropsychologia*.

Castiello, U., Paulignan, Y., & Jeannerod, M. (1991). Temporal dissociation of motor responses and subjective awareness. *Brain, 114*, 2639–2655.

Chieffi, S. M., Gentilucci, M., Allport, A., Sasso, E., & Rizzolatti, G. (1993). Study of selective reaching and grasping in a patient with unilateral parietal lesion. *Brain, 116,* 1119–1137.

Connolly, J. D., Andersen, R. A., & Goodale, M. A. (2003). FMRI evidence for a 'parietal reach region' in the human brain. *Experimental Brain Research, 153*, 140–145.

Culham, J. (2004). Human brain imaging reveals a parietal area specialized for grasping. In N. Kanwisher & J. Duncan (Eds.), *Attention and Performance XX: Functional brain imaging of human cognition* (pp. 415–436). Oxford: Oxford University Press.

Culham, J. C., & Kanwisher, N. G. (2001). Neuroimaging of cognitive functions in human parietal cortex. *Current Opinion in Neurobiology, 11*, 157–163.

Culham, J. C., Danckert, S. L., DeSouza, J. F. X., Gati, J. S., Menon, R. S., & Goodale, M. A. (2003). Visually-guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. *Experimental Brain Research, 153*, 180–189.

Darling, W. G., Rizzo, M., & Butler, A. J. (2001). Disordered sensorimotor transformations for reaching following posterior cortical lesions. *Neuropsychologia, 39*, 237–254.

Desmurget, M., & Prablanc, C. (1997). Postural control of three-dimensional prehension movements. *Journal of Neurophysiology, 77*, 452–464.

Desmurget, M., Epstein, C. M., Turner R. S., Prablanc, C., Alexander, G. A., & Grafton, S. T. (1999). Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nature Neuroscience, 2,* 563–567.

Dijkerman, H. C., & Milner, A. D. (1997). Copying without perceiving: Motor imagery in visual form agnosia. *NeuroReport, 8*, 729–732.

Dijkerman, H. C., Milner, A. D., & Carey, D. P. (1996). The perception and prehension of objects oriented in the depth plane: I. Effects of visual form agnosia. *Experimental Brain Research, 112*, 442–451.

Dijkerman, H. C., Milner, A. D., & Carey, D. P. (1998). Grasping spatial relationships: Loss of allocentric visual coding in a patient with visual form agnosia. *Consciousness & Cognition, 7*, 424–437.

Dijkerman, H. C., Lê, S., Démonet, J.-F., & Milner, A. D. (2004). Visuomotor performance in a patient with visual agnosia due to an early lesion. *Cognitive Brain Research, 20*, 12–25.

Ellison, A., Schindler, I., Pattison, L. L., & Milner, A. D. (2004). An exploration of the role of the superior temporal gyrus in visual search and spatial perception using TMS. *Brain, 127*, 2307–2315.

Ettlinger, G., & Kalsbeck, J. E. (1962). Changes in tactile discrimination and in visual reaching after successive and simultaneous bilateral posterior parietal ablations in the monkey. *Journal of Neurology, Neurosurgery and Psychiatry, 25,* 256–268.

Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature, 392*, 568–601.

Farnè, A., Rossetti, Y., Toniolo, S., & Ladavas, E. (2002). Ameliorating neglect with prism adaptation: Visuo-manual and visuo-verbal measures. *Neuropsychologia, 40*, 718–729.

Farnè, A., Roy, A. C., Paulignan, Y., Rode, G., Rossetti, Y., Boisson, D., et al. (2003). Visuo-motor control of the ipsilateral hand: Evidence from right brain-damaged patients. *Neuropsychologia, 41*, 739–757.

Faugier-Grimaud, S., Frenois, C., & Stein, D. G. (1978). Effects of posterior parietal lesions on visually guided behavior in monkeys. *Neuropsychologia, 16,* 151–168.

Ferrier, D., & Yeo, G. F. (1884). A record of experiments on the effects of lesion of different regions of the cerebral hemispheres. *Philosophical Transactions of the Royal Society of London, 175*, 479–564.

Frassinetti, F., Angeli, V., Meneghello, F., Avanzi, S., & Ladavas, E. (2002). Long-lasting amelioration of visuospatial neglect by prism adaptation. *Brain, 125,* 608–23.

Garcin, R., Rondot, P., & de Recondo, J. (1967). Ataxie optique localisee aux deux hemichamps visuels homonymes gauches. *Revue Neurologique, 116*, 707–714.

Glickstein, M., & May, J. G. (1982). Visual control of movement: The circuits which link visual to motor areas of the brain with special reference to the visual input to the pons and cerebellum. In W. D. Neff (Ed.), *Contributions to Sensory Physiology*, Vol. 7 (pp. 103–145). New York: Academic Press.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences, 15*, 20–25.

Goodale, M. A., & Milner, A. D. (2004). *Sight Unseen: An exploration of conscious and unconscious vision*. Oxford: Oxford University Press.

Goodale, M. A., Pélisson, D., & Prablanc C. (1986). Large adjustments in visually guided reaching do not depend on vision of the hand and perception of target displacement. *Nature, 320,* 748–750.

Goodale, M. A., Milner, A. D., Jakobson, L. S., & Carey D. P. (1990). Kinematic analysis of limb movements in neuropsychological research: Subtle deficits and recovery of function. *Canadian Journal of Psychology, 44,* 180–195.

Goodale, M. A., Milner, A. D., Jakobson, L. S., & Carey, D. P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature, 349*, 154–156.

Goodale, M. A., Jakobson, L. S., & Keillor, J. M. (1994). Differences in the visual control of pantomimed and natural grasping movements. *Neuropsychologia, 32*, 1159–1178.

Gréa, H., Desmurget, M., Prablanc, C. (2000). Postural invariance in three-dimensional reaching and grasping movements. *Experimental Brain Research*, *134*, 55–62.

Gréa, H., Pisella, L., Rossetti, Y., Desmurget, M., Tilikete, C., & Grafton, S. et al. (2002). A lesion of the posterior parietal cortex disrupts on-line adjustments during aiming movements. *Neuropsychologia, 40*, 2471–2480.

Habib, M., & Sirigu, A. (1987). Pure topographic disorientation. A definition and anatomical basis. *Cortex, 23,* 73–85.

Harvey M., Milner A. D., & Roberts R. C. (1994). Spatial bias in visually-guided reaching and bisection following right cerebral stroke. *Cortex, 30,* 343–350.

Harvey, M. (1995). Translation of 'Psychic paralysis of gaze, optic ataxia, and spatial disorder of attention' by Rudolph Bálint. *Cognitive Neuropsychology, 12*, 261–282.

Harvey, M., Jackson, S. R., Newport, R., Krämer, T., Morris, D. L., & Dow, L. (2002). Is grasping impaired in hemispatial neglect? *Behavioural Neurology, 13,* 17–28.

Harvey, M., Hood, B., North, A., & Robertson, I. H. (2003). The effects of visuomotor feedback training on the recovery of hemispatial neglect symptoms: Assessment of a 2-week and follow-up intervention. *Neuropsychologia, 41*, 886–893.

Heider, B. (2000). Visual form agnosia: Neural mechanisms and anatomical foundations. *Neurocase, 6*, 1–12.

Himmelbach, M., & Karnath, H.-O. (2003). Goal-directed hand movements are not affected by the biased space representation in spatial neglect. *Journal of Cognitive Neuroscience, 15*, 972–980.

Himmelbach, M., Clavagnier, S., Perenin, M.-T., & Karnath, H.-O. (2003). fMRI of delayed pointing in a patient with optic ataxia: The ventral stream is not the solitary actor. *Acta Neurobiologiae Experimentalis, 63* (Suppl.), 86.

Hyvärinen, J., & Poranen, A. (1974). Function of the parietal associative area 7 as revealed from cellular discharges in alert monkeys. *Brain, 97,* 673–692.

Ishihara, M., Pisella, L., Blangero, A., Luaute, J., Krolak-Salmon, P., Rode, G., et al. (2004). Posterior parietal contributions in motor programming for peripheral visual targets. *Perception, 33* (Suppl.), 165–166.

Jackson, S. R., Newport, R., Husain, M., Harvey, M and Hindle, J. V. (2000). Reaching movements may reveal the distorted topography of spatial representations after neglect. *Neuropsychologia*, *38,* 500–507.

Jakobson, L. S., Archibald, Y. M., Carey, D. P., & Goodale, M. A. (1991). A kinematic analysis of reaching and grasping movements in a patient recovering from optic ataxia. *Neuropsychologia, 29*, 803–809.

James, T. W., Culham, J., Humphrey, G. K., Milner, A. D., & Goodale, M. A. (2003). Ventral occipital lesions impair object recognition but not object-directed grasping: A fMRI study. *Brain, 126*, 2463–2475.

Jeannerod, M. (1986). Mechanisms of visuo-motor coordination: A study in normal and brain-damaged subjects. *Neuropsychologia, 24*, 41–78.

Jeannerod, M. (1988). *The neural and behavioural organization of goal-directed movements*. Oxford: Oxford University Press.

Jeannerod, M., & Rossetti, Y. (1993). Visuomotor coordination as a dissociable visual function: Experimental and clinical-evidence. In C. Kennard (Ed.), Visual perceptual defeets. *Baillieres Clinical Neurology, 2,* 439–460. London, Bailliere Tindall.

Jeannerod, M., Decety, J., & Michel, F. (1994). Impairment of grasping movements following bilateral posterior parietal lesion. *Neuropsychologia, 32*, 369–380.

Karnath, H.-O., Dick, H., & Konczak, J. (1997). Kinematics of goal-directed arm movements in neglect: Control of hand in space. *Neuropsychologia, 35*, 435–444.

Karnath, H.-O., Ferber, S., & Himmelbach, M. (2001). Spatial awareness is a function of the temporal not the posterior parietal lobe. *Nature, 411*, 950–953.

Karnath, H.-O., Frűhmann Berger, M., Kuker, W., & Rorden, C. (2004). The anatomy of spatial neglect based on voxelwise statistical analysis: A study of 140 patients. *Cerebral Cortex, 14*, 1164–1172.

Karnath, H.-O., & Perenin, M. T. (2005). Cortical control of visually guided reaching: Evidence from patients with optic ataxia. *Cerebral Cortex, 15*, 1561–1569.

Kerkhoff, G. (2000). Multiple perceptual distortions and their modulation in leftsided visual neglect. *Neuropsychologia, 38*, 1073–1086.

Khan, A. Z., Pisella, L., Vighetto, A., Cotton, F., Luaute, J., Boisson, D., et al. (2005). Optic ataxia errors depend on remapped, not viewed, target location. *Nature Neuroscience, 8*, 418–420.

Khan, A. Z., Pisella, L., Rossetti, Y., Vighetto, A., & Crawford, J. D. (2005). Impairment of gaze-centered updating of reach targets in bilateral parietal-occipital damaged patients. *Cerebral Cortex, 15*, 1547–1560.

Konczak, J., & Karnath, H.-O. (1998). Kinematics of goal-directed arm movements in neglect: Control of hand velocity. *Brain and Cognition, 37*, 387–403.

Konczak, J., Himmelbach, M., Perenin, M. T., & Karnath, H.-O. (1999). Do patients with neglect show abnormal hand velocity profiles during tactile exploration of peripersonal space? *Experimental Brain Research, 128*, 219–223.

Landis, T., Cummings, J. L., Benson, D. F. and Palmer, E. P. (1986). Loss of topographic familiarity. An environmental agnosia. *Archives of Neurology, 43,* 132–136.

Lê, S., Cardebat, D., Boulanouar, K., Hénaff, M.-A., Michel, F., & Milner, A. D. et al. (2002). Seeing, since childhood, without ventral stream: A behavioural study. *Brain, 125*, 58–74.

Leibovitch, F. S., Black, S. E., Caldwell, C. B., Ebert, P. L., Ehrlich, L. E., & Szalai, J. P. (1998). Brain-behavior correlations in hemispatial neglect using CT and SPECT: The Sunnybrook Stroke Study. *Neurology, 50*, 901–908.

Levine, D. N., Kaufman, K. J., & Mohr, J. P. (1978). Inaccurate reaching associated with a superior parietal lobe tumor. *Neurology, 28*, 556–561.

Malhotra, P., Jager, H. R., Parton, A., Greenwood, R., Playford, E. D., & Brown, M. M. et al. (2005). Spatial working memory capacity in unilateral neglect. *Brain, 128*, 424–435.

Marotta, J. J., Behrmann, M., & Goodale, M. A. (1997). The removal of binocular cues disrupts the calibration of grasping in patients with visual form agnosia. *Experimental Brain Research, 116*, 113–121.

Mattingley, J. B., & Driver, J. (1997). Distinguishing sensory and motor deficits after parietal damage: An evaluation of response selection biases in unilateral neglect. In P. Thier & H.-O. Karnath (Eds.), *Parietal lobe contributions to orientation in 3D space* (pp. 309–337). Heidelberg: Springer-Verlag.

Mattingley, J. B., Husain, M., Rorden, C., Kennard, C., & Driver, J. (1998). Motor role of human inferior parietal lobe revealed in unilateral neglect patients. *Nature, 392*, 179–182.

McIntosh, R. D., Dijkerman, H. C., Mon-Williams, M., & Milner, A. D. (2000). Visuomotor processing of spatial layout in visual form agnosia. Paper presented at the Experimental Psychology Society, Cambridge, April.

McIntosh, R. D., Pritchard, C. L., Dijkerman, H. C., Milner, A. D., & Roberts, R. C. (2002). Prehension and perception of size in left visuospatial neglect. *Behavioural Neurology, 13*, 3–15.

McIntosh, R. D., McClements, K. I., Dijkerman, H. C., Birchall, D., & Milner, A. D. (2004a). Preserved obstacle avoidance during reaching in patients with left visual neglect. *Neuropsychologia, 42*, 1107–1117.

McIntosh, R. D., McClements, K. I., Schindler, I., Cassidy, T. P., Birchall, D., & Milner, A. D. (2004b). Avoidance of obstacles in the absence of visual awareness. *Proceedings of the Royal Society of London B, 271*, 15–20.

McIntosh, R. D., Dijkerman, C. D., Mon-Williams, M., & Milner, A. D. (2004c). Grasping what is graspable: Evidence from visual form agnosia. *Cortex, 40*, 695–702.

McIntyre, J., Stratta, F., & Lacquaniti, F. (1997). Viewer-centered frame of reference for pointing to memorized targets in three-dimensional space. *Journal of Neurophysiology, 78*, 1601–1618.

Milner, A. D. (1997). Neglect extinction, and cortical streams of visual processing. In P. Thier and H. O. Kornath (Eds.), *Parietal lobe contributions to orientation in 3D space* (pp. 3–22). Heidelberg: Springer-Verlag.

Milner, A. D., & Dijkerman, H. C. (1998). Visual processing in the primate parietal lobe. In A. D. Milner (Ed.), *Comparative neuropsychology* (pp. 70–94). Oxford: Oxford University Press.

Milner, A. D., & Dijkerman, H. C. (2001). Direct and indirect visual routes to action. In B. De Gelder, E. De Haan & C. A. Heywood (Eds.), *Out of Mind: Varieties of unconscious processes* (pp. 241–264). Oxford: Oxford University Press.

Milner, A. D., & Goodale, M. A. (1995). *The Visual Brain in Action*. Oxford: Oxford University Press.

Milner, A. D., Perrett, D. I., Johnston, R. S., Benson, P. J., Jordan, T. R., & Heeley, D. W. et al. (1991). Perception and action in 'visual form agnosia'. *Brain, 114*, 405–428.

Milner, A. D., Brechmann, M., & Pagliarini, L. (1992). To halve and halve not: An analysis of line bisection judgements in normal subjects. *Neuropsychologia, 30*, 515–526.

Milner, A. D., Harvey, M., Roberts, R. C., & Forster, S. V. (1993). Line bisection errors in visual neglect: Misguided action or size distortion? *Neuropsychologia, 31*, 39–49.

Milner, A. D., Harvey, M., & Pritchard, C. L. (1998). Visual size processing in spatial neglect. *Experimental Brain Research, 123,* 192–200.

Milner, A. D., Dijkerman, H. C., & Carey, D. P. (1999a). Visuospatial processing in a pure case of visual-form agnosia. In N. Burgess, K. J. Jeffery & J. O'Keefe (Eds.), *The hippocampal and parietal foundations of spatial cognition* (pp. 443–466). Oxford: Oxford University Press.

Milner, A. D., Paulignan, Y., Dijkerman, H. C., Michel, F., & Jeannerod, M. (1999b). A paradoxical improvement of optic ataxia with delay: New evidence for two separate neural systems for visual localization. *Proceedings of the Royal Society of London, B 266*, 2225–2230.

Milner, A. D., Dijkerman, H. C., McIntosh, R. D., Rossetti, Y., & Pisella, L. (2003). Delayed reaching and grasping in patients with optic ataxia. *Progress in Brain Research, 142*, 225–242.

Mon-Williams, M., Tresilian, J. R., McIntosh, R. D., & Milner, A. D. (2001a). Monocular and binocular distance cues: Insights from visual form agnosia. I. *Experimental Brain Research, 139*, 127–136.

Mon-Williams, M., McIntosh, R. D., & Milner, A. D. (2001b). Vertical gaze angle as a distance cue for programming reaching: Insights from visual form agnosia. II. *Experimental Brain Research, 139*, 137–142.

Mon-Williams, M., Tresilian, J. R., Coppard, V. L., & Carson, R. G. (2001c). The effect of obstacle position on reach-to-grasp movements. *Experimental Brain Research, 137*, 497–501.

Morel, A., & Bullier, J. (1990). Anatomical segregation of two cortical visual pathways in the macaque monkey. *Visual Neuroscience, 4*, 555–578.

Mort, D. J., Molhotra, P., Mannan, S. K., Rorden, C., Pambakian, A., Kennard, C., et al. (2003). The anatomy of visual neglect. *Brain, 126* 1986–1997.

Mort, D. J., Malhotra, P., Mannan, S. K., Pambakian, A., Kennad, C., & Husain, M. (2004). Reply to: Karnath, H.-O., Frűhmann Berger, M, Zopf, R. and Kueker, W. (2004). Using SPM normalization for lesion analysis in spatial neglect. *Brain, 127,* e11.

Mountcastle, V. B., Lynch, J. C., Georgopoulos, A. P., Sakata, H., & Acuca, C. (1975). Posterior parietal association cortex of the monkey: Command function of operations within extrapersonal space. *Journal of Neurophysiology, 38,* 871–907.

Murphy, K. J., Carey, D. P., & Goodale, M. A. (1998). The perception of spatial relations in a patient with visual form agnosia. *Cognitive Neuropsychology, 15*, 705–722.

Pélisson, D., Prablanc, C., Goodale, M. A, Jeannerod, M. (1986). Visual control of reaching movements without vision of the limb. Part II. Evidence of fast unconscious processes correcting the trajectory of the hand to the final position of a double step stimulus. *Experimental Brain Research, 62,* 303–311.

Perenin, M.-T. (1997). Optic ataxia and unilateral neglect: Clinical evidence for dissociable spatial functions in posterior parietal cortex. In P. Thier & H.-O. Karnath (Eds.), *Parietal lobe contributions to orientation in 3D space* (pp. 289–308). Heidelberg: Springer-Verlag.

Perenin, M.-T., & Vighetto, A. (1988). Optic ataxia: A specific disruption in visuomotor mechanisms. I. Different aspects of the deficit in reaching for objects. *Brain, 111*, 643–674.

Perenin, M. T., Revol, P., Paulignan, Y., & Vighetto, A. (1999). Optic ataxia is improved in conditions of 'indirect' pointing: Further evidence for two modes of spatial localization. *Neural Plasticity, S1*, 153–154.

Pisella, L., Tiliket, C., Rode, G., Boisson, D., Vighetto, A., & Rossetti, Y. (1999). Automatic corrections prevail in spite of an instructed stopping response. In M. Grealy & J. A. Thomson (Eds.), *Studies in perception and action* (pp. 275–279). Hillsdale, NJ: Erlbaum.

Pisella, L., Gréa, H., Tiliket, C., Vighetto, A., Desmurget, M., & Rode, G. et al. (2000). An 'automatic pilot' for the hand in human posterior parietal cortex: Toward reinterpreting optic ataxia. *Nature Neuroscience, 3*, 729–736.

Pisella, L., Berberovic, N., & Mattingley, J. B. (2004). Impaired working memory for location but not for colour or shape in visual neglect: A comparison of parietal and non-parietal lesions. *Cortex, 40*, 379–390.

Pitzalis, S., Di Russo, F., Figliozzi, F., & Spinelli, D. (2004). Underestimation of contralateral space in neglect: A deficit in the "where" task. *Experimental Brain Research, 159*, 319–328.

Prablanc, C., Pelisson, D., & Goodale, M. A. (1986). Visual control of reaching movements without vision of the limb. *Experimental Brain Research, 62*, 293–302.

Pritchard, C. L., Milner, A. D., Dijkerman, H. C., & MacWalter, R. S. (1997). Visuospatial neglect: Veridical coding of size for grasping but not for perception. *Neurocase, 3*, 437–443.

Ratcliff, G., & Davies-Jones, G. A. B. (1972). Defective visual localization in focal brain wounds. *Brain, 95,* 49–60.

Revol, P., Rossetti, Y., Vighetto, A., Rode, G., Boisson, D., & Pisella, L. (2003). Pointing errors in immediate and delayed conditions in unilateral optic ataxia. *Spatial Vision, 16*, 347–364.

Ricci, R., Pia, L., & Gindri, P. (2004). Effects of illusory spatial anisometry in unilateral neglect. *Experimental Brain Research, 154*, 226–237.

Rice, N. J., McIntosh, R. D., Schindler, I., Démonet, J.-F., & Milner, A. D. (in press). Automatic avoidance of obstacles in patients with visual form agnosia.

Rizzolatti, G., & Gentilucci, M. (1988). Motor and visual-motor functions of the premotor cortex. In P. Rakic & W. Singer (Eds.), *Neurobiology of neocortex* (pp. 269–284). Chichester: Wiley.

Robertson, I. H., Nico, D., & Hood, B. (1995). The intention to act improves unilateral left neglect: Two demonstrations. *NeuroReport, 7*, 246–248.

Robertson, I. H., Nico, D., & Hood, B. M. (1997). Believing what you feel: Using proprioceptive feedback to reduce unilateral neglect. *Neuropsychology, 11*, 53–58.

Rossetti, Y., Rode, G., Pisella, L., Farnè, A., Li, L., & Boisson, D. et al. (1998). Prism adaptation to a rightward optical deviation rehabilitates left visuospatial neglect. *Nature, 40*, 1597–1599.

Rossetti, Y., Pisella, L., & Vighetto, A. (2003). Optic ataxia revisited: Visually guided action versus immediate visuomotor control. *Experimental Brain Research, 153*, 171–179.

Rossetti, Y., McIntosh, R. D., Revol, P., Pisella, L., Rode, G., & Danckert, J. et al. (2005). Visually guided reaching: Bilateral posterior parietal lesions cause a switch from fast visuomotor to slow cognitive control. *Neuropsychologia, 43*, 162–177.

Schenk, T., Schindler, I., McIntosh, R. D., & Milner, A. D. (2005). The use of visual feedback is independent of visual awareness: Evidence from visual extinction. *Experimental Brain Research, 167*, 95–102.

Schindler, I., Ellison, A., Pattison, L. L., & Milner, A. D. (under revision). Simulation of spatial and object-based neglect using transcranial magnetic stimulation.

Schindler, I., Rice, N. J., McIntosh, R. D., Rossetti, Y., Vighetto, A., & Milner, A. D. (2004). Automatic avoidance of obstacles is a dorsal stream function: Evidence from optic ataxia. *Nature Neuroscience, 7*, 779–784.

Snyder, L. H., Batista, A. P., & Andersen, R. A. (1997). Coding of intention in the posterior parietal cortex. *Nature, 386*, 167–170.

Tresilian, J. R. (1998). Attention in action or obstruction of movement? A kinematic analysis of avoidance behaviour in prehension. *Experimental Brain Research, 120*, 352–368.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT Press.

Vallar, G., & Perani, D. (1987). The anatomy of unilateral neglect after right-hemisphere stroke lesions. A clinical / CT-scan correlation study in man. *Neuropsychologia, 24*, 609–622.

Van Essen, D. C., & DeYoe, E. A. (1995). Concurrent processing in the primate visual cortex. In M. S. Gazzaniga (Ed.), *The Cognitive Neurosciences* (pp. 383–400). Cambridge, MA: MIT Press.

Young, M. P. (1992). Objective analysis of the topological organization of the primate cortical visual system. *Nature, 358*, 152–155.

CHAPTER 4.3

# Visual peripersonal space

Andrea Serino, Alessandro Farnè, and Elisabetta Làdavas

## Introduction

A stable representation of external space requires integration of information stemming from multiple sensory modalities. As we typically receive a simultaneous flow of information from each of our senses in real word situations, our perception of space is the product of an integrated multisensory processing. It seems entirely adaptive that the multiple sources of information, derived from the different modalities, could be combined to yield the best estimate of the external events (Driver & Spence 2000).

The last two decades of neurophysiological research have brought a large body of evidence to support the notion that multisensory integration at single-neuron level is a frequent feature in spatial representation, especially in the coding of near-peripersonal space (Hyvarinen & Poranen 1974; Rizzolatti et al. 1981, 1998; Duhamel et al. 1991, 1998; Graziano & Gross 1995, 1998). For instance, animal experiments have revealed an ever-growing body of evidence supporting the notion that visual space surrounding the body (near peripersonal space) in the monkey is coded through multisensory integration at the single-neuron level. It is now widely accepted that a number of structures and cortical areas of the monkey brain, like putamen, the post-central gyrus and parietal areas 7b and VIP, as well as premotor areas play some special role in representing the space that closely surrounds the animal's body. These areas contain a high proportion of multimodal neurons that have a tactile and visual and/or auditory receptive fields and display a quite good level of spatial register among them. For example, visual and auditory RFs match the location of the somatosensory RF, extending only a few centimeters outward from the skin. These neurons respond to both tactile and visual (or auditory) stimuli provided that visual (or auditory) stimuli are presented immediately adjacent to a particular body part (e.g., head or hand).

The main functional properties of these multimodal neurons can be summarized as follows: (1) The visual RFs, which are in approximate spatial register with the tactile RFs, operate to some degree in body part centered coordinates, moving with the body-part when it moves, and not when the eye moves; (2) The extent of the visual RFs is typically restricted to the space immediately surrounding the body part; (3) The strength of the visual response decreases with distance from the body part.

On the basis of these functional properties, several authors have suggested that premotor cortex, parietal areas and putamen form an interconnected system for integrated multisensory coding of near-peripersonal space (Colby et al. 1993; Duhamel et al. 1998; Fogassi et al. 1996, 1998; Graziano et al. 1997), whereby multisensory responses are observed, as opposed to a far-peripersonal space that is outside the range of bimodal response sensitivity.

*An integrated visuo-tactile system coding near peripersonal space in humans*

Recent neuropsychological findings from our laboratory provided the first evidence that the human brain forms integrated visual-tactile representations of the space closely surrounding the body. This was shown by taking advantage of a neuropsychological condition called 'extinction', which provided considerable insight into the behavioral characteristics of multimodal spatial representation in humans. Extinction (Loeb 1885; Oppenheim 1885) is a pathological sign following brain damage whereby some patients fail to report a stimulus presented to the contralesional affected side only when a concurrent stimulus is presented on the ipsilesional side of the body, that is, under conditions of double simultaneous stimulation (Bender 1952). The fact that patients fail to report the presence of a contralesional stimulus only when an ipsilesional stimulus is concurrently presented, has been taken as hallmark of the "competitive" nature of the extinction phenomenon (di Pellegrino & De Renzi 1995; Ward et al. 1994).

Extinction emerges as a consequence of an uneven competition between spared and affected representations of space, whereby ipsi- and contra-lesional stimuli benefit from competitive weights of different strength, for accessing a limited pool of attentional resources (di Pellegrino & De Renzi 1995; Diver et al. 1997; Driver 1998; Duncan 1980, 1996). When two opposite stimuli are engaged in competition in patients affected by extinction, the ipsilesional stimulus benefits from a higher weight as compared to the contralesional stimulus, whose competitive strength has been reduced by the lesion of a brain area representing a portion of contralateral space. As a result, when two simultaneous stimuli are engaged in competition, the contralesional stimulus evokes a weaker activation of that portion of space, thus loosing the competition and appearing to be extinguished by the relatively stronger ipsilesional stimulus.

*Visual peripersonal space near the hand*

In a series of studies from our laboratory, we have tried to verify whether the presentation of a visual stimulus in the right ipsilesional field can extinguish the tactile stimulus presented on the contralesional hand, which is otherwise well detected by patients when presented alone. The prediction of these studies was that if a multisensory (visuo-tactile) system processing tactile and visual stimuli near the body is in charge of coding left and right spatial representations, then delivering visual stimuli close to a body part ($\leq$ 7 cm) would be more effective in producing cross-modal visuo-tactile extinction than presenting the same visual stimuli at larger distances ($\geq$ 35 cm). We

refer to these locations as, respectively, the near-peripersonal and the far-peripersonal space of a given body part.

The results of these studies showed strong effects of cross-modal modulation of tactile perception, which appeared to be 1) remarkably dependent upon the spatial congruence of visuo-tactile inputs relative to the affected side and, 2) most consistently manifest when visuo-tactile interaction occurred in the near peripersonal space. In agreement with the predictions of our hypothesis, the results can be considered a strong neuropsychological evidence that the human brain represents near peripersonal space through an integrated multisensory visuo-tactile system. Due to its activity, visual stimulation nearby the ipsilesional hand strongly activates its somatosensory representation. Concerning the phenomenon of extinction, the nearby visual stimulus produces the same behavioural consequence as if a tactile stimulus were delivered to the ipsilesional hand. In patients with left tactile extinction, in whom spatial competition is biased ipsilesionally, the somatosensory representation of the left and right hand, activated by tactile and a visual stimuli, largely extinguishes contralesional tactile stimuli. This because the processing of the somatosensory stimulation of the contralesional hand is disadvantaged in terms of competitive weights, and gives rise to a comparatively weaker representation.

To examine the spatial co-ordinates used by this integrated visuo-tactile system to code near-peripersonal space, a patient with tactile extinction was asked to cross the hands such that the left hand was in the right hemispace and the right hand in the left hemispace (di Pellegrino et al. 1997). A visual stimulus presented near the right hand (in the left space) extinguished tactile stimuli applied to the left hand (in right hemispace). Thus, the cross-modal visuo-tactile extinction was not modulated by the position of the hands in space, as far as the visual-right hand/tactile-left hand stimulus mapping is kept constant. This finding, by showing that the visual peripersonal space remains anchored to the hand when this is moved, strongly suggests that the near peripersonal space is at least partially coded in a hand-centred co-ordinate system.

*Visual peripersonal space near the face*

The pattern of results observed in the case of visual-tactile stimulation of the hand is highly consistent with the functional properties of the multisensory system that has been described in monkeys, further suggesting that human and non-human primates might share, at some level, similar cerebral mechanisms for near space representation. One way to further investigate this issue consists of assessing whether other properties that pertain to monkeys' multisensory system can also be revealed in human behaviour. In this respect, one interesting question is whether humans represent near-peripersonal space not only in relation to hands, but also to other body parts. Neurophysiological findings have demonstrated a somatotopic distribution of multisensory neurons' RFs, which are known to be mostly located on the animal hand/arm, trunk, and face. These latter neurons seem to be particularly relevant, since a specific multimodal area of the parietal lobe (VIP) is mainly devoted to representing space near the face (Colby et al. 1993; Duhamel et al. 1991, 1998). Therefore, we reasoned that a

multisensory mechanism, similar to that operating in the case of the hand, might also be involved in representing near-peripersonal space in relation to the human face.

Therefore, analogously to the previous studies, we investigated whether the presentation of ipsilesional visual stimuli near the face may modulate left tactile extinction (Làdavas et al. 1998). We also expected that cross-modal modulation of extinction would be stronger by presenting visual stimuli near the patients' face, compared to far from it. This hypothesis, which has been assessed in a group of RBD patients with left unimodal tactile extinction, was clearly supported. As for the hand, visual stimuli presented to the ipsilesional side produced a decrease in the detection of contralesional tactile stimuli, particularly when visual stimuli were presented near the ipsilesional cheek. In this condition, patients reported only few touches of the left cheek, which were otherwise well perceived when delivered alone. Again, the cross-modal reduction produced by nearby visual stimulation of the right cheek was so strong that the amount of contralesional touches that patients were able to report was comparable to that obtained following bilateral tactile stimulation. This phenomenon was much less severe when visual stimuli were delivered far from the face; in this case patients were still able to report the majority of contralesional touches.

Thus, these studies suggest the existence of an integrated system that controls both visual and tactile inputs within near-peripersonal space of the face and the hand, which can be functionally separated from that controlling visual information in the far-peripersonal space (Farnè & Làdavas 2002; Làdavas 2002).

*Unitary vs. modular representation of visual peripersonal space*

One question that needs to be answered is whether the modular organisation of space, which seems to operate as a general principle governing spatial perception, also applies to the representation of the near peripersonal space. Paraphrasing Graziano & Gross's metaphor of near peripersonal space, should we conceive this 'gelatinous medium' surrounding the body as a unitary, homogeneous sector of space encompassing the whole body, or as a collection of modules, each coding for the space immediately adjacent to a specific body-part?

In a recent study (Farnè et al., 2005) we tried to answer this question by testing the unitary vs. modular representation hypothesis. As the two hypotheses make opposite predictions, we tested them directly by investigating cross-modal visual-tactile extinction in a group of right brain-damaged patients. We reasoned that, if the unitary hypothesis were true, then tactile stimuli delivered on the contralesional hand would be comparably extinguished by ipsilesional visual stimuli irrespective of the stimulated body-part (either the hand or the face), provided that the visual stimulus were presented *near* the body. Alternatively, if near peripersonal space is represented in a modular way, then tactile stimuli delivered on the contralesional hand would be more severely extinguished when ipsilesional visual stimuli are presented near the homologous body part (i.e., the right hand), than near the non homologous body part (i.e., the right side of the face). Additionally, the two hypotheses also differ with respect to the near-far modulation of cross-modal extinction. While the near-far modulation is

expected when stimulating homologous sectors, its presence in the case of stimulation of non homologous sectors would support the unitary hypothesis; in contrast, its absence would favor the modular organization hypothesis.

The results showed a stronger V-T extinction between homologous than non homologous combinations and how the effect was selectively present when visual stimuli were presented *near* the ipsilesional side of the patients' body. In sharp contrast, when visual stimuli were presented *far* from the ipsilesional side of the patients' body, the amount of V-T extinction obtained in homologous and non homologous combinations was absolutely comparable. This suggests that the modular organization of the 'gelatinous medium surrounding our bodies' may be specifically limited to the most proximal, near peripersonal sectors.

*Functional characteristics of visual peripersonal space:*
*Plasticity of the peripersonal space*

Taken together, the neurophysiological and neuropsychological findings reviewed above converge in showing that peripersonal space, instead of univocally correspond to the reaching space, may be further decomposed in a near and far peripersonal space sectors. However, there are many interesting questions, such as the following ones, that deserve to be answered. Is the extension of the peripersonal space fixed in space or can it be modified? If it can be modified, according to what kind of experience? Is a simple change of our visual body-image sufficient to dynamically re-map far space as near, or is some kind of visuo-motor activity necessary to produce this re-mapping?

These important questions concerning near-peripersonal space in humans are tightly linked to, and partially suggested by, available neurophysiological evidence. Recent animal studies have examined whether the near-peripersonal space of monkeys' hands, and especially its spatial extension and location, can be modified through different kinds of sensorimotor experience. So far, the manipulations attempted have mainly concerned the use of a tool as an extension of the peri-personal space (Iriki et al. 1996, 2001; Obayashi et al 2000).

A re-coding of relatively far visual stimuli as near ones has been observed in monkey single-cells studies, after extensive experience with the use of a tool. In these studies, a rake-shaped tool was used to connect the animal's hand with objects located outside its reaching distance, with the result of actually extending the hand's reachable space. Once the monkeys were trained to use the rake to retrieve distant food, a few minutes of tool-use induced an expansion of visual RFs of bimodal neurons recorded in the parietal cortex. This rapid expansion along the tool axis seemed to incorporate the tool into the hand's peripersonal space representation. The extended visual RF contracted back to pre-tool-use dimensions after a short rest, even if the monkey was still passively holding the rake (Iriki et al. 1996). Therefore, the tool-use related expansion of the visual RFs was strictly dependent upon the intended use of the rake to reach distant objects. No modification was ever found when the monkey was just passively holding the tool.

A similar effect of re-coding of visual stimuli located in far-peripersonal space, as if they were closer to the participants' body, has been found behaviourally in a group of right brain-damaged patients with tactile extinction by Farnè and Ladavas (2000). In this study, the amount of cross-modal visual-tactile extinction was assessed by presenting visual stimuli far from the patients ipsilesional hand, at the distal edge of a 38 cm-long rake passively held in their hand. The patients' performance was evaluated before tool use, immediately after a 5 minutes period of tool use, and after a further ±10 min. resting period. To isolate any possible effect due to mere motor activity, cross-modal extinction was also assessed immediately after a 5 min. period of hand pointing movements. We found that visual stimuli, presented at the tip of a 38 cm long rake statically held in the patients' ipsilesional hand, induced more contralesional tactile extinction immediately after tool-use (retrieving distant objects with the rake), than before tool-use, when they just hold the rake passively. This evidence of an expansion of near-peripersonal space of the hand lasted only few minutes after tool use. After the 5 minutes resting period, the amount of cross-modal extinction had regained a pre-tool-use level, suggesting that the spatial extension of the hand's near-peripersonal space contracted back towards patients' hand. Finally, the amount of cross-modal extinction found immediately after the execution of pointing movements toward distant objects was entirely comparable to that obtained in the pre-tool-use condition. Further neuropsychological evidence of expansion of peri-hand space in humans has been reported by other authors, yielding similar results (Maravita et al. 2001; Berti & Frassinetti 2000).

Several reports have now shown that tool-use can change space perception both in normal subjects and in brain damaged patients, thus raising several questions about the crucial determinants and the characteristics of peri-hand space extension. Is a passive change of the corporeal configuration (hand+tool) sufficient, or is some goal-directed activity needed? A crucial question concerns the critical determinant of the extent to which peri-hand space increase. Does this depend upon the physical, absolute length of the tool, or the length of the tool that can be effectively used to act on objects? Finally a third question concerns the actual shape of the expansion of the peri-hand space after tool use: does it consist in a real elongation of the multisensory integrative area along the axis of the tool or in a shift of these proprieties to the tip of the tool?

When considering the first issue, i.e. the role played by passive or active experience, the results of a recent study (Farnè et al. 2005a) were clear in showing that a relatively prolonged, but passive experience with a tool is not sufficient to induce such a dynamic remapping of far space as near space. Indeed, when cross-modal effects were assessed in the far space after a short period of passive exposure to the proprioceptive and visual experience of wielding a rake, the severity of visual-tactile extinction was absolutely comparable to that obtained when the tool was actually absent. This favours the idea that plastic modifications of the body schema (Head & Holmes 1911) are not the product of passive changes in proprioceptive/kinesthesic, or visual inputs *per se*. An artificial extension of our reachable space by a hand-held tool would not

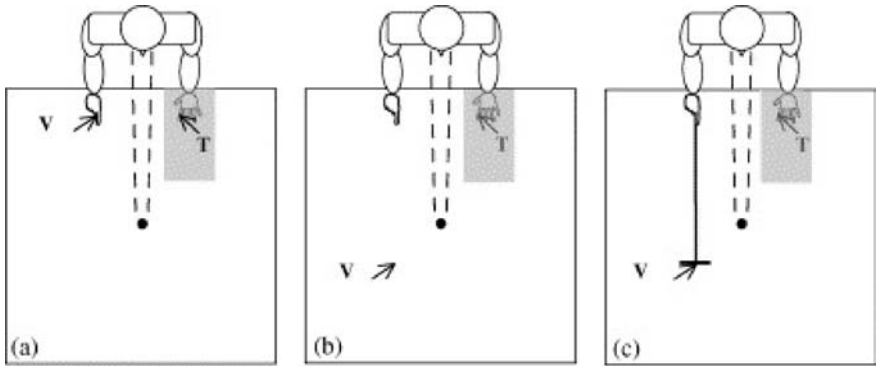



**Figure 1.** Schematic illustration of the experimental setting for assessing visual–tactile extinction as a function of the cross-modal conditions, viewed from above (Farnè et al. 2005). The visual stimulus (V) could be located near (a) or far (b and c) from the patient's right hand. Tactile (T) stimuli were delivered to the patients' left hand screened from view (grey rectangle). Note that the visual stimulus was presented at the same distant position (60 cm from the hand) in both the far condition (b) without any tool and (c) after passive visual/proprioceptive exposure to the 60 cm long tool. (With permission from Farnè at al. 2005).

necessarily imply a tool incorporation phenomenon, unless the tool is used in some active way. Indeed, when cross-modal extinction was assessed equally far in space, but immediately after the active use of a long tool, we observed a significant increase of cross-modal extinction. These findings considerably extend our knowledge about dynamic tool incorporation in humans, by making clear that the plastic modifications are tightly linked to the active, purposeful use of a tool as physical extension of the body, which allows to interact with otherwise non reachable objects.

As a second question we asked whether the absolute or the operative length of the tool would be crucial in extending peri-hand space (Farnè et al. 2005b). In this respect, we found that the differential amount of cross-modal extinction obtained with different tools was not determined by the absolute length of the tool, but by its operative length. Therefore, these results constitute the first evidence that peri-hand space elongation is directly related to the functionally effective length of the tool, i.e. by the distance at which the operative part of the tool was located with respect to the hand.

Finally, as far as the third question is concerned, we asked whether the expansion of the peri-hand space after tool use consists in an actual elongation of the visual-tactile integrative area along the tool axis, encompassing the whole tool (Farnè & Làdavas 2000; Farnè et al. 2005a, b), or in a selective incorporation of the tool-tip, due to the shift or the creation of a new integrative area at the distal edge of the used tool (Holmes et al. 2004). To shed light on this issue, we recently assessed cross-modal visual-tactile extinction in a RBD patient while she was wielding a 60 cm long rake, before and immediately after its use to retrieve distant objects. At variance with previous patients

studies, visual-tactile extinction was assessed near the ipsilesional hand (holding the rake handle), near the distal edge of the rake, as well as in a middle position between the hand and the distal end of the rake. After tool-use, crossmodal extinction increased both at the distal edge as well as midway between the hand and the tool-tip, whereas it remains constant near the hand. This result suggests that after tool use the visuo-tactile peri-hand space is expanded to incorporate the whole tool rather than it is displaced to a restricted area around the tip of the tool. (Farnè et al., in press).

Another way to extend our own visual peripersonal space has been shown by Iriki and colleagues (2001). In this interesting study the authors trained the monkey to recognize the image of the hand in a video monitor. Before the training, no neuron responded to visual stimuli presented around the image of the hand in the monitor screen, but immediately after the monkey learned to recognize the self-image in the monitor, a group of neurons appeared with new visual RFs formed around the screen-image of the hand. A similar re-coding of far visual stimuli as near ones has recently been observed in a patient with tactile extinction and normal subjects (Maravita et al. 2000, 2002). In this patient, a flash of light actually delivered close to the right hand, but appearing in far space due to observation via a mirror, produced closely similar effects to that produced by a light which was directly viewed near the hand in peripersonal space. Thus, seeing his own hand via a mirror activates a representation of the peripersonal space around that hand, not of the extrapersonal space as suggested by the distant visual image in the mirror. Thus, a mirror can be considered a different kind of tool which allows objects located in the far space to be treated as falling close to the actual location of the patient's hand.

In conclusion, neurophysiological and neuropsychological findings converge in showing that the representation of peri-hand space can be expanded along the axis of a tool to include its length, this re-mapping being achieved through a re-sizing of the peri-hand area where visual-tactile integration occurs. Tools enable human beings, as well as other animals, to act on objects that would otherwise not be reachable by hands. Acting on distant objects by means of a physical tool requires sensory information that is mainly provided by vision and touch. The expansion of the peri-hand area whereby vision and touch are integrated would render the possibility of reaching and manipulating far objects as if they were near the hand.

*Action-related representation of near peripersonal space*

In recent studies of spatially specific cross-modal extinction (Farnè et al. 2003) it was found that the activation of the visuo-tactile integrated system can occur rather automatically, following a rather bottom-up flow of information, which is not necessarily affected by top-down conscious regulation of sensory processing. The results of a group study clearly showed that visual stimuli presented in the near-peripersonal space of the ipsilesional hand induced strong cross-modal extinction of tactile stimuli simultaneously delivered on the contralesional hand, independent of the patients' knowledge concerning the real possibility of being touched (Farnè et al. 2003). Crucially, the amount of cross-modal extinction was comparable, no matter whether the

patient's hand was physically protected by a transparent barrier or not against the approaching visual stimulus.

Moreover, the human brain can form visual representations of the near-peripersonal space of a non owned body part, like a rubber hand, as if it were a real hand (Farnè et al. 2000). A rubber hand can deceive the integrated system in such a way that a visual stimulus, actually presented far from patients' real hand, is processed as if it were in the near-peripersonal space. Critically, the system coding the space surrounding the body can be deceived by the vision of a fake hand, provided that its appearance looks plausible with respect to subject's body. Although this deception may seem surprising, it can be better understood as the results of a normal adaptive process. Because the visual response of the monkey's bimodal neurons does not change after repeated stimulation (Graziano et al. 1997), it has been suggested that the basic functional properties of these neurons, e.g. the distance-dependent gradient of firing, are hard-wired and that the spatial correspondence between visual and tactile RFs can be further calibrated through experience (Salinas & Abbot 1995; Graziano et al. 1997).

Overall, these findings confirm the notion that the activation of the visuo-tactile integrated system can occur automatically, following a bottom-up flow of information, which is not necessarily affected by top-down conscious regulation of sensory processing. By considering the functional role that multisensory systems have been proposed to deserve, i.e. acting as sensory-motor interfaces, one may suggest that this reluctance to top-down modulation might have an adaptive valence. Indeed, movements of the head and arm directed both towards the body and away from the body are controlled by multisensory structures in the monkey, and can do so by relying both on cutaneous and visual information coming from nearby objects. Many of our movements aimed at avoiding a stimulus coming towards the face or the head are fast and occur without conscious planning, which would ultimately be detrimental to a potentially defensive aim. Humans studies of pathological escaping actions (Denny-Brown et al. 1952) indirectly support a bottom-up control of visually-driven withdrawal reactions. The automatic nature of exaggerated withdrawal reactions is underlined in a report of a patient, affected by a right parietal lobe infarction, who presented with a dense hemianesthesia and hemiplegia of the left hand when vision was prevented. However, "with eyes open, visual stimuli induced withdrawal of the arm and burning pain in the numb side" (Hoogenraad et al. 1994).

Space representation involves considerable integration among senses. Here, we reviewed neuropsychological findings that shed light onto the functioning of brain mechanisms coding near-peripersonal space in humans on the basis of multisensory integration. Our findings are fully consistent with multiple representations of space, in which a set of space-related neuronal structures code different sectors of space, in different co-ordinates, across different combination of modalities, and for different behavioral purposes (Rizzolatti et al. 1998). Among these maps, the representation of near-peripersonal space in humans clearly appears to parallel the functioning of the circuit of multisensory areas that has been well documented in monkeys. Direct evidence from functional anatomy for the existence of brain structures responsible for

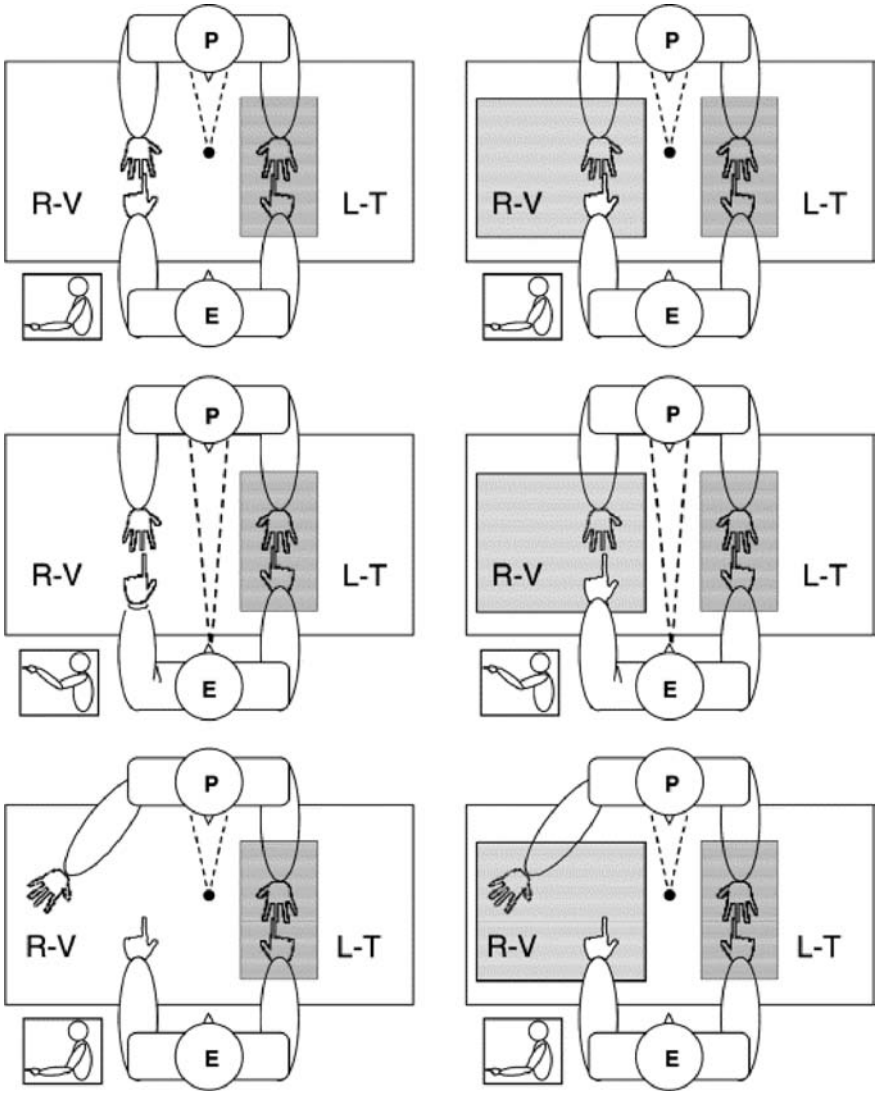



**Figure 2.** Schematic illustration of the crossmodal visuo-tactile conditions, and the experimental setting with the patient (P) and examiner (E) relative positions, viewed from above (Farnè et al. 2003). The visual stimulus (V) could be located near (first row), or far from the patient's right (R) hand, which could be located either below (second row) or aside (third row) the visual stimulus. Tactile (T) stimuli were delivered to the patients' left (L) hand. Note that in the first and latter case (first and third row) the position of the visual stimulus with respect to the patient's body parts other than the hand (i.e. the eye, the head and the midline) is identical. Left column: No-Glass conditions; right column: Glass conditions. (With permission from Farnè et al. 2003).

similar multisensory integrative processes in humans has recently become available and confirmed, that both monkeys and humans may share similar multimodal areas (Bremmer et al. 2001a, b; Macaluso et al. 2000a, b). Taken together, the inferences we derived from our neuropsychological studies show a remarkably high degree of convergence with neurophysiological, cognitive, and functional imaging studies.

## References


Bender, M. B. (1952). *Disorders in perception*. Springfield: CC Thomas.

Berti, A., & F. Frassinetti. (2000). When far becomes near: remapping of space by tool use. *Journal of Cognitive Neuroscience, 3,* 415–420.

Bremmer, F., A. Schlack, N. J. Shah, O. Zafiris, M. Kubischik, K. Hoffmann, K. Zilles, & G. R. Fink (2001). Polymodal motion processing in posterior parietal and premotor cortex: A human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron, 29*, 287–296.

Bremmer, F., A. Schlack A., J. R. Duhamel, W. Graf, & G. R. Fink (2001). Space coding in primate posterior parietal cortex. *NeuroImage, 14*, S46–S51.

Colby, C. L., J. R. Duhamel & M. E. Goldberg (1993). Ventral intraparietal area of the macaque: Anatomic location and visual response properties. *Journal of Neurophysiology, 69*, 902–914.

Danny-Brown, D., J.S. Meyer & S. Horenstein (1952). The significance of perceptual rivalry resulting from parietal lesion. *Brain, 75*, 433–471.

Di Pellegrino, G., & E. De Renzi (1995). An experimental investigation on the nature of extinction. *Neuropsychologia, 33*, 153–170.

Di Pellegrino, G., E. Làdavas, & A. Farnè (1997). Seeing where your hands are. *Nature, 338*, 730.

Driver, J. (1998). The neuropsychology of spatial attention. In Pashler H. (Ed.), *Attention* (pp. 57–71). Hove: Psychology Press.

Driver, J., J. B. Mattingley, C. Rorden, & G. Davis (1997). Extinction as a paradigm measure of attentional bias and restricted capacity following brain injury. In Thier P. & H. O. Karnath (Eds.), *Parietal lobe contribution to orientation in 3D space* (pp. 401–429). Heidelberg: Springer Verlag.

Driver, J., & C. Spence (2002). Multisensory perception: Beyond modularity and convergence. *Current Biology, 10,* R731–735.

Duhamel, J. R., C. L. Colby, & M. E. Goldberg (1991). Congruent representation of visual and somatosensory space in single neurons of monkey ventral intra-parietal area (VIP). In Paillard J. (Ed.), *Brain and Space* (pp. 223–236). Oxford: Oxford University Press.

Duhamel, J. R., C. L. Colby, & M. E. Goldberg (1998). Ventral intraparietal area of the macaque: Congruent visual and somatic response properties. *Journal of Neuropsysiology, 79,* 126–136.

Duncan, J. (1980). The locus of interference in the perception of simultaneous stimuli. *Psychological Review, 87,* 272–300.

Duncan, J. (1996). Coordinated brain systems in selective perception and action. In Inui T. & J. L. McClelland (Eds.), *Attention and Performance* (pp. 549–578). Cambridge: MIT Press.

Farnè, A., & E. Làdavas (2000). Dynamic size-change of hand peripersonal space following tool use. *Neuroreport, 85*, 1645–1649.

Farnè, A., F. Pavani, F. Meneghello, & E. Làdavas (2000). Left tactile extinction following visual stimulation of a rubber hand. *Brain, 123,* 2350–2360.

Farnè, A., & E. Làdavas. (2002). Auditory peripersonal space in humans. *Journal of Cognitive Neuroscience, 14*, 1030–1043.

Farnè, A., M. L. Demattè, E. Làdavas (2003). Beyond the window: Multisensory representation of peripersonal space across a trasparent barrier. *International journal of Psychophysiology, 50I*, 51–61.

Farnè, A., M. L. Demattè, & E. Làdavas (2005). Neuropsychological evidence of modular organization of the near peripersonal space. *Neurology, 65*, 1754–1758.

Farnè, A., A. Iriki, & E. Làdavas (2005). Shaping multisensory action-space with tools: Evidence from patients with cross-modal extinction. *Neuropsychologia, 43*, 238–248.

Farnè, A., A. Serino, & E. Làdavas (in press). Dynamic size-change of perihand space following tool-use: Determinants and spatial characteristics revelead through cross-modal extinction. *Cortex.*

Fogassi, L., V. Gallese, L. Fadiga, G. Luppino, M. Matelli, & G. Rizzolatti (1996). Coding of peripersonal space in inferior premotor cortex (area F4). *Journal of Neurophysiology, 76*, 141–157.

Fogassi, L., V. Raos, G. Franchi, V. Gallese, G. Luppino, & M. Matelli. (1998). Visual responses in the dorsal premotor area F2 of the macaque monkey. *Experimental Brain Research, 128,* 194–199.

Graziano, M. S. A., & Gross C. G. (1995). The representation of extrapersonal space: A possible role for bimodal, visuo-tactile neurons. In Gazzaniga M. S. (Ed.), *The Cognitive Neuroscience* (pp. 1021–1034). Cambridge: MIT Press.

Graziano, M. S. A., & Gross C. G. (1998). Visual responses with and without fixation: Neurons in premotor cortex encode spatial locations independently of eye position. *Experimental Brain Research, 118*, 373–380.

Graziano, M. S. A., X. T. Hu, & C. G. Gross (1997). Visuospatial properties of ventral premotor cortex. *Journal of Neurophysiology, 77*, 2268–2292.

Head, H., & G. Holmes (1991). Sensory disturbances from cerebral lessons. *Brain*, *34*, 102–254.

Holmes, N. P., & C. Spence (2004). Extending or projecting space with tools? Multisensory interactions highlight only the distal and proximal ends of tools. *Neuroscience Letters*, *372*, 62–67.

Hoogenraad, T. U., L. M. Ramos, & J. van Gijn (1994). Visually induced central pain and arm withdrawal after right parietal lobe infarction. *Journal of Neurology, Neurosurgery and Psychiatry, 57*, 850–852.

Hyvarinen, J., & A. Poranen (1974). Function of the parietal associative area 7 as revealed from cellular discharged in alert monkeys. *Brain, 97*, 673–692.

Iriki, A., M. Tanaka, & Y. Iwamura (1996). Coding of modified body schema during tool use by macaque postcentral neurons. *Neuroreport, 7*, 2325–2330.

Iriki, A., M. Tanaka, S. Obayashi, & Y. Iwamura (2001). Self-images in the video monitor coded by monkey intraparietal neuron. *Neuroscience Research*, *40*, 163–173.

Làdavas, E., G. Zeloni, & A. Farnè (1998). Visual peripersonal space centered on the face in humans. *Brain, 121,* 2317–2326.

Làdavas, E. (2002). Functional and dynamic properties of visual peripersonal space in humans. *Trends in Cognitive Science, 6*, 17–22.

Loeb, J. (1885). Die elementaren Storungen einfacher Funktionen nach ober-flachlicher, umschriebener Verletzung des Großhirns. *Pfluger Archiv, 37*, 51–56.

Macaluso, E., C. D. Frith, & J. Driver (2000a). Modulation of human visual cortex by crossmodal spatial attention. *Science, 289,* 1206–1208.

Macaluso, E., C. D. Frith, & J. Driver (2000b). Selective spatial attention in vision and touch. Unimodal and multimodal mechanisms revealed by PET. *Journal of Neurophysiology, 63,* 3062–3085.

Maravita, A., M. Husain, K. Clarke, & J. Driver (2001). Reaching with the tool extends visual-tactile interactions into far space: Evidence from cross-modal extinction. *Neuropsychologia, 39*, 580–585.

Maravita, A., C. Spence, K. Clarke, M. Husain, & J. Driver (2000). Vision and touch through the looking glass in a case of crossmodal extinction. *Neuroreport, 169,* 3521–3526.

Maravita, A., C. Spence, S. Kennett, & J. Driver (2002). Tool-use changes multimodal spatial interactions between vision and touch in normal humans. *Cognition, 83*, B25–B34.

Obayashi, S., M. Tanaka, & A. Iriki (2000). Subjective image of invisible hand coded by monkey intraparietal neurons. *Neuroreport, 11*, 3499–3505.

Oppenheim, H. (1885). Uber eine durch eine klinisch bisher nicht verwetete Untersuchungsmethode ermittelte Sensibilitatsstorung bei einseitigen Erkrakungen des Großhirns. *Neurologiches Centralblatt, 37*, 51–56.

Rizzolatti, G., G. Luppino, & M. Matelli (1998). The organization of the cortical motor system: New concepts. *Electroencephalographic Clinical Neurophysiology, 106*, 283–296.

Rizzolatti, G., C. Scandolara, M. Matelli, & M. Gentilucci (1981). Afferent properties of periarcuate neurons in macaque monkeys. II Visual responses. *Behavioral Brain Research, 2*, 147–163.

Salinas, E., & L. F. Abbot (1995). Transfer of coded information from sensory to motor networks. *Journal of Neuroscience, 15,* 6461–6474.

Ward, R., S. Goodrich, & J. Driver (1994). Grouping reduces visual extinction: Neuropsychological evidence for weight-linkage in visual selection. *Visual Cognition, 1*, 101–129.

CHAPTER 4.4

# Visual perceptual processing in unilateral spatial neglect

## The case of visual illusions

Giuseppe Vallar and Roberta Daini

### Introduction

Since the syndrome of unilateral spatial neglect has been definitely included in the province of neuropsychological cognitive disorders, in the early 1970s of the last century (Bisiach & Vallar 1988, for a review), it has been a widely shared *tenet* that early sensory and perceptual processing may be spared in brain-damaged patients suffering from neglect, because the basic mechanism of the disorder is not an impairment at lower-levels of analysis and integration of sensory input (see for such a view Denny-Brown, Meyer, & Horenstein 1952). The main argument supporting interpretations of unilateral spatial neglect as a deficit of higher processing levels comes from the observation that, although brain-damaged patients with neglect frequently show associated neurological deficits (such as hemiplegia, hemianopia, and hemianaesthesia), the two sets of disorders are double-dissociated. Neglect may occur in the absence of these primary sensory motor-disorders, that, in turn, are not necessarily associated with it (Bisiach, Perani, Vallar, & Berti 1986; Bisiach, Vallar, Perani, Papagno, & Berti 1986; Vallar & Perani 1986). Furthermore, not only neglect is independent of primary sensory and motor deficits, but it may even be a main component of them. Hemianopia (Kooistra & Heilman 1989; Vallar, Sandroni, Rusconi, & Barbieri 1991), hemiplegia (Rode et al. 1992; Rode, Perenin, Honoré, & Boisson 1998; Vallar, Bottini, & Sterzi 2003; Vallar, Guariglia, Nico, & Pizzamiglio 1997), and hemianaesthesia (Bottini et al. 2005; Smania & Aglioti 1995; Vallar, Bottini, Rusconi, & Sterzi 1993; Vallar, Bottini, Sterzi, Passerini, & Rusconi 1991) may be partly caused by the spatial cognitive impairment of neglect. This has been shown by studies both in individual cases and in small series of brain-damaged patients, such as those quoted above. There is, however, also evidence that the role of neglect in increasing the frequency and severity of sensory and motor deficits may be clinically relevant. Hemianopia, hemiplegia and hemianaesthesia are more frequent after right-brain-damage, compared with left-brain-damage

(Sterzi et al. 1993). This hemispheric asymmetry suggests a role for neglect, since this disorder is more closely associated with right- than with left-brain damage (Bisiach & Vallar 2000).

## Sensory and perceptual processing in unilateral spatial neglect

When considering the relationships between sensory and perceptual processing on the one hand, and unilateral spatial neglect on the other, the available data suggest two conclusions. In brain-damaged patients with neglect, the *absence* of a peripheral sensory or motor deficit may be unambiguously taken as evidence that neglect is independent of these lower-level disorders. The *presence* of sensory or motor deficits is ambiguous, however, in that they may be *primary* (namely due to a sensory or motor associated, but causally unrelated, disorder), or *secondary* (namely a manifestation of neglect itself). Secondary disorders may differ from primary deficits in important respects, including their amenability to manoeuvres such as the physiological lateral manipulation of the sensory input, through vestibular and optokinetic stimulation, transcutaneous muscle vibration, prism adaptation (Rossetti & Rode 2002; Vallar, Guariglia, & Rusconi 1997). The spatial, neglect-related, feature of hemianopia, tactile extinction and somatosensory deficits has been shown also by dissociating retinotopic and somatosensory coordinates from spatial reference frames, by requiring the patient to look rightwards or crossing the forearms, so that the visual and somatosensory stimuli are delivered on the right side, with respect to the mid-sagittal plane of the body. These manoeuvres may temporarily improve left-sided visual and somatosensory deficits (Kooistra & Heilman 1989; Moro, Zampini, & Aglioti 2004; see also Moscovitch & Behrmann 1994, for related findings; Smania & Aglioti 1995).

In the light of this evidence, in recent years a number of studies have attempted at exploring the view that the processing of sensory input is largely preserved in patients with unilateral spatial neglect, with the aim of defining in more detail the extent of analysis undergone by information delivered to the neglected side. In general, the available data suggest that information may be processed up to the level of semantic analysis, provided that the conditions of the task do not require a declarative explicit report about the stimulus (Berti 2002; McGlinchey-Berroth 1997, for reviews).

Plotting the empirical evidence onto the internal information processing model of perception of Urlich Neisser (1976, Figure 1) the locus of functional impairment of neglect appears to be located near "consciousness", with this component of the flow chart being selectively defective, such as in Bisiach et al.'s "representational scotoma" (Bisiach, Bulgarelli, Sterzi, & Vallar 1983), or access to it being prevented (Vallar, Bottini et al. 1991). The dissociation between non-conscious, preserved, and conscious, defective, processing in patients with unilateral spatial neglect may be envisaged in different theoretical frames. According to an attentional perspective (Umiltà 2001), the non-conscious systems spared in patients with neglect may be conceived as independent of attention, which, in turn, supports perceptual awareness (Posner 1994). Within

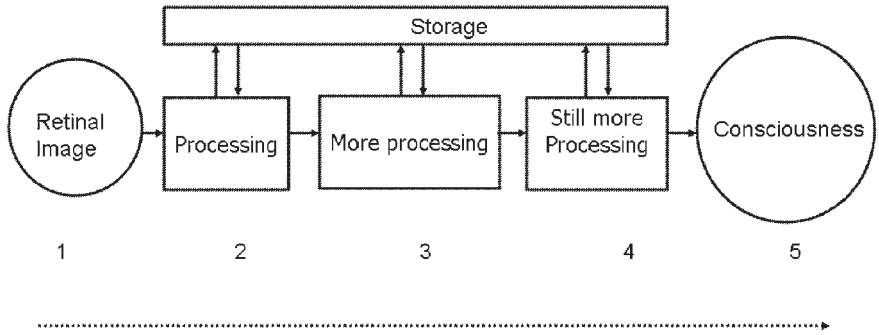



**Figure 1.** The internal information-processing model of perception of Neisser (1976) applied to the syndrome of spatial unilateral neglect (Halligan et al. 2003; Vallar 1998), whose locus of impairment may be located at stage 5 (consciousness, and, more specifically, spatial awareness, both on the premotor and on the perceptual side), at the connection between stages 4 and 5 or both.

a representational account, awareness is an intrinsic feature of the representation of space, disrupted in neglect (Bisiach & Vallar 2000). The attention vs. representation debate in the context of unilateral neglect appears at present much less relevant than it was thought to be in the late 1980s of the last century (Bisiach & Vallar 1988). First, it is a widely accepted view that many manifestations of neglect may be interpreted within both an attentional and a representational theoretical frame, suggesting a substantial overlapping of these two (often vaguely defined) theoretical constructs (Bisiach & Vallar 2000). Secondly, current multi-component accounts of the manifold manifestations of neglect allow for multiple (possibly interacting) pathological mechanisms, including, for instance, defective directed attention and corruption, or loss, within the representational medium (Benke, Luzzatti, & Vallar 2004).

This chapter considers one specific aspect of visual perceptual processing in patients with unilateral spatial neglect, namely the case of visual illusions. Studying the processing of visual illusions in neglect patients is of interest in three main respects. First, the observation that processing of illusions is spared vs. defective in such patients elucidates the role of spatial awareness (putatively defective in neglect) in the analysis of illusory configurations. In addition, illusory effects may be assessed both explicitly and implicitly, testing the view that unilateral spatial neglect is a disorder of spatial awareness. Second, a particular type of illusions, namely illusions of length and position, mimic some aspects of neglect (illusions of neglect, see Vallar & Daini 2002), therefore elucidating possible mechanisms of some aspects of the disorder. Third, anatomo-clinical correlation studies in brain-damaged patients provide evidence concerning the localization of brain regions involved in with the processing of visual illusory stimuli.

## Processing of illusions in patients with spatial neglect

Visual illusions are a time-honoured tool, that have long been used to explore the functional properties of the perceptual system (Coren & Gircus 1978a; Kanisza 1979). In patients with visual neglect, investigations concerning illusory phenomena have produced three main sets of results: (i) processing of visual illusions may be preserved (*illusions in neglect*) or defective, suggesting a dissociation between the functional and neural underpinnings of visual and spatial processes; (ii) visual illusions of length and position simulate in neurologically unimpaired subjects some manifestations of the disorder (*illusions of neglect*), providing, therefore, insights into some putative pathological mechanisms, such as a distortion of perceptual space (Gainotti & Tiacci 1971; Halligan & Marshall 1991; Milner & Harvey 1995); (iii) anatomo-clinical correlations in neglect patients, showing preserved vs. disrupted illusory effects, provide information concerning their neural basis.

## Illusions in neglect

### *Illusions of length and position*

The figure of Müller-Lyer (Boring 1942; Müller-Lyer 1889; Porac 1994) and its variants (Coren & Gircus 1978b) consist in the phenomenon whereby two identical lines are seen as different in physical length, because of the presence at the line ends of fins with a particular orientation. The line with outgoing fins is seen as expanded, the line with ingoing fins as compressed (Figure 2-B, 2-C). Illusory effects are present also when non-symmetrical figures are used, and the manual setting of the subjective midpoint of the line is required (see Post, Welch, & Caufield 1998, and references therein). A stimulus with a left-sided ingoing fin (2-D) brings about an illusory shortening of the left side of the line, with a rightward bisection error. A stimulus with a right-sided outgoing fin (2-G) has a similar effect, by an illusory expansion of the right side of the line. A stimulus with a right-sided ingoing fin (2-E) brings about an illusory shortening of the right side of the line, while a stimulus with a left-sided outgoing fin (2-F) induces a lengthening of the left side, both resulting in a leftward bisection error. In the *Judd or Holding illusion*, fins oriented in the same direction are added to the ends of the line (Holding 1970; Judd 1899), and the stimulus is displaced leftwards (Figure 2-H), resulting in a leftward transection error, or rightwards (Figure 2-I), with a rightward error. The *Brentano* or *combined form* of the *Müller-Lyer figure* induces a leftward bisection error when its left side is expanded and its right side compressed (Figure 2-J). A Brentano figure with an expanded right side and a compressed left side (Figure 2-K) brings about a rightward error.

The first study addressing the issue of processing of illusory stimuli by patients with neglect was made by Mattingley, Bradshaw and Bradshaw (1995), who investigated in seven right brain-damaged patients the bisection of horizontal lines with unilateral fins and of Judd illusion stimuli (Figure 2-D to 2-I). A group analysis revealed

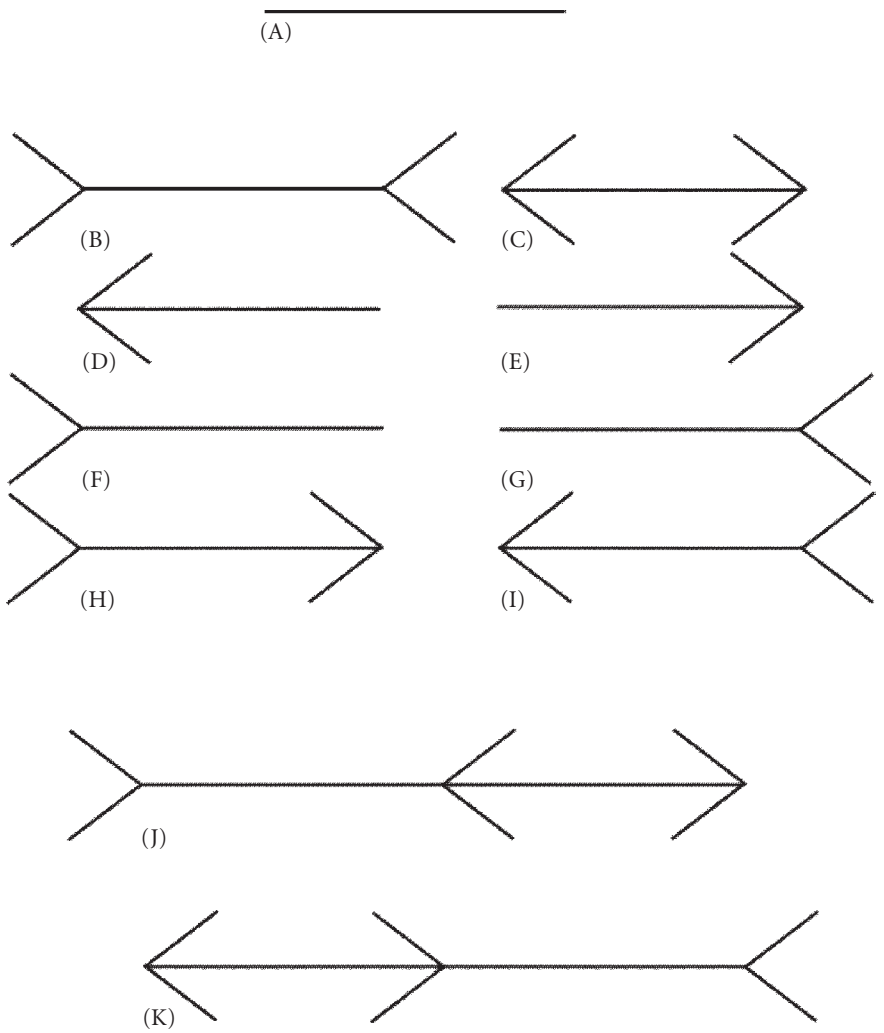



**Figure 2.** Illusory stimuli used in line bisection. Horizontal baseline segment (A); Müller-Lyer illusion with bilateral outward-projecting fins (B), and with bilateral inward-projecting fins (C); unilateral left-sided inward-projecting fin (D); unilateral right-sided inward-projecting fin (E); unilateral left-sided outward-projecting fin (F); unilateral right-sided outward-projecting fin (G); Judd illusion with fins pointing rightwards (H), and leftwards (I); Brentano or combined forms (J and K), resulting from the embedding of two opposite Müller-Lyer illusions (B and C) (reprinted with kind permission from Oxford University Press, Vallar & Daini 2002).

that the patients' subjective midpoint was affected not only by right-sided (Figures 2-E and 2-G), but also by left-sided fins (Figures 2-D and 2-F), although the latter fell within a putatively neglected region of visual space. Not all patients had a consistent

performance in all conditions, but at least one patient (#2) exhibited preserved illusory effects, with both left-sided and right-sided fins. These largely preserved illusory effects may be contrasted with the patients' inability to report verbally the presence of left-sided fins, regardless of whether they occurred alone (Figures 2-D and 2-F) or with right-sided fins (Figures 2-H and 2-I).

Subsequent studies confirmed and extended these results. In a single right-brain-damaged patient with left neglect, Ro and Rafal (1996), who used the Judd figure (see Figure 2-H and 2-I), found the expected directional effects in a bisection task, although no data from control subjects were provided. Fins pointing rightwards (Figure 2-H) displaced the patient's subjective midpoint leftwards, fins pointing leftwards (Figure 2-I) had a rightward directional effect. In a same-different discrimination task, by contrast, the patient failed to detect left-sided differences (e.g., Figures 2-B vs. 2-I, or 2-C vs. 2-H), as patients with left neglect typically do (Vallar, Rusconi, & Bisiach 1994), though stimuli differing in their right side (e.g., Figures 2-B vs. 2-H, or 2-C vs. 2-I) were correctly judged as "different".

A group study by Olk et al. (2001), again using stimuli with unilateral fins and Judd stimuli, confirmed (experiment 1) that right-brain-damaged patients with left neglect may show illusory effects with fins pointing both rightwards (Figure 2-H) and leftwards (Figure 2-I), as well as with unilateral fins (Figure 2-D to 2-G). Five out of the 12 patients were able to report left-sided fins on every trial, four patients on over 80% of the trials, two patients made only a few errors, and one patient (J.C.) never reported left-sided fins. J.C. showed in most conditions the expected illusory effects, which, however, proved to be not significant, as analysed in the individual patient. In experiment 2, group analyses revealed illusory effects in the 12 neglect patients, in neurologically unimpaired controls and in right-brain-damaged patients without neglect, with both the leftward and the rightward pointing Judd illusion. In this experiment awareness of the left-side of the stimulus was assessed by a "same-different" judgement task similar to the one used by Ro and Rafal (1996). Two out of the 12 neglect patients of Olk et al. (2001) erroneously judged as "same" pairs of figures differing in their left side (e.g., Figure 2-B vs. 2-I, or 2-C vs. 2-H) on each trial. One such patient (B.M.), in line with Ro and Rafal' s earlier findings (1996), showed preserved illusory effects, though no statistical analysis could be made, due to the limited number of trials.

The error in manual bisection is also affected by two background lines arranged to make an isosceles triangle with its vertex on the left or the right end of a 13 cm horizontal line. The set of stimuli included complete items, and partial stimuli. The bisection error of six right-brain-damaged patients was modulated by the position of the vertex, as in the unilateral left-sided- (2-D) and right-sided inward-projecting fins (2-E) of the Müller-Lyer figure. Patients and neurologically unimpaired subjects made an error in the direction opposite to the side of the vertex of the triangle. The performance of neglect patients was overall biased rightwards, with the effect of the background reducing (right-sided vertex) or increasing (left-sided vertex) the rightward bias related to neglect. The main factor that modulated the bisection error leftwards or rightwards was the presence of the vertex of the triangle, suggesting a mechanism similar

to that of the partial Müller-Lyer figure shown in Figures 2-D and 2-E (Esterman, McGlinchey-Berroth, Alexander, & Milberg 2002).

Using the Brentano version of the Müller-Lyer figure, Vallar, Daini and Antonucci (2000), found completely preserved illusory effects in six right-brain-damaged-patients with left neglect, both when the left half of the segment was illusorily made longer (Figure 2-J), bringing about a leftward directional error, and when it was made shorter (Figure 2-K), resulting in a rightward error. In a second experiment Vallar et al. (2000) investigated the role of the spatial position of the stimulus. In patients with left neglect a presentation of the stimulus in the left side of space (with respect to the mid-sagittal plane of the body) increased, as it has long been known (Bisiach et al. 1983; Heilman & Valenstein 1979), the rightward bisection error, compared to a centre or right-sided position. This manipulation did not affect, however, the magnitude of the illusory effects induced by either version of the Brentano-Müller-Lyer illusion (Figures 2-J and 2-K). Control subjects, by contrast, exhibited the illusory effect, but were not affected by the spatial position of the stimulus.

The bisection performance of right brain-damaged-patients with left neglect is affected in a similar fashion by the Oppel-Kundt illusion, in which a horizontal line interrupted by vertical cross-bars seems longer as the bars are closer (Figure 3-A vs. 3-B). The configuration which brings about an illusory expansion of the left side of the line (Figure 3-C) reduces the rightward bisection error, which, in turn, is increased by a pattern inducing an illusory lengthening of the right side of the segment (Figure 3-D). In a study performed in 28 right-brain-damaged patients and in 28 neurologically unimpaired control subjects, Ricci, Pia and Gindri (2004) found illusory effects in both groups, with the background affecting the bisection error of the two subjects' groups in the same direction. Congruent illusory effects were also found in a line extension task. Ricci et al. (2004) also devised an Oppel-Kundt circle cancellation task, in which the targets (little ellipses) were evenly distributed, or their density increased horizontally towards the left or the right side. Patients, in line with their reduced bisection error when the density of the background was greater on the left side, showed a reduction of the neglected area, which, in turn, increased when the background was more dense on the right side.

In two of the studies considered earlier (Olk & Harvey 2002; Ro & Rafal 1996) symmetrical figures were also used (i.e., the Müller-Lyer illusion shown in figure 2-B and 2-C). A consistent finding was that the bilateral outward-projecting fins stimulus (Figure 2-B), which is illusorily perceived as longer, brought about a greater rightward error in bisection, compared to the inward-projecting fins stimulus (Figure 2-C). Control subjects did not show this effect (Olk & Harvey 2002). This *illusory line length effect* (Vallar & Daini 2002) sheds light into the mechanisms underlying a phenomenon frequently shown by patients with left neglect, namely the disproportionate increase of the ipsilesional error in the bisection of lines of increasing length (Bisiach et al. 1983; Vallar et al. 2000). A similar effect of the perceived length of the line on the bisection error of patients with left neglect has been also found by Ricci, Calhoun and Chatterjee (2000), using a symmetrical version of the Oppel-Kundt illusion (Figures 3-A, and 3-

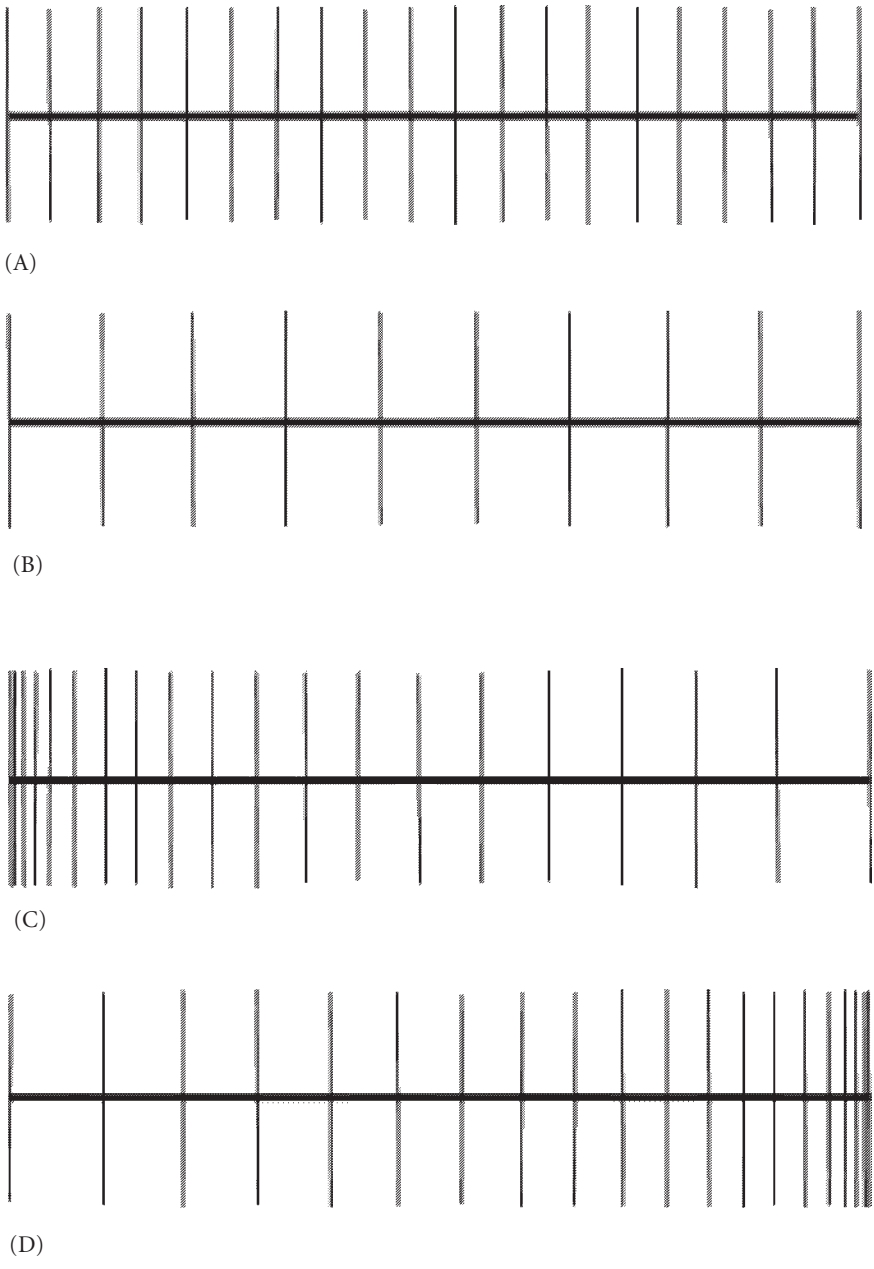



**Figure 3.** The Oppel-Kundt illusion. Density of the vertical lines: evenly distributed, with different rates (A, and B), leftward higher density (C), and rightward higher density (D) (reprinted with kind permission from Oxford University Press, Vallar & Daini 2002).

B), which, like the Müller-Lyer illusion, may increase or reduce the perceived length of the line (Watt 1994). These findings suggest that the pathological bias producing the line length effect applies not only to physical, but also to perceived, represented length.

*Figures delimited by subjective contours*

In one patient (V.R.) (Mattingley, Davis, & Driver 1997) with a left-sided visual extinction to double simultaneous stimulation, caused by an extensive lesion in the vascular territory of the middle cerebral artery, left extinction was less severe when the bilateral stimuli formed a subjective figure (Kanisza 1979; Kanizsa 1976) across the visual field, compared to conditions where such a fill-in did not take place. Kartsounis and Warrington (1989) had previously found that continuous, or meaningfully integrated, stimuli may overcome neglect. Processing of figures with subjective contours was subsequently investigated by Vuilleumier and Landis (1998) in three right brain-damaged patients with left visual neglect. The rightward error in a line bisection task was comparable across stimulus type (horizontal lines, bars and rectangles delimited by real or subjective contours, as shown in Figure 4), with a similar length effect in all stimulus conditions. This suggests that real and subjective contours had been processed in a comparable fashion, before the rightward bias of spatial neglect took place. The control condition was a task requiring the bisection of a horizontal empty space, delimited by two dots or vertical segments, with neither real nor subjective contours: the three patients did not show any evidence of left neglect in this bisection task, with, if anything, a leftward error. This finding replicates previous observations that the rightward bisection error of patients with left neglect is reduced when the stimulus is a virtual line (namely, an empty space between two dots), compared to canonical line bisection (Bisiach, Pizzamiglio, Nico, & Antonucci 1996; Bisiach, Rusconi, Peretti, & Vallar 1994, though see patient A.S., whose rightward error was greater in virtual line bisection; McIntosh, McClements, Dijkerman, & Milner 2004).

Vuilleumier and Landis (1998) assessed awareness of the presence of the left-sided stimuli used as inducers of the subjective contours by "same\different" judgements. Patients, consistently and erroneously, judged as "same" configurations, including figures delimited by subjective contours, which differed in the left-sided inducers. Their performance was errorless both with figures delimited by subjective contours, in which the differences were right-sided, and with similar configurations, not inducing subjective contours. In this latter, non-illusory, condition the patients were able to detect both left and right-sided differences. This finding shows that bilateral inducers generating subjective contours worsen the patients' ability to detect the left, contralesional component stimuli, at least when a "same\different" judgement response is required. This result differs from the performance of patient V.R. (Mattingley et al. 1997), who showed less left extinction when bilateral stimuli generated a figure with subjective contours across the visual field, compared to sets of similar stimuli, which did not induce such an illusory effect. No definite conclusions can be drawn, however. Different tasks were used ("same\different" judgements vs. detection), the stimuli were not identical, and Mattingley et al.'s (1997) patient V.R. showed no left neglect. This, in turn,

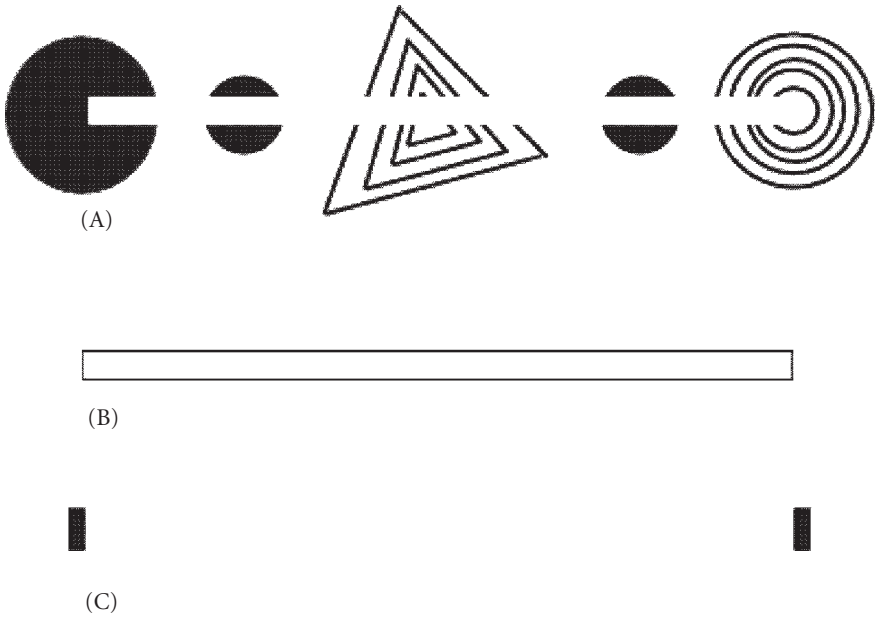



**Figure 4.** Figures with subjective contours. Anomalous surface (horizontal bar) with subjective contours generated by inducers (A); a surface with real contours (B); a virtual line, namely, an empty space between two vertical bars (C) (reprinted with kind permission from Oxford University Press, Vallar & Daini 2002).

was a selection criterion for Vuilleumier and Landis' (1998) patients, who also showed left extinction. These findings suggest, nevertheless, that the presence of subjective contours does not systematically facilitate perceptual awareness of left-sided stimuli.

These findings from patients with neglect indicate that processing of illusory contours does not require spatial directed attention. This conclusion is supported by the reverse dissociation. Patient N.M. (Ricci, Vaishnavi, & Chatterjee 1999), who was likely to suffer from diffuse brain damage due to head injury, though no structural abnormality was revealed by MRI, had no or minimal evidence of left neglect, but was unable to process illusory contours (see also Vecera & Behrmann 1997, for related evidence).

*Preserved processing of illusions in neglect patients*

There is definite converging evidence from different studies to the effect that both subjective figures and illusions of length and position may be adequately processed in patients with left unilateral spatial neglect. The studies reviewed earlier, investigating the effects of illusions of length and position (the Müller-Lyer figure and its variants, the Oppel-Kundt figure), have revealed that the illusory displacement of the subjective centre of the line subtracts from (with configurations bringing about a leftward expansion/rightward compression or a leftward displacement of the line: see Figure 2-E, 2-F, 2-H; 3-C) or adds to (with configurations bringing about a rightward expan-

sion/leftward compression or a rightward displacement of the line: see Figure 2-D, 2-G, 2-I, 3-D) the rightward bias, which characterizes the bisection performance of patients with left neglect. This preserved processing has been qualified as *pre-attentive*, or not requiring perceptual awareness, on the basis of the observation that patients show, on the one hand, preserved illusory effects on line bisection, but, on the other hand, may fail to detect and report left-sided details of the illusory figures (see patient #2, who never reported left-sided fins, but showed complete illusory effects, in Mattingley et al. 1995; but see Olk & Harvey 2002; Vuilleumier & Landis 1998). This dissociation in the processing of illusory stimuli may be interpreted in the light of the distinction between *direct* vs. *indirect* tasks (Palmer 1999: 639). A direct task is designed to assess the subjects' conscious awareness of a visual presentation, e.g., through detection. An indirect task is designed to assess some process that can be influenced by registered information about the stimulus, even when there is no visual awareness of it. Line bisection may be regarded as a task which taps illusions of length and position in an indirect fashion. By contrast, detection and "same\different" judgements, concerning the same illusory stimuli or portions of them, may be considered direct tasks. In patients with left spatial neglect the level of representation of horizontal extent at which the illusory effects occur appears, therefore, to be preserved. The indirect/direct task dissociation suggests that this preserved processing may take place without perceptual awareness (Berti 2002).

This level of visual representation, preserved in many neglect patients, involves *non-spatial* and *retinotopic* reference frames. In the study by Vallar et al. (2000) the spatial position of the Brentano version of the Müller-Lyer figure modulated the bisection error of neglect patients. A right-sided position of the stimulus with respect to the mid-sagittal plane of the subject's trunk reduced, as found many times before (Heilman & Valenstein 1979), the rightward bisection error. This hemi-spatial effect, absent in neurologically unimpaired subjects, supports the view that an egocentric pathological mechanism contributes to the bisection error of patients with left neglect. The spatial position of the stimulus, by contrast, did not affect the extent of the illusory effects shown by either neglect patients or neurologically unimpaired subjects, suggesting that these visual phenomena (preserved in patients with neglect) occur within a retinotopic reference frame.

## Illusions of horizontal extent as models of neglect: Illusions of neglect

Illusion of horizontal extent, such as the non-symmetrical versions of the Müller-Lyer figures, the Oppel-Kundt configuration (Figures 2 and 3), and the isosceles triangular background induce in neurologically unimpaired individuals a rightward or leftward displacement of the subjective mid-point, according to the side of the expansion/compression of the horizontal segment. These illusory effects, as noted by Watt (1994), who used the Oppel-Kundt illusion as an illustrative example, mimic the line bisection performance of patients with left unilateral neglect.

Following a similar logic, Fleming and Behrmann (1998) used Judd illusion displays (Figure 2-H and 2-I) to assess the performance of neurologically unimpaired subjects in manual line bisection, and in a task which required to place the two fins at the ends of an imaginary shaft. In this study the illusion-inducing properties of the Judd figures were investigated varying orthogonally the direction and the angles of the fins. Results showed that illusory displacements of the shaft induce in neurologically unimpaired subjects a directional error similar to the one committed by neglect patients. Such an error is also produced by non-symmetrical Müller-Lyer and Brentano configurations (Figure 2-D vs. 2-E, 2-F vs. 2-G, 2-J vs. 2-K) (Mattingley et al. 1995; Olk et al. 2001; Post et al. 1998; Vallar et al. 2000).

For the Judd figure (an illusion of position, in which the stimulus is displaced), the analogy may be regarded as compatible with the view that one pathological mechanism underlying contralesional neglect involves the ipsilesional pathological orientation of spatial attention, with the illusory displacement mimicking the ipsilesional shift of lateral spatial attention (discussion in Bisiach & Vallar 2000; Kinsbourne 1993). For the Müller-Lyer illusion, the analogy is consistent with the view that one pathological mechanism underlying some abnormal behaviours exhibited by right brain-damaged-patients with left neglect is a rightward compression of the internal representation of space, at an even rate (Halligan & Marshall 1991), or a shrinkage or compression in size perception, confined to, or affecting disproportionately, the left contralesional side of perceived space (Gainotti & Tiacci 1971; Milner, Harvey, Roberts, & Forster 1993). Alternatively, the spatial medium may be pathologically expanded contralesionally (leftwards in patients with left neglect), and compressed ipsilesionally (rightwards), making objects in the left side of space, or the left side of objects, disproportionately shorter in their horizontal dimension (Bisiach, Neppi-Mòdona, & Ricci 2002; Bisiach & Vallar 2000). Distortions of this sort would account for a number of pathological phenomena found in patients with left neglect. These include the patients' rightward error in line bisection, their judging the left half of a horizontal line as shorter than the right (Milner et al. 1993), and their underestimation of the horizontal extent of stimuli presented in the left side of egocentric space (Ferber & Karnath 2001; Gainotti & Tiacci 1971; Irving-Bell, Small, & Cowey 1999; Kerkhoff 2000; Milner & Harvey 1995).

Another pathological phenomenon that is present in the performance of some right-brain-damaged patients (the contralesional – leftward in right-brain-damaged patients – overextension of a line) is simulated by visual illusions. In the study by Ricci et al. (2004) an Oppel-Kundt background with a line density increasing leftwards or rightwards (e.g., Figure 3-C and 3-D), that brought about a bias in bisection towards the more dense background, produced, in the line extension task, an overestimation of the length of the line lying on the more dense background. This effect was found both in right-brain-damaged patients with neglect and in neurologically unimpaired individuals, and was independent of the side (leftward or rightward) of the extension. This illustrates one main feature of these simulations, namely their symmetrical effects, that differ from the asymmetrical nature of the neglect disorder. It should be also noted that, as a group, the neglect patients of Ricci et al. (2004) did not show

the leftward contralesional hyperextension, that – it had been suggested (Bisiach et al. 2002) – is a main component of neglect. A perusal of the patients' individual data (see Table 1 of Ricci et al. 2004) shows variable patterns of extension. These appear also unrelated to visual field deficits, that may play a main role in producing the phenomenon, as Doricchi and colleagues suggested (Doricchi & Angelelli 1999; Doricchi, Guariglia, Figliozzi, Magnotti, & Gabriele 2003; Doricchi, Onida, & Guariglia 2002).

These simulations of neglect through illusory stimuli are mere analogies, however, even though they provide suggestions concerning the possible pathological mechanisms producing the ipsilesional displacement of the subjective mid-point in line bisection. These illusory effects, are, as discussed earlier, preserved in patients with left unilateral neglect. Illusions of length and position, and figures with subjective contours are likely to arise at a non-spatial, retinotopic, level of representation (Vallar et al. 2000). The anatomical correlates of the preserved illusory effects in right-brain-damaged patients with left unilateral neglect provide converging evidence, which supports this conclusion.

## The anatomical basis of visual illusions

As to illusory contours, neurophysiological studies in the monkey (Grosof, Shapley, & Hawken 1993; Lee & Nguyen 2001; Peterhans & von der Heydt 1989; von der Heydt & Peterhans 1989; von der Heydt, Peterhans, & Baumgartner 1984) and functional imaging experiments in humans (Ffytche & Zeki 1996; Hirsch et al. 1995; Larsson et al. 1999; Mendola, Dale, Fischl, Liu, & Tootell 1999) have provided evidence that the neural basis of visual illusions includes the occipital regions (the visual association and the primary visual cortices). More specifically, a main role of the lateral occipital extrastriate visual cortex has been suggested, on the basis of fMRI activation studies (Mendola et al. 1999), of studies with visual evoked potentials (Murray, Foxe, Javitt, & Foxe 2004; Proverbio & Zani 2002), and of experiments combining both methods (Murray et al. 2002). The posterior parietal cortex may also play a role (Murray et al. 2004; Proverbio & Zani 2002). The suggestion has also been made that effects seen in the striate visual cortex V1, and in V2 (Lee & Nguyen 2001; Peterhans & von der Heydt 1989), may reflect feedback modulation from the lateral occipital complex (Halgren, Mendola, Chong, & Dale 2003; Murray et al. 2004; Murray et al. 2002).

Using repetitive Transcranic Magnetic Stimulation (rTMS), Brighina, Ricci, Piazza et al. (2003) found that 1 Hz stimulation of the extra-striate area in the right hemisphere, but not in the left hemisphere, disrupts perception of illusory contours in neurologically unimpaired subjects. In line with these findings, in migraineurs, in whom there is evidence for an hyper-excitability of the primary visual cortex (Aurora 2001; Aurora, Barrodale, Chronicle, & Mulleners 2005), 1 Hz rTMS over the right extra-striate cortex reduces latencies in a task requiring the discrimination of regular and irregular real and illusory contours (Fierro et al. 2003). These studies suggest a role of the extra-striate visual cortex in the processing of illusory contours, with an

asymmetry indicating a critical involvement of the right hemisphere (see also the visual evoked potentials and fMRI study of Murray et al. 2002, providing evidence for a contribution of the lateral occipital cortex of both hemispheres).

Based on these suggestions, the anatomical correlates of the processing of visual illusions in patients with left neglect may be considered, focusing on the damage vs. sparing of the occipital regions.

*Illusions of length and position*

In the study by Mattingley et al. (1995) a group analysis revealed that right-sided fins induced illusory effects in all conditions, as in control subjects. Left-sided fins, by contrast, brought about only partial effects. This is likely to reflect variability among patients. Mattingley et al.'s (1995) patient #1, who had severe hypoperfusion in the vascular territory of the right middle cerebral artery, made a systematic left-sided bisection error with left-sided fins, which were presumably treated as visual cues, with no illusory effect. Patient #2, who had a temporo-parietal and subcortical stroke lesion, by contrast, showed completely preserved illusory effects with left-sided fins. The other five patients had lesions involving the frontal, temporal, parietal or subcortical regions; the occipital lobe was damaged in patient #4. In the study by Olk et al. (2001), where the group analysis showed overall preserved illusory effects, two out of the 12 right-brain-damaged patients with left neglect had lesions extending to the occipital lobe: one patient (K.G.) showed largely preserved illusory effects, the other (L.C.) had a much less consistent performance. The six right-brain-damaged patients studied by Esterman et al. (2002), whose performance, as that of neurologically unimpaired subjects, was modulated by an isosceles triangular background, had lesions sparing the occipital region, and showed visual extinction, but no hemianopia.

The study by Ricci et al. (2004) with the Oppel-Kundt illusion suggests a role of the occipital regions. A single-patient perusal of the performance of the 28 right-brain-damaged patients with left neglect showed that the 19 patients with illusory effects (in line bisection, in line extension, or in both tasks) had lesions sparing the occipital regions, that were damaged in the four patients in whom the illusory effect was absent. Three of these four patients had a left hemianopia on a clinical confrontation exam.

In two other studies more precise anatomical information was provided, including lesion maps. The patient of Ro and Rafal (1996) had an extensive temporo-parietal lesion, which spared the optic radiations and the occipital cortex. In the study of Vallar et al. (2000) one patient (G.M.) showed no illusory effects with left-sided outward-projecting fins (Figure 2-J). G.M. was the only patient in this series with right hemisphere damage extending to the visual association and primary visual cortices. These findings have been replicated and extended in a larger series of right brain-damaged neglect patients with lesions including the optic radiations, the occipital cortex, or both, and behavioural and electrophysiological evidence of left visual half-field deficits (Daini, Angelelli, Antonucci, Cappa, & Vallar 2002). This group of right brain-damaged patients with neglect and hemianopia was compared with neglect patients without left visual-half field deficits, and lesions sparing the optic radiations and

the occipital cortex. Patients with damage extending caudally to the occipital regions showed no illusory effects, which, in turn, were preserved in patients with more anterior damage (see Figure 5). These patients, as neurologically unimpaired controls exhibited the illusory effects in both directions. The rightward bias of neglect was further increased when the Brentano figure was rightward-expanded (Figure 2-K), reduced when the expansion was towards the left side (Figure 2-J). This difference was independent of the severity of spatial unilateral neglect, as assessed by cancellation and reading tasks, but patients with more posterior damage, as reported previously (Binder, Marshall, Lazar, Benjamin, & Mohr 1992; D'Erme, De Bonis, & Gainotti 1987, for related evidence; Doricchi & Angelelli 1999), showed a greater rightward bias in line bisection (see Figure 5).

*Figures delimited by subjective contours*

The three patients of Vuilleumier and Landis (1998), who showed preserved processing of subjective figures, had cortical or subcortical lesions, which spared the primary and secondary visual areas. In a second study, Vuilleumier et al. (2001) replicated their earlier findings in a larger series of 12 patients, including the three previously reported cases (Vuilleumier & Landis 1998), with a complete group analysis showing that the rightward bisection error diminished with gap stimuli (an empty space between two dots), compared with horizontal bars formed by either real or illusory contours (Bisiach et al. 1996; Bisiach et al. 1994; McIntosh et al. 2004). Vuilleumier et al. (2001), looking at the individual data, found that their series fractionated into two subgroups, differing with respect to their bisection performance with gap stimuli. One subgroup, in which lesions clustered in the inferior-posterior parietal lobule (BA 40), showed the general pattern, characterized by a reduction of the rightward bias with gap stimuli. In the other subgroup, in which lesions extended more posteriorly to the lateral occipital lobe (BAs 18 and 19), the bisection error was comparable in all conditions, including gap stimuli. This may suggest that the reduction of the bisection error in neglect patients with gap stimuli may be related to visual features of the stimulus, whose processing is disrupted by occipital damage, together with attention cueing (McIntosh et al. 2004). The average bisection error of subjective vs. real figures was however similar in both subgroups, the difference concerning instead a very different stimulus (a gap). Vuilleumier et al. (2001) also found a significant correlation between the bisection performances of figures with subjective and real contours in the parietal, but not in the parieto-occipital subgroup. Taken together, these findings suggest, from a neuropsychological perspective, a role of the lateral occipital cortex in the generation of subjective figures.

## Conclusions

The available empirical evidence concerning the processing of visual illusions (figures delimited by subjective contours, illusions of length and position) in right-brain-

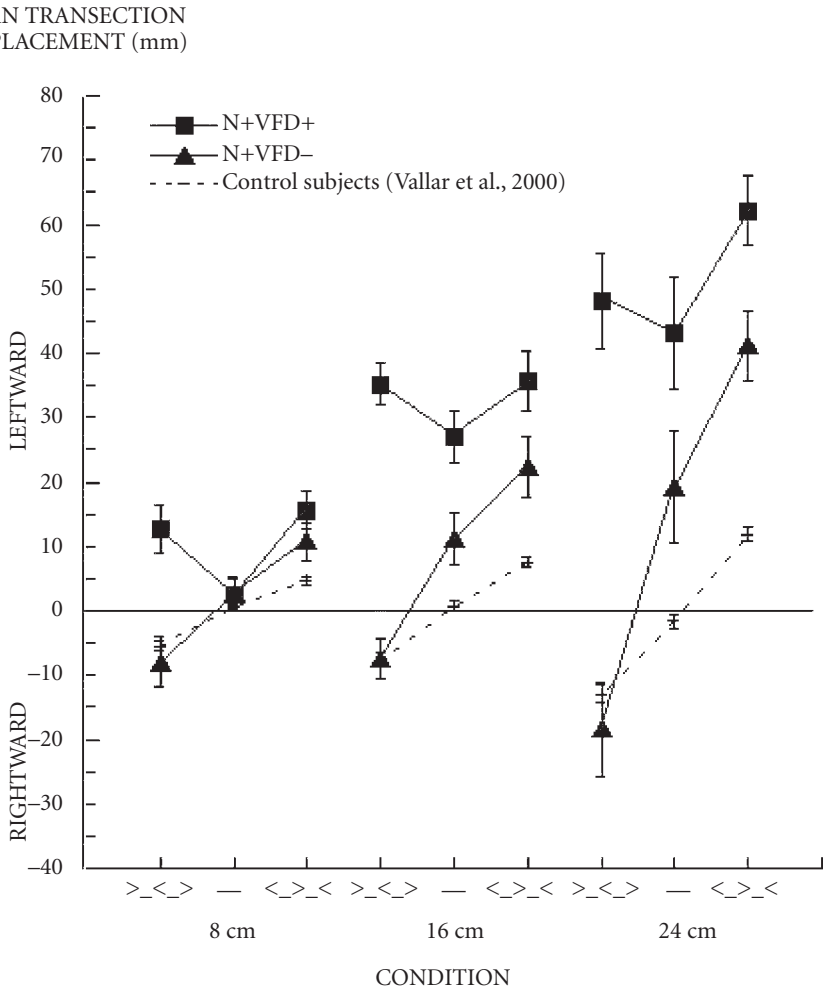



**Figure 5.** Mean transection displacement (mm) and standard error, by group (patients with neglect, N+, with and without visual field deficits VFD+/VFD–), line length (8 cm, 16 cm, and 24 cm), and condition (baseline control, left-, right-expanded Brentano-Müller-Lyer illusion). Control data from Vallar et al.'s (2000) study are shown (reprinted with kind permission from Springer Science and Business Media Daini et al. 2002).

damaged patients with left neglect consistently suggests that the levels of representation where these visual phenomena arise are largely preserved. This behavioural evidence has an anatomical counterpart. Illusory effects are disrupted in patients with left neglect when the lesions extend from the posterior-inferior parietal region at the temporo-parietal junction, which represents the main anatomical correlate of this disorder (Halligan, Fink, Marshall, & Vallar 2003, and references therein), more caudally to the occipital regions. Perceptual analysis of visual input, including grouping and

figure-ground segmentation (as suggested by experiments using illusory contours), and a relevant part of the multi-component processes (Coren & Gircus 1978b) underpinning estimation of length (as suggested by experiments using variants of the Müller-Lyer and Oppel-Kundt illusions) are likely to take place at a retinotopic level of representation, in the visual cortex. These operations are largely independent of the spatial representations, dysfunctional in patients with left neglect, which have more anterior neural correlates (Halligan et al. 2003). This functional and anatomical independence is supported also by the finding that the presence or absence of illusory effects in neglect patients is unrelated to the overall severity of neglect itself, as assessed by standard diagnostic test batteries (Daini et al. 2002; Vallar et al. 2000; Vuilleumier et al. 2001). In the study by Ricci et al. (2004), in neglect patients the Oppel-Kundt illusory effects in the bisection and cancellation tasks were correlated positively with the response bias in the landmark task, negatively with the perceptual bias (Bisiach, Ricci, Lualdi, & Colombo 1998). This task, where subjects are required to indicate the shorter or the longer segment of a horizontal line, is used to disentangle perceptual vs. response biases in neglect (Milner et al. 1993). Ricci et al. (2004) interpreted this pattern of correlations as an indication that illusory effects are more likely to take place in neglect patients whose functional impairment spares input processes (namely, neglect is brought about mainly by an output bias), that may partly overlap with those concerned with the illusory effects themselves. It should be noted, however, that the illusory effects found by Ricci et al. (2004), Vallar et al. (2000), Daini et al. (2002), Esterman et al. (2002) include both rightward and leftward biases, and, in the latter case, the rightward response bias of neglect is to be defeated. Accordingly, the response bias assessed by the Landmark task (Bisiach, Ricci, Lualdi et al. 1998; Milner et al. 1993) appears to be specific for that particular experimental condition, rather than being a general reluctance on the patients' part to perform leftward contralesional movements (directional hypokinesia, see Heilman, Watson, & Valenstein 2003).

In the studies considered in this review the preserved illusory effects were demonstrated through *indirect* (Palmer 1999), *procedural* or *implicit* tasks (Roediger & McDermott 1993), in which patients where required to communicate that stimulus processing had taken place through a behavioural response (line bisection), rather than by explicitly declaring the detection of the left-sided components of the illusory configurations. A number of studies have emphasised the indirect nature of the preserved illusory effects, showing that patients were unable to explicitly process the left side of the stimulus, as assessed by "same/different" judgements or detection direct tasks (Mattingley et al. 1995, see patient #2; see, however, Olk et al. 2001; Ro & Rafal 1996; Vuilleumier & Landis 1998; Vuilleumier et al. 2001). These findings may be taken as evidence that illusory contours and illusions of length and position arise at levels of representation which do not entail perceptual awareness: *pre-attentional* (Mattingley et al. 1995; Vuilleumier et al. 2001), involving what has been termed *intermediate* vision (Humphreys et al. 1994; Ricci et al. 2004; Ricci et al. 1999). These phenomena may be also referred to as based on *bottom-up attentional* processing, rather than *top-down* (Connor, Egeth, & Yantis 2004), aware, mechanisms (Dennett 1991; Palmer 1999).

The perceptual processes involved in the illusory effects may, nevertheless, affect the subjects' visuo-motor behaviour, such as their error in line bisection, with effects adding to, or subtracting from, the rightward shift brought about by unilateral neglect (Daini et al. 2002; Mattingley et al. 1995; Ricci et al. 2004; Ro & Rafal 1996), independent of the presence of motor biases, such as those revealed by the Landmark task (Ricci et al. 2004).

A further issue concerns illusions of length and position as a simulation model of the mechanisms underlying spatial neglect. The simulation appears to include the lateral pathological displacement of spatial attention (the Judd illusion of position), and the relative compression of objects in the left portion of space, compared to right-sided objects, or of the left side of objects, compared to their right side (the Müller-Lyer figure and its variants, the Oppel-Kundt background).

On the one hand, data from neurologically unimpaired individuals indicate that these illusions provide an effective simulation of two aspects of left spatial neglect, namely: the rightward displacement of the subjective mid-point of a horizontal segment, and the contralesional leftward overextension in the line extension task. The very nature of illusions of length, furthermore, simulates a horizontal size distortion (see, e.g., Cohen, Gray, Meyrignac, Dehaene, & Degos 1994; Ferber & Karnath 2001; Frassinetti, Nichelli, & di Pellegrino 1999; Restle & Decker 1977), which characterizes some manifestations of unilateral spatial neglect. More specifically, the expansion of the right side of a line, and the compression of its left side, induced by appropriately arranged fins, provide an analogue of the anisometric distortion of space representation in left neglect, that may bring about a rightward ipsilesional error in line bisection, and a leftward contralesional overextension. In brain-damaged patients with left neglect, however, the mechanisms underlying the ipsilesional bisection and the contralesional overextension biases are likely to be independent, since dissociations between the two disorders have been found (Bisiach, Ricci, & Neppi Mòdona 1998; Doricchi & Angelelli 1999).

On the other hand the consistent neuropsychological observation of preserved illusory effects of length and position in neglect patients, and of their disruption after damage involving the occipital regions, suggests that such a simulation, plausible as it may be, takes place at a different level of representation, and in different regions of the brain.

The view that multiple representations of lateral extension may exist in the brain, within different reference frames, is compatible with the finding that a related perceptual disorder (the underestimation of the horizontal size of contralesional visual objects) has been observed in right-brain-damaged patients with unilateral neglect: a tendency to "overvalue" the size of ipsilesional drawings (Gainotti & Tiacci 1971), a "size distortion" (Milner & Harvey 1995). These deficits have been found also in right-brain-damaged patients without neglect (hemimicropsia, Cohen et al. 1994, case #1) (horizontal dysmetropsia, Frassinetti et al. 1999), as well as after damage to the left hemisphere (Cohen et al. 1994, case #2).

To summarize, there is evidence that the occipital lobe, and, more specifically, the extra-striate visual cortex (Cohen et al. 1994; Frassinetti et al. 1999) constitutes a neural basis for the processing of horizontal length. Consistent with these findings, illusions of length and position are likely, as discussed earlier, to arise in the occipital regions.

The evidence from brain-damaged-patients with neglect suggests that the processing of visual illusions (of length and position, subjective contours) is consistently spared, provided the damage does not include the occipital regions. This conclusion may be taken as evidence that brain regions anterior to the striate and extra-striate visual cortices provide little, if any, contribution to the processing of illusions. In the study by Daini et al. (2002), however, in neglect patients without hemianopia the size of the illusory effect was larger on the contralesional left side, compared with the right side (Figure 6). This suggests that, while "bottom up" processing of visual illusions such as the Brentano-Müller-Lyer is independent of spatial representational and focal attention systems (impaired in neglect), these same "top down" processes may nevertheless exert a modulation effect, which may reduce the size of the illusion. The view that spatial attention may inhibit some perceptual effects is consistent with an observation by Chatterjee, Ricci and Calhoun (2000), who asked two patients with left neglect to judge the relative heaviness of pairs of weights placed in the two hands. They found that contextual effects of previous weights induced a leftward bias in their judgement. Chatterjee et al. (2000) concluded that in neglect patients contextual effects, which are normally mitigated by attention, may have a greater influence on the formation of representations of the left, neglected, side, resulting in a paradoxical leftward bias. Consistent with this interpretation, brain-damaged patients with hemianopia without neglect did not show any lateral bias in the illusory effects. The observation that in neglect patients without visual field defects the illusory effects were larger contralesionally is also compatible with developmental data showing that the magnitude of the Müller-Lyer illusion and of its Brentano form decreases with age (Predebon 1984). This age trend may reflect a developmental change in perceptual cognitive processing (Girgus, Coren, & Fraenckel 1975).

In patients with unilateral neglect illusory effects are greater in the contralesional side, where "top down" attentional modulation, based on the activity of regions typically damaged in such patients, such as the posterior-inferior parietal region and the temporo-parietal junction, is made disproportionately weak by the unilateral brain damage. Interestingly, for illusory contours it has been suggested that higher-tier visual areas (the lateral occipital complex, parietal structures) modulate backwards lower-tier visual areas (V1, V2) (Halgren et al. 2003; Murray et al. 2004; Murray et al. 2002). Taken together, these findings suggest an interpretation of the developmental reduction of the magnitude of the Müller-Lyer illusion in terms of age-related changes in spatial directed attention.

In conclusion, studies investigating the perception of visual illusions (length, position, and subjective contours) in brain-damaged patients with unilateral spatial neglect definitely indicate that their processing is largely independent, both behaviourally

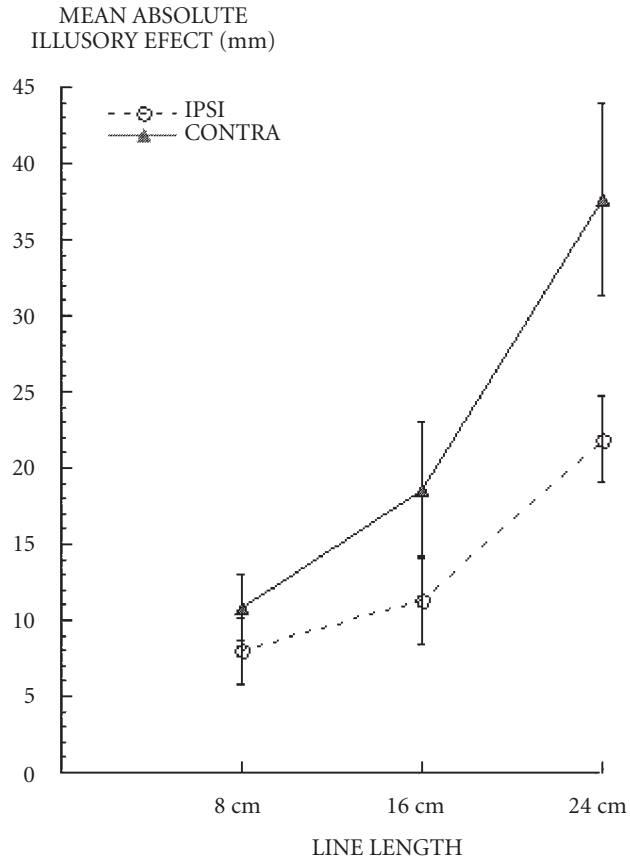



**Figure 6.** Mean absolute illusory effect (mm) and standard error in seven N+VFD– patients, by line length (8 cm, 16 cm, and 24 cm). IPSI: illusion size with ipsilesional, right-expanded stimuli. CONTRA: illusion size with contralesional, left-expanded stimuli (reprinted with kind permission from Springer Science and Business Media Daini et al. 2002).

and anatomically, of the spatial representations whose damage brings about unilateral spatial neglect. There is however also some evidence, based on illusions of length, for a modulation from the extra-occipital regions, damaged in neglect patients. This may suggests a role for visuo-spatial attention and may be related to developmental changes.

## References


Aurora, S. K. (2001). Pathophysiology of migraine headache. *Current Pain Headache Reports, 5*, 179–182.

Aurora, S. K., Barrodale, P., Chronicle, E. P., & Mulleners, W. M. (2005). Cortical inhibition is reduced in chronic and episodic migraine and demonstrates a spectrum of illness. *Headache, 45*, 546–552.

Benke, T., Luzzatti, C., & Vallar, G. (2004). Hermann Zingerle's "Impaired perception of the own body due to organic brain disorders". An introductory comment, and an abridged translation. *Cortex, 40*, 265–274.

Berti, A. (2002). Unconscious processing in neglect. In H.-O. Karnath, A. D. Milner & G. Vallar (Eds.), *The cognitive and neural bases of spatial neglect* (pp. 313–326). Oxford: Oxford University Press.

Binder, J., Marshall, R., Lazar, R., Benjamin, J., & Mohr, J. P. (1992). Distinct syndromes of hemineglect. *Archives of Neurology, 49*, 1187–1194.

Bisiach, E., Bulgarelli, C., Sterzi, R., & Vallar, G. (1983). Line bisection and cognitive plasticity of unilateral neglect of space. *Brain and Cognition, 2*, 32–38.

Bisiach, E., Neppi-Mòdona, M., & Ricci, R. (2002). Space anisometry in unilateral neglect. In H.-O. Karnath, A. D. Milner & G. Vallar (Eds.), *The cognitive and neural bases of spatial neglect* (pp. 145–152). Oxford: Oxford University Press.

Bisiach, E., Perani, D., Vallar, G., & Berti, A. (1986). Unilateral neglect: Personal and extra-personal. *Neuropsychologia, 24*, 759–767.

Bisiach, E., Pizzamiglio, L., Nico, D., & Antonucci, G. (1996). Beyond unilateral neglect. *Brain, 119*, 851–857.

Bisiach, E., Ricci, R., Lualdi, M., & Colombo, M. R. (1998). Perceptual and response bias in unilateral neglect: Two modified versions of the Milner landmark task. *Brain and Cognition, 37*, 369–386.

Bisiach, E., Ricci, R., & Neppi Mòdona, M. (1998). Visual awareness and anisometry of space representation in unilateral neglect: A panoramic investigation by means of a line extension task. *Consciousness and Cognition, 7*, 327–355.

Bisiach, E., Rusconi, M. L., Peretti, V., & Vallar, G. (1994). Challenging current accounts of unilateral neglect. *Neuropsychologia, 32*, 1431–1434.

Bisiach, E., & Vallar, G. (1988). Hemineglect in humans. In F. Boller & J. Grafman (Eds.), *Handbook of neuropsychology* (Vol. 1, pp. 195–222). Amsterdam: Elsevier.

Bisiach, E., & Vallar, G. (2000). Unilateral neglect in humans. In F. Boller, J. Grafman & G. Rizzolatti (Eds.), *Handbook of neuropsychology* (2 ed., Vol. 1, pp. 459–502). Amsterdam: Elsevier Science, B.V.

Bisiach, E., Vallar, G., Perani, D., Papagno, C., & Berti, A. (1986). Unawareness of disease following lesions of the right hemisphere: Anosognosia for hemiplegia and anosognosia for hemianopia. *Neuropsychologia, 24*, 471–482.

Boring, E. G. (1942). *Sensation and perception in the history of experimental psychology*. New York: D. Appleton-Century Company.

Bottini, G., Paulesu, E., Gandola, M., Loffredo, S., Scarpa, P., & Sterzi, R. et al. (2005). Left caloric vestibular stimulation ameliorates right hemianesthesia. *Neurology, 65*, 1278–1283.

Brighina, F., Ricci, R., Piazza, A., Scalia, S., Giglia, G., & Fierro, B. (2003). Illusory contours and specific regions of human extrastriate cortex: Evidence from rTMS. *European Journal of Neuroscience, 17*, 2469–2474.

Chatterjee, A., Ricci, R., & Calhoun, J. (2000). Weighing the evidence for cross over in neglect. *Neuropsychologia, 38*, 1390–1397.

Cohen, L., Gray, F., Meyrignac, C., Dehaene, S., & Degos, J. D. (1994). Selective deficit of visual size perception: Two cases of hemimicropsia. *Journal of Neurology Neurosurgery and Psychiatry, 57*, 73–78.

Connor, C. E., Egeth, H. E., & Yantis, S. (2004). Visual attention: Bottom-up versus top-down. *Current Biology, 14* (R850–R852).

Coren, S., & Gircus, J. S. (1978a). *Seeing is deceiving: The psychology of visual illusions*. Hillsdale, New Jersey: Lawrence Erlbaum.

Coren, S., & Gircus, J. S. (1978b). Visual illusions. In R. Held, H. W. Leibowitz, & H.-L. Teuber (Eds.), *Handbook of sensory physiology. Perception* (Vol. 8, pp. 548–568). Heidelberg: Springer-Verlag.

D'Erme, P., De Bonis, C., & Gainotti, G. (1987). Influenza dell'emi-inattenzione e dell'emianopsia sui compiti di bisezione di linee nei pazienti cerebrolesi. *Archivio di Psicologia, Neurologia e Psichiatria, 48*, 193–207.

Daini, R., Angelelli, P., Antonucci, G., Cappa, S. F., & Vallar, G. (2002). Exploring the syndrome of spatial unilateral neglect through an illusion of length. *Experimental Brain Research, 144*, 224–237.

Dennett, D. C. (1991). *Consciousness explained*. London: Allen Lane, The Penguin Press.

Denny-Brown, D., Meyer, J. S., & Horenstein, S. (1952). The significance of perceptual rivalry resulting from parietal lesion. *Brain, 75*, 433–471.

Doricchi, F., & Angelelli, P. (1999). Misrepresentation of horizontal space in left unilateral neglect. Role of hemianopia. *Neurology, 52*, 1845–1852.

Doricchi, F., Guariglia, P., Figliozzi, F., Magnotti, L., & Gabriele, G. (2003). Retinotopic modulation of space misrepresentation in unilateral neglect: Evidence from quadrantanopia. *Journal of Neurology, Neurosurgery and Psychiatry, 74*, 116–119.

Doricchi, F., Onida, A., & Guariglia, P. (2002). Horizontal space misrepresentation in unilateral brain damage II. Eye-head centered modulation of visual misrepresentation in hemianopia without neglect. *Neuropsychologia, 40*, 1118–1128.

Esterman, M., McGlinchey-Berroth, R., Alexander, M. P., & Milberg, W. (2002). Triangular backgrounds shift line bisection performance in hemispatial neglect: The critical point. *Journal of the International Neuropsycholological Society, 8*, 721–726.

Ferber, S., & Karnath, H.-O. (2001). Size perception in hemianopia and neglect. *Brain, 124*, 527–536.

Ffytche, D. H., & Zeki, S. (1996). Brain activity related to the perception of illusory contours. *Neuroimage, 3*, 104–108.

Fierro, B., Ricci, R., Piazza, A., Scalia, S., Giglia, G., & Vitello, G. et al. (2003). 1 Hz rTMS enhances extrastriate cortex activity in migraine: Evidence of a reduced inhibition? *Neurology, 61*, 1446–1448.

Fleming, J., & Behrmann, M. (1998). Visuospatial neglect in normal subjects: Altered spatial representations induced by a perceptual illusion. *Neuropsychologia, 36*, 469–475.

Frassinetti, F., Nichelli, P., & di Pellegrino, G. (1999). Selective horizontal dysmetropsia following prestriate lesion. *Brain, 122*, 339–350.

Gainotti, G., & Tiacci, C. (1971). The relationships between disorders of visual perception and unilateral spatial neglect. *Neuropsychologia, 9*, 451–458.

Girgus, J. S., Coren, S., & Fraenckel, R. (1975). Levels of perceptual processing in the development of visual illusions. *Developmental Psychology, 11*, 268–273.

Grosof, D. H., Shapley, R. M., & Hawken, M. J. (1993). Macaque V1 neurons can signal 'illusory' contours. *Nature, 365*, 550–552.

Halgren, E., Mendola, J., Chong, C. D. R., & Dale, A. M. (2003). Cortical activation to illusory shapes as measured with magnetoencephalography. *Neuroimage, 18*, 1001–1009.

Halligan, P. W., Fink, G. R., Marshall, J. C., & Vallar, G. (2003). Spatial cognition: Evidence from visual neglect. *Trends in Cognitive Sciences, 7*, 125–133.

Halligan, P. W., & Marshall, J. C. (1991). Spatial compression in visual neglect: A case study. *Cortex, 27*, 623–629.

Heilman, K. M., & Valenstein, E. (1979). Mechanisms underlying hemispatial neglect. *Annals of Neurology, 5*, 166–170.

Heilman, K. M., Watson, R. T., & Valenstein, E. (2003). Neglect and related disorders. In K. M. Heilman & E. Valenstein (Eds.), *Clinical neuropsychology* (4 ed., pp. 296–346). New York: Oxford University Press.

Hirsch, J., Delapaz, R. L., Relkin, N. R., Victor, J., Kim, K., & Li, T. et al. (1995). Illusory contours activate specific regions in human visual cortex. Evidence from functional magnetic-resonance-imaging. *Proceedings of the National Academy of Sciences, USA, 92*, 6469–6473.

Holding, D. H. (1970). A line illusion with irrelevant depth cues. *American Journal of Psychology, 83*, 280–282.

Humphreys, G. W., Riddoch, M. J., Donnelly, N., Freeman, T., Boucart, M., & Muller, H. M. (1994). Intermediate visual processing and visual agnosia. In M. Farah & G. Ratcliff (Eds.), *The neuropsychology of high-level vision* (pp. 63–101). Hillsdale, New Jersey: Lawrence Erlbaum Associates.

Irving-Bell, L., Small, M., & Cowey, A. (1999). A distortion of perceived space in patients with right-hemisphere lesions and visual hemineglect. *Neuropsychologia, 37*, 919–925.

Judd, C. H. (1899). A study of geometrical illusions. *Psychological Review, 6*, 241–261.

Kanisza, G. (1979). *Organization in vision*. New York: Praeger.

Kanizsa, G. (1976). Subjective contours. *Scientific American, 234*, 48–52.

Kartsounis, L. D., & Warrington, E. K. (1989). Unilateral visual neglect overcome by cues implicit in stimulus arrays. *Journal of Neurology, Neurosurgery, and Psychiatry, 52*, 1253–1259.

Kerkhoff, G. (2000). Multiple perceptual distortions and their modulation in leftsided visual neglect. *Neuropsychologia, 38*, 1073–1086.

Kinsbourne, M. (1993). Orientational bias model of unilateral neglect: Evidence from attentional gradients within hemispace. In I. H. Robertson & J. C. Marshall (Eds.), *Unilateral neglect: Clinical and experimental studies* (pp. 63–86). Hove: Erlbaum.

Kooistra, C. A., & Heilman, K. M. (1989). Hemispatial visual inattention masquerading as hemianopia. *Neurology, 39*, 1125–1127.

Larsson, J., Amunts, K., Gulyas, B., Malikovic, A., Zilles, K., & Roland, P. E. (1999). Neuronal correlates of real and illusory contour perception: Functional anatomy with PET. *European Journal of Neuroscience, 11*, 4024–4036.

Lee, T. S., & Nguyen, M. (2001). Dynamics of subjective contour formation in the early visual cortex. *Proceedings of the National Academy of Sciences USA, 98* 1907–1911.

Mattingley, J. B., Bradshaw, J. L., & Bradshaw, J. A. (1995). The effects of unilateral visuospatial neglect on perception of Müller-Lyer illusory figures. *Perception, 24*, 415–433.

Mattingley, J. B., Davis, G., & Driver, J. (1997). Preattentive filling-in of visual surfaces in parietal extinction. *Science, 275*, 671–674.

McGlinchey-Berroth, R. (1997). Visual information processing in hemispatial neglect. *Trends in Cognitive Sciences, 1*, 91–97.

McIntosh, R. D., McClements, K. I., Dijkerman, H. C., & Milner, A. D. (2004). "Mind the gap": The size-distance dissociation in visual neglect is a cueing effect. *Cortex, 40*, 339–346.

Mendola, J. D., Dale, A. M., Fischl, B., Liu, A. K., & Tootell, R. B. (1999). The representation of illusory and real contours in human cortical visual areas revealed by functional magnetic resonance imaging. *Journal of Neuroscience 19*, 8560–8572.

Milner, A. D., & Harvey, M. (1995). Distortion of size perception in visuospatial neglect. *Current Biology, 5*, 85–89.

Milner, A. D., Harvey, M., Roberts, R. C., & Forster, S. V. (1993). Line bisection errors in visual neglect: Misguided action or size distortion? *Neuropsychologia, 31*, 39–49.

Moro, V., Zampini, M., & Aglioti, S. M. (2004). Changes in spatial position of hands modify tactile extinction but not disownership of contralesional hand in two right brain-damaged patients. *Neurocase, 10*, 437–443.

Moscovitch, M., & Behrmann, M. (1994). Coding of spatial information in the somatosensory system: Evidence from patients with neglect following parietal lobe damage. *Journal of Cognitive Neuroscience, 6*, 151–155.

Müller-Lyer, F. C. (1889). Optische Urtheilstäuschungen. *Archiv für Anatomie und Physiologie, Physiologische Abteilung (Supplement-Band), 2*, 263–270.

Murray, M. M., Foxe, D. M., Javitt, D. C., & Foxe, J. J. (2004). Setting boundaries: Brain dynamics of modal and amodal illusory shape completion in humans. *Journal of Neuroscience, 24*, 6898–6903.

Murray, M. M., Wylie, G. R., Higgins, B. A., Javitt, D. C., Schroeder, C. E., & Foxe, J. J. (2002). The spatiotemporal dynamics of illusory contour processing: Combined high-density electrical mapping, source analysis, and functional magnetic resonance imaging. *Journal of Neuroscience, 22*, 5055–5073.

Neisser, U. (1976). *Cognition and reality. Principles and implications of cognitive psychology*. San Francisco, CA: W. H. Freeman and Co.

Olk, B., & Harvey, M. (2002). Effects of visible and invisible cueing on line bisection and Landmark performance in hemispatial neglect. *Neuropsychologia, 40*, 282–290.

Olk, B., Harvey, M., Dow, L., & Murphy, P. J. S. (2001). Illusion processing in hemispatial neglect. *Neuropsychologia, 39*, 611–625.

Palmer, S. E. (1999). *Vision science. Photons to phenomenology*. Cambridge, MA: The MIT Press.

Peterhans, E., & von der Heydt, R. (1989). Mechanisms of contour perception in monkey visual cortex. II. Contours bridging gaps. *Journal of Neuroscience, 9*, 1749–1763.

Porac, C. (1994). Comparison of the wings-in, wings-out, and Brentano variants of the Mueller-yer illusion. *American Journal of Psychology, 107*, 69–83.

Posner, M. I. (1994). Attention: The mechanisms of consciousness. *Proceedings of the National Academy of Sciences of the United States of America, 91*, 7398–7403.

Post, R. B., Welch, R. B., & Caufield, K. (1998). Relative spatial expansion and contraction within the Müller-Lyer and Judd illusions. *Perception, 27*, 827–838.

Predebon, J. (1984). Age trends in The Mueller-Lyer and Ponzo illusions. *British Journal of Developmental Psychology, 3*, 99–103.

Proverbio, A. M., & Zani, A. (2002). Electrophysiological indexes of illusory contours perception in humans. *Neuropsychologia, 40*, 479–491.

Restle, F., & Decker, J. (1977). Size of the Mueller-Lyer illusion as a function of its dimensions: Theory and data. *Perception and Psychophysics, 21*, 489–503.

Ricci, R., Calhoun, J., & Chatterjee, A. (2000). Orientation bias in unilateral neglect: Representational contributions. *Cortex, 36*, 671–677.

Ricci, R., Pia, L., & Gindri, P. (2004). Effects of illusory spatial anisometry in unilateral neglect. *Experimental Brain Research, 154*, 226–237.

Ricci, R., Vaishnavi, S., & Chatterjee, A. (1999). A deficit of intermediate vision: Experimental observations and theoretical implications. *Neurocase, 5*, 1–12.

Ro, T., & Rafal, R. D. (1996). Perception of geometric illusions in hemispatial neglect. *Neuropsychologia, 34*, 973–978.

Rode, G., Charles, N., Perenin, M. T., Vighetto, A., Trillet, M., & Aimard, G. (1992). Partial remission of hemiplegia and somatoparaphrenia through vestibular stimulation in a case of unilateral neglect. *Cortex, 28*, 203–208.

Rode, G., Perenin, M. T., Honoré, J., & Boisson, D. (1998). Improvement of the motor deficit of neglect patients through vestibular stimulation: Evidence for a motor neglect component. *Cortex, 34*, 253–261.

Roediger, H. L., & McDermott, K. B. (1993). Implicit memory in normal human subjects. In F. Boller & J. Grafman (Eds.), *Handbook of neuropsychology* (Vol. 8, pp. 63–131). Amsterdam: Elsevier.

Rossetti, Y., & Rode, G. (2002). Reducing spatial neglect by visual and other sensory manipulations: Non-cognitive (physiological) routes to the rehabilitation of a cognitive disorder. In H.-O. Karnath, A. D. Milner & G. Vallar (Eds.), *The cognitive and neural bases of spatial neglect* (pp. 375–396). Oxford: Oxford University Press.

Smania, N., & Aglioti, S. (1995). Sensory and spatial components of somaesthetic deficits following right brain damage. *Neurology, 45*, 1725–1730.

Sterzi, R., Bottini, G., Celani, M. G., Righetti, E., Lamassa, M., & Ricci, S. et al. (1993). Hemianopia, hemianaesthesia, and hemiplegia after left and right hemisphere damage: A hemispheric difference. *Journal of Neurology, Neurosurgery, and Psychiatry, 56*, 308–310.

Umiltà, C. (2001). Mechanisms of attention. In B. Rapp (Ed.), *The handbook of cognitive neuropsychology* (pp. 135–158). Philadelphia: Psychology Press.

Vallar, G. (1998). Spatial hemineglect in humans. *Trends in Cognitive Sciences, 2*, 87–97.

Vallar, G., Bottini, G., Rusconi, M. L., & Sterzi, R. (1993). Exploring somatosensory hemineglect by vestibular stimulation. *Brain, 116*, 71–86.

Vallar, G., Bottini, G., & Sterzi, R. (2003). Anosognosia for left-sided motor and sensory deficits, motor neglect, and sensory hemiinattention: Is there a relationship? *Progress in Brain Research, 142*, 289–301.

Vallar, G., Bottini, G., Sterzi, R., Passerini, D., & Rusconi, M. L. (1991). Hemianesthesia, sensory neglect and defective access to conscious experience. *Neurology, 41*, 650–652.

Vallar, G., & Daini, R. (2002). Illusions in neglect, illusions of neglect. In H.-O. Karnath, A. D. Milner & G. Vallar (Eds.), *The cognitive and neural bases of spatial neglect* (pp. 209–224). Oxford: Oxford University Press.

Vallar, G., Daini, R., & Antonucci, G. (2000). Processing of illusion of length in spatial hemineglect. A study of line bisection. *Neuropsychologia, 38*, 1087–1097.

Vallar, G., Guariglia, C., Nico, D., & Pizzamiglio, L. (1997). Motor deficits and optokinetic stimulation in patients with left hemineglect. *Neurology, 49*, 1364–1370.

Vallar, G., Guariglia, C., & Rusconi, M. L. (1997). Modulation of the neglect syndrome by sensory stimulation. In P. Thier & H.-O. Karnath (Eds.), *Parietal lobe contributions to orientation in 3D space* (pp. 555–578). Heidelberg: Springer-Verlag.

Vallar, G., & Perani, D. (1986). The anatomy of unilateral neglect after right hemisphere stroke lesions. A clinical CT/Scan correlation study in man. *Neuropsychologia, 24*, 609–622.

Vallar, G., Rusconi, M. L., & Bisiach, E. (1994). Awareness of contralesional information in unilateral neglect: Effects of verbal cueing, tracing and vestibular stimulation. In C. Umiltà & M. Moscovitch (Eds.), *Attention and performance XV. Conscious and nonconscious information processing* (pp. 377–391). Cambridge, MA: MIT Press.

Vallar, G., Sandroni, P., Rusconi, M. L., & Barbieri, S. (1991). Hemianopia, hemianesthesia and spatial neglect. A study with evoked potentials. *Neurology, 41*, 1918–1922.

Vecera, S. P., & Behrmann, M. (1997). Spatial attention does not require preattentive grouping. *Neuropsychology, 11*, 30–43.

von der Heydt, R., & Peterhans, E. (1989). Mechanisms of contour perception in monkey visual cortex. I. Lines of pattern discontinuity. *Journal of Neuroscience, 9*, 1731–1748.

von der Heydt, R., Peterhans, E., & Baumgartner, G. (1984). Illusory contours and cortical neuron responses. *Science, 224*, 1260–1262.

Vuilleumier, P., & Landis, T. (1998). Illusory contours and spatial neglect. *Neuroreport, 9*, 2481–2484.

Vuilleumier, P., Valenza, N., & Landis, T. (2001). Explicit and implicit perception of illusory contours in unilateral spatial neglect: Behavioural and anatomical correlates of preattentive grouping mechanisms. *Neuropsychologia, 39*, 597–610.

Watt, R. (1994). Some points about human vision and visual neglect. *Neuropsychological Rehabilitation, 4*, 213–219.

CHAPTER 4.5

# The impairment of the body image in the unilateral neglect syndrome

Gabriella Bottini, Martina Gandola,
Lorenzo Pia, and Anna Berti

## Introduction

In this chapter we shall discuss some theoretical issues on the mental representation of the body, illustrating the main competences of the left and the right hemisphere in this cognitive domain. The attention will mainly focus on the "non semantic" components of the body representation which are particularly related to the right hemisphere. Finally, the symptoms associated to the desegregation of the body schema which typically occur when unilateral neglect is present, will be described in their neuropsychological and anatomical aspects.

## The body representation: Theoretical issues

The concept of body representation is a topic of debate not only in the psychological domain. It is also extensively discussed for example at the philosophical level. In neuropsychology the impairment of the body representation may cause a wide range of symptoms very different in their nature. Various hypotheses have been proposed on the mechanisms underlying the several disorders of the body representation. Some of them are spatial in their nature (De Renzi & Faglioni 1963; De Renzi & Scotti 1970; Reed & Farah 1995), other relay on more conceptual/linguistic theories (Denes 1989; Semenza 1988; Semenza & Goodglass 1985).

Recent works suggest that our knowledge of the body is mediated by at list three different types of representations (Buxbaum & Coslett 2001; Coslett, Saffran, & Schwoebel 2002; Schwoebel & Coslett 2005; Schwoebel, Coslett, & Buxbaum 2001).

The ***body image*** includes semantic, propositional, and lexical information such as the name of body parts, the association between body parts and artefacts and the function of different parts. This information are verbally coded and are accessible to consciousness.

The ***body structural description*** is a representation that includes information about the shape and contours of the body and the local relationship between different body parts. This representation derives primary from visual input.

The ***body schema***, the third type of body representation, is a dynamic representation of the body in the space modulated by the motor systems which controls action and posture. The "body schema" is an on-line representation grounded on the integration of somatosensory, vestibular and visual stimuli that provide information about the body posture and its interaction with the space.

This three types of representation may be selectively impaired and cause different deficits. While an impairment at the "body image" level may produce the Gerstmann syndrome (Gerstmann 1924), autotopagnosia (Pick 1908, 1915, 1922) is supposed to reflect a disorder at the "body structural description" level of representation. Finally, a "body schema" deficit may cause neglect related to the personal-body space (Coslett et al. 2002).

## Disorders of the body representation

Body related deficits are usually classified in bilateral or unilateral. In general, while lesions of the left hemisphere cause bilateral symptoms such as autotopagnosia or finger agnosia, lesions of the right hemisphere induce unilateral symptoms (Poeck & Orgass 1971).

*Bilateral deficits*

A typical bilateral body–related deficit is autotopagnosia (Pick 1908, 1915, 1922) which manifests as the inability to point both verbally and under imitation commands to body parts on its own body or on other persons or on a human schematic configuration. Especially because this deficit is not exclusively concerning their own body Gerstmann proposed the term somatotopagnosia instead of autotopagnosia (Gerstmann 1942). Conversely in this syndrome the ability to name and recognize the body segments is preserved. Several times this specific impairment is associated to mental deterioration or other cognitive deficits such as aphasia, visuo-spatial and motor deficits and the inability to perceive the global stimulus in its subcomponents (reviews in Denes 1989; Poeck & Orgass 1971). The frequent co-occurrence with other symptoms makes sometimes difficult the identification of "pure" cases of autotopagnosia. Indeed there is evidence in the literature of rare pure cases not associated to other confounding cognitive dysfunctions (Denes, Cappelletti, Zilli, Dalla Porta, & Gallana 2000; Guariglia, Piccardi, Puglisi Allegra, & Traballesi 2002; Ogden 1985; Semenza 1988; Sirigu, Grafman, Bressler, & Sunderland 1991). Patients show normal performance on point to both animals' and other objects' parts, this confirms that autotopagnosia is a selective deficit of a cognitive process strictly related to the body representation (Denes et al. 2000; Ogden 1985; Semenza 1988; Sirigu et al. 1991). Lesions typically associated to this symptom are in the left frontal lobe (Denes 1989).

An even more selective bilateral deficit is finger agnosia which consists of the inability to recognize, identify, name and localize hand's fingers (Gerstmann 1924).

Autotopagnosia does not appear as a semantic deficit as subjects know for example what a nose is and are perfectly able to associate objects related to it (e.g. handkerchief). Thus autotopagnosia seems to be a selective deterioration of the structure of the body intended as the correct localization of its segments in its schema.

*Unilateral deficits: From somatosensory perception to body ownership*

As mentioned before, this deficits are typically associated to right brain damage. Thus, it is very common that patients with left neglect may present a wide variety of body schema impairments. This spectrum of disorders includes a range of symptoms from ***personal neglect***, which is the inability to orient toward, explore and perceive the contralesional side of the body, to the lack of awareness for motor and sensory impairment of the contralesional half of the body (***anosognosia***). Vallar has distinguished in a recent review on neglect, ***defective*** and ***productive*** symptoms related to the personal (bodily) space. The first group of deficits includes for example hemisomatoagnosia which is due to a defective awareness of the contralesional side of the body, and anosognosia which manifests with the denial of the motor, visual and somesthetic deficits. Among the productive manifestations there is somatoparaphrenia (Vallar 1988). All those symptoms will be treated separately.

*Personal neglect*

Patients with extrapersonal neglect typically fail to respond to stimuli presented in the contralesional space and to explore that side of the space in absence of elementary sensory or motor deficits (Heilman 1979). However spatial neglect may also concern the contralesional half of the body. In this case subjects are unable to orient toward, explore, perceive and represent this part of the body (personal neglect, Zingerle 1913). When personal neglect is clinically evident patients become unable to use common objects on the left side of the body so they may wash, shave, comb hair only on the right side (Critchley 1953). Sometimes they do not use the contralesional limb even in absence of primary motor deficits, mimicking a left hemi-paresis (motor neglect, Critchley 1953). Personal and extrapersonal neglect may be clinically double dissociated although relatively few cases with personal neglect without extrapersonal neglect have been described in literature both in the acute and in the chronic phase (Beschin & Robertson 1997; Bisiach, Perani, Vallar, & Berti 1986; Guariglia & Antonucci 1992; McIntosh, Brodie, Beschin, & Robertson 2000; Zoccolotti & Judica 1991). Interestingly enough only a single case (L.D.) of right personal without extrapersonal neglect, anosognosia and somatoparaphrenia after a left hemispheric lesion has been reported (Peru & Pinna 1997). The evidence of these behavioural dissociations suggests that the representation of different parts of the space (extrapersonal, peripersonal versus personal, bodily space) may be subserved by functionally distinct and independent systems (Bisiach et al. 1986; Guariglia & Antonucci 1992).

The body related deficit is not easily quantifiable. In the classical test proposed by Bisiach and co-worker patients are required to touch the contralesional parts of the body (hand) with their ipsilateral hand without visual control (Bisiach et al. 1986). Patients' performance is scored in a four-point scale ranging from 0 (the patient promptly reaches for the target; absence of personal neglect) to 3 (absence of movements towards the target; severe personal neglect). Intermediate score are assigned when the target is reached with hesitation and searching behaviour (score:1) or when the search is interrupted before the target is reached (score:2). Score 2 and 3 respectively correspond to medium and severe personal neglect. Personal neglect may also be assessed using a more ecological test such as the "comb and razor test" (Zoccolotti & Judica 1991) in which patients perform three simple and common daily activities such as using a comb, a razor (men) or a facial compact (women), and wearing glasses. Patients' performance is scored in a four-point scale ranging from 0 (normal performance) to 3 (severe deficit). A modified and more quantified version of this test has been proposed by Beschin and Robertson (Beschin & Robertson 1997): patients are asked to perform personal grooming behaviour for a fixed period of time (30 second) and the proportion of activity made on the left side of the body is estimate using a simple formula (% left = left activity / left + ambiguous + right activity). The formulation of this test has been further improved by McIntosh and co-workers (McIntosh et al. 2000) using a different formula in which personal neglect is considered as a lateral bias of behaviour rather then as a lateralised deficit (% bias = left – right activity / left + ambiguous + right activity). The more sensitive the used test the higher the number of reported cases of personal neglect (Beschin & Robertson 1997; McIntosh et al. 2000) compared with previous evidence (Bisiach et al. 1986; Pizzamiglio et al. 1992; Zoccolotti & Judica 1991).

While the anatomy of peri and extrapersonal neglect has been extensively studied (review in Vallar, Bottini, & Paulesu 2003) only few studies have concerned the anatomical substrate of personal neglect. The difficulty to identify isolated cases of personal neglect (i.e. dissociated by extrapersonal neglect) has made very complex any exhaustive and definitive conclusion on the anatomical correlates of this specific symptom. It seems, in fact, that personal neglect is associated with posterior brain lesions involving the infero-posterior parietal areas or subcortical regions such as the basal ganglia, the thalamus and white matter fibre tracts (Bisiach et al. 1986; Guariglia & Antonucci 1992; Peru & Pinna 1997); it is important to note however that the reported anatomical correlates concern only very few cases of pure personal neglect. The areas involved are those classically associated with peri and extrapersonal neglect as well. Studies on primates demonstrate that the monkey's brain contains well distinguished regions subserving the exploration of different sectors of space (Rizzolatti, Berti, & Gallese 2000; Rizzolatti & Camarda 1987; Rizzolatti, Matelli, & Pavesi 1983). The hypothesis of a similar organization in the human brain, although already suggested (Berti & Frassinetti 2000; Cowey, Small, & Ellis 1994; Halligan & Marshall 1991), deserves more research especially to better define possible dissociations within the peripersonal space which includes the bodily space. A more systematic investi-

gation of the anatomical correlates of this spatial sector is needed with appropriate tests to distinguish personal neglect by other confounding clinical manifestations such as hypokinesia and with a proper lesional mapping methodology including statistical comparisons of the extension of the lesions between the different groups of patients (Rorden & Karnath 2004). A more theoretical question might be arose on which personal neglect is as its definition and identification mainly relies on clinical descriptions. However the boundary between personal neglect, sensory imperception, motor neglect (pseudo-hemiplegia) still needs to be clarify.

*Anosognosia for hemiplegia*

Patients affected by neurological disorders may not acknowledge their deficits despite unambiguous evidence. This behaviour has been described in sensory-motor domains (e.g. cortical blindness, cortical deafness, hemianopia and hemiplegia), cognitive domains (e.g. language and memory deficits), in schizophrenia and Alzheimer's disease (see Prigatano & Schacter 1991). One instance of this phenomenon can be found in right-brain-damaged patients, affected by left-sided hemiplegia, who may deny their paralysis and claim that their contralesional limbs can still move. This distorted or absent perception of what affects *one side of the body* has been termed anosognosia or denial of motor deficit (Babinski 1914). Anosognosia for hemiplegia has important clinical and theoretical implications. From a clinical point of view, anosognosia can have a negative impact on rehabilitation. Indeed, the denial of left side hemiplegia has been shown to be the worst prognostic factor for functional recovery of the motor disorders in right brain-damaged patients (Gialanella & Mattioli 1992). Thus, a better understanding of the mechanisms underlying the denial symptoms might help in the clinical treatment of these patients. Anosognosia also has *theoretical* implications for the study of higher cognitive functions. It has been shown that the detailed study of patients' denial can disclose implicit mental contents and can shed light on the structure underlying conscious mental processes (Berti, Làdavas, Stracciari, Giannarelli, & Ossola 1998).

The symptomatology of anosognosia for hemiplegia can vary in different patients. Sometimes when explicitly questioned about the condition of their limbs, anosognosic patients may display different degrees of denial ranging from emotional indifference (anosodiaforia), in which the motor problems may be admitted but without any concerns, to resolute and intractable unawareness of the disease. Additionally, productive symptoms, as verbal confabulations about their limbs, and delusional beliefs may coexist. In this latter case, patients may claim that the limbs are far from the body or belong to someone else, e.g. to another patient or to the doctor (*somatoparaphrenia*). The content of the confabulation can be very bizarre and patients may even claim that somebody else is lying on their beds or may show violent attitude against those 'alien' limbs (*misoplegia*).

Many interpretation of the denial behaviour, although theoretically distant, have in common the fact of not considering the disturbance as a *specific* cognitive disorder. For instance, anosognosia has been explained in terms of a generalized defensive

mechanism or psychological denial that should protect the patients from the disease. However, many different data falsify this hypothesis. First, anosognosia for hemiplegia is more frequent after right-brain damages and during the acute and post-acute phases of the illness (Bisiach & Geminiani 1991; Pia, Neppi-Mòdona, Ricci, & Berti 2004). These finding does not support a defense mechanisms view because a defensive mechanism should be active for both right and left hemiplegic disturbances and should increase with time: a goal-directed mechanisms would take time to consolidate. Furthermore, anosognosia can be temporally eliminated by caloric stimulation of one ear (Geminiani & Bottini 1992). Again, a defensive reaction should not be influenced by vestibular activation. Finally, data showing that anosognosia can be selective (see below) are themselves against a motivational account of the disorder. Other interpretation, although admitting that anosognosia is a disorder related to the cognitive system, explain it away as due to the presence of multiple concomitant neurocognitive disorders. Many authors pointed to the role of somatosensory deficit associated with intellectual impairment or memory problems (e.g. Levine, Calvanio, & Rinn 1991) or considered anosognosia as due to neglect of contralateral side of space involving also the detection of the left side of the body (Bisiach & Berti 1987). These accounts of anosognosia would receive support only by finding the coexistence of the denial behaviour with severe somatosensory deficits, intellectual impairment, memory problems or neglect. On the other hand, this account would be falsified by finding double dissociations between all these deficits. Berti et al. (Berti, Làdavas, & Della Corte 1996), Small and Ellis (Small & Ellis 1996) and Berti et al., (Berti et al. 2005) found that, although most patients with anosognosia are affected by sensory problems of the plegic arm, there are a few anosognosic patients who showed neither sensory impairment nor intellectual derangement. Moreover, most patients do not show any sign of memory loss or neglect symptoms (Berti et al. 2005; Berti et al. 1996). Conversely, many patients with sensory, memory and intellectual deficit are not anosognosic. These double dissociations show that, although the concomitant presence of various neurological/neuropsychological impairments may aggravate and shape the manifestations of anosognosia, their presence is neither necessary nor sufficient to cause the disorder (Berti 2001). Therefore, anosognosia cannot be explained away ascribing it to other deficits, but instead it seems to be a *specific* cognitive disorder affecting self-awareness of one side of the body.

There are data suggesting that anosognosia can be also *selective* (i.e. domain-specific). Indeed, it has been described limited to one limb (either the upper or the lower, Berti et al. 1996; Berti et al. 1998), affecting only some kind of movements (Marcel, Tegner, & Nimmo-Smith 2004) and evident in particular kind of task response and not in other: there are patients who are anosognosic in personal reports, when they are asked why they are in the hospital and what is the matter with their left arm or leg, but in a self-evaluation task they judge with very low score their capacity of making movements with the contralesional limbs. On the other hand, there are patients who verbally admit their motor impairment, but give very high score to their potential ability of clapping hands or using the left hand for moving an object (Berti et

al. 1996; Berti et al. 1998; Marcel et al. 2004; see also House & Hodges 1988). Finally, it has also been shown (Berti et al. 1996) that when patients have different concomitant neurological disorders (e.g. neglect dyslexia, drawing neglect and motor impairment), awareness can be damaged in one domain and not in the other. For instance, we found that some patients were anosognosic for the motor problem, but admitted their spatial deficit (drawing neglect or neglect dyslexia), whereas other patients did not admit their cognitive deficit but were aware of the hemiplegia.

The fact that anosognosia is not only *specific*, but also *selective* implies that it cannot be explained as a generalized disturbance of awareness (related, for instance, to massive damage to prefrontal areas) because this would imply a lack of monitoring for all concomitant deficits, both in the somatosensory domain (unawareness for upper and lower limb paresis) and in the cognitive domain (unawareness for hemiplegia and all concomitant neglect and related disorders). On the contrary, the selectivity of anosognosia strongly suggest that awareness can have a composite structure, revealing even at the level of thought processes the modular organization of the cognitive system (Bisiach & Berti 1995). This hypothesis would predict different neural basis for different form of awareness and not a unique cerebral localization for monitoring processes (such as pre-frontal areas). A recent review of the literature on the neural basis of anosognosia for hemiplegia has shown that its occurrence is related to frontal and parietal lobes damages. The authors suggested that anosognosia can be conceived as a disorder of motor awareness implemented in a fronto-parietal circuit related to space and motor representation where the parietal component may be responsible for the spatial computation necessary to act in space (Pia et al. 2004). However, an important limit of this study was the lack of anatomical details because most of the studies cited in the review did not report lesional maps of the damaged brains. This prevented to draw conclusions about the specific Brodmann areas involved in this putative fronto-parietal circuit. A prospective study, however, investigated the lesion distribution in a group of patients showing left spatial neglect, left hemiplegia and anosognosia for the motor deficit, with those of patients showing neglect, left hemiplegia but not anosognosia. The study clearly showed that the brain areas whose lesion causes anosognosia are localized mainly in the pre-motor frontal cortex (Berti et al. 2005). These areas are known to be closely linked to motor programming both in humans and monkeys (Rizzolatti, Luppino, & Matelli 1998; Tanji 1996), motor imagery (Jeannerod 1994; Roth et al. 1996) and even interpretation of others' actions (Jackson & Decety 2004; Rizzolatti & Craighero 2004). Our data expands this knowledge by providing evidence of an involvement of pre-motor areas in the conscious monitoring of body acts and is relevant for models of motor control in particular and consciousness in general. Indeed, the involvement of pre-motor areas in self-monitoring of body movements implies that, at least for motor functions, monitoring is neither the prerogative of some kind of central executive system, hierarchically superimposed to sensory-motor and cognitive functions, nor a function that is physiologically and anatomically separated from the primary process that has to be monitored. Instead, the anatomical correlates of anosognosia show that monitoring can be implemented in the same neural network

responsible for the process that has to be controlled and not in a central-superimposed and anatomically-separated system. The study also showed that some pre-motor areas were selectively spared by the lesions (e.g. the supplementary motor areas). The authors speculated that the possibility of normally activating these areas might generate a distorted representation of one side of the body generating the false belief of being able to move. Finally, because body movements occur in egocentric space, the association observed between anosognosia, neglect and parietal lesion may reflect the damage to common components of a fronto-parietal network, specifically related to spatiomotor integration. The lesion to a single component of this network gives raise to selective, and spatially constrained, disorders of awareness, either related to the conceiving of contralesional extrapersonal space (causing neglect) or of contralesional awareness of body space (giving raise to anosognosia and related disorder).

*Somatoparaphrenia*

On the basis of the symptomatological classification proposed by Vallar in 1998 (Vallar 1988), somatoparaphrenia (Gerstmann 1942) should be considered as a productive disorder characterized by a selective delusion about the paralyzed limbs. It occurs mostly in case of right hemispheric lesions, on our knowledge, in fact there is only one case described in the literature with this symptom induced by a left hemispheric lesion (Neilsen 1938); although it may be noted that the exploration of this disorder is mainly based on patients' interviews, and the frequent association of aphasia to left hemispheric damage may prevent a deep investigation of this phenomenon. Patients with somatoparaphrenia (Gerstmann 1942) typically claim that their contralesional limbs belong to another person, for example parents (Bisiach, Rusconi, & Vallar 1991; Bottini, Bisiach, Sterzi, & Vallar 2002) or may report experience of detachment or reduplication of body parts (Halligan, Marshall, & Wade 1995). Somatoparaphrenia is generally associated to unawareness or denial of hemiplegia (anosognosia) and neglect (Bisiach et al. 1991). The selectivity of somatoparaphrenia is corroborated by the fact that patients show normal believes about other parts of the body (Bisiach et al. 1991). The literature on this topic is quite scanty and generally consists of the description of this disorder. As a systematic investigation of the occurrence of somatoparaphrenia still lacks, there is no evidence of a specific anatomical correlates. There is not a convergent opinion on the origin of this peculiar disorder. Halligan and coll. (Halligan et al. 1995) for example hypothesize that the brain damage "contaminate" central reasoning processes, leading thereby to believes that stretch reason to the breaking point". If this is the truth it might be expected that somatoparaphrenia is particularly associated with lesion in the frontal cortex. Bisiach (Bisiach 1995) has attempted to explain the behaviour of somatoparaphrenic patients in term of a disruption of the Topological Representation of Egocentric Space (TRES) cognitive model of spatial configuration and in particular of body schema. This model assumes that the representation of space is implemented in three layers with different competences: layer 1 which is sensory driven; layer 2 which produces autochthonous not sensory driven spatial representations, and is partially inhibited by 1 when normally functioning; and layer 3 which only

has a diagrammatic function as it symbolizes layers 1 and 2 products (Bisiach 1995). In this model body-related representation may remain at an unconscious level or at least "not conscious with the mainstream of the subject's ideation" (Bisiach 1995). The damage of this cognitive system provokes a mismatch between the sensory driven and the endogenous processes of body representation which explains the alternation of rational and delusional attitude of the most somatoparaphrenic patients towards their paralyzed limbs.

The body representation is the result of different cognitive processes which are hierarchically organized from the more "elementary" levels such as perception of visual, vestibular and somatosensory stimuli to the more cognitive in their nature processes such as the ownership of their own body. These components seem to be grounded in a modular structure as there is evidence that, at least in the right hemisphere, different neural systems subserve diverse cognitive functions concerning the perception, exploration and representation of the personal, peripersonal and extrapersonal space (see Vallar 1988). The interactions among these modules have still to be clarified and the coexistence or dissociation of elementary or more cognitive defective or productive deficits of the body representation reflect, at the behavioural level, the still unclear neurophysiological organization of the bodily and extrapersonal spatial configuration.

When a lesion in the right somatosensory parietal cortex occurs tactile imperception (hemianesthesia) for the contralateral limbs which is the typical clinical consequence, is sometimes accompanied by delusional phenomenon concerning the contralesional paralyzed body. This pathological condition offers the opportunity of exploring the role of the sense of body ownership in somatosensory awareness.

One of these cases, F.B., has been recently described (Bottini et al. 2002). This is a woman who suffered from a right subcortical haemorrhagic stroke, inducing a dense left hemiplegia and hemianesthesia associated to a wide range of body awareness deficits such as anosognosia, personal neglect and somatoparaphrenia: patient in fact claimed that her left paralyzed hand, on which she was not able to perceive any tactile stimuli, belonged to her niece. The global intellective functioning of FB was within the normal range. The relationship between her hemianesthesia and her delusional symptom was explored through a simple, apparently paradoxical verbal modulation: the patient was required to report tactile stimuli delivered to "her niece's hand" instead then to her left hand. In this case F.B.'s hemianesthesia dramatically recovered. Also in this case, as observed by other authors who report in somatoparaphrenic patients the tendency to give weak explanations to the examiners' questions about the delusional behaviour, FB was very elusive and only if very pressed she said that she was taking care of her niece's hand as she forgot it on the bed after having kindly massaged the painful shoulder of the aunt.

FB case may contribute in clarifying at least some aspects of body ownership. Body parts representations relies onto somatosensory and motor cortices and these representations are resistant to the absence of the corresponding body segments as demonstrated by the well known phenomenon of the phantom limb. The author suggest that somatoparaphrenia may be considered the opposite phenomenon as in the

presence of the although paralyzed limb the subjects claim it does not belong them. Although FB apparently lost her ability to perceive touches on her left limb, she, under adequate semantic modulation, still demonstrated a residual spared somatosensory perception which probably depends on some elementary sensory functions comparable to the type mapped onto the somatosensory cortices. The problem arises when the patient has to recognize the hand on which she is still able to perceive touch as her own hand. At this point this residual sensory function does not seem to be able to elicit this sense of hand ownership. The verbal instructions of the examiners are coherent with her delusion ("Do you feel touches on your niece's hand?"), and cause a dramatic recover of the lack of perception. This behaviour is in many ways similar to allochiria which induces a symmetrical allocation of stimuli delivered on the contralesional bodily or peripersonal space to the ipsilesional side (Obersteiner 1882). In this case the phenomenon is more complex as FB needs to refer tactile stimuli on someone else's body image (a kind of "allantropia"...). Cases as FB suggest that the awareness of somatosensory perception intermingle with higher-level processes such as the sense of ownership.

*Somatosensory neglect*

At the more elementary level, lesions of the somatosensory parietal cortex may induce an impairment to report tactile stimuli delivered to the contralateral side of the body: remianesthesia (Paulesu, Frackowiak, & Bottini 1997; Pause, Kunesch, Binkofski, & Freund 1989; Roland 1987). Left hemianesthesia following right brain lesions, is frequently associated with some of the body awareness deficits previously described such as anosognosia, somatoparaphrenia and personal neglect. Left somatosensory deficit, at least in some cases, may reflect not only a primary sensory impairment but also a more complex and higher-order deficit of spatial representation of the body (review in Vallar 1997). This fact derives from many neurophysiological and clinical evidences. It has been for example demonstrated in a retrospective study on cohort of patients with stroke, that somatosensory deficits occurred significantly more frequently in right brain damaged subjects (Sterzi et al. 1993). Furthermore different physiological manipulations (caloric vestibular, electrical transcutaneous, and optokinetic stimulation) may produce a transient recovery of contralateral sensory deficits (Vallar, Bottini, Rusconi, & Sterzi 1993; Vallar, Rusconi, & Bernardini 1996; Vallar, Sterzi, Bottini, Cappa, & Rusconi 1990). Amongst these procedures the most extensively investigated, for its remarkably effect, is caloric vestibular stimulation (CVS) with iced water in the external ear canal contralateral to the brain lesion. Classical studies showed that in right brain damaged patients left CVS temporary ameliorates contralesional hemianesthesia (Bottini et al. 1995; Vallar et al. 1993; Vallar et al. 1990). Interestingly enough, the same stimulation in the right ear does not produce the same effect on left brain damaged patients with the notable exception of few cases of patients who manifest right visuo-spatial neglect with a probable non canonical hemispheric lateralization of spatial functions (Vallar et al. 1993). The observation of this behavioural asymmetry had suggested in case of right hemispheric lesion that hemianesthesia also contains an

attentional-spatial component which is strictly related to the neglect syndrome, and that this particular component which is not typical of right hemianesthesia associated to left hemispheric lesion, may be modulated and transiently reduced by CVS. Another hypothesis might be taken into account, that the right hemisphere plays a special role in monitoring visuo-spatial functions in general and more specifically in the representation of the body in all its components including attention for tactile stimuli. To support this hypothesis, Meador et al. (Meador et al. 1988) have demonstrated that during pharmacological inhibition with sodium amobarbital, in case of right hemisphere inactivity the degree of tactile perception impairment (in particular extinction) was significantly more severe than in case of left inhibition. This result has been confirmed by a different experimental paradigm performed by Pardo and coworkers (Pardo, Fox, & Raichle 1991) who, exploring with PET the human anatomical areas involved in the vigilance aspects of normal attention to sensory stimuli, found a significant higher activation primarily in the prefrontal and superior parietal of the right hemisphere. Furthermore patients with left neglect may present physiological preserved response (skin conductance response or evoked potentials) to undetected contralesional tactile stimuli (Vallar, Bottini, Sterzi, Passerini, & Rusconi 1991; Vallar, Sandroni, Rusconi, & Barbieri 1991). This observation suggest that patient's hemianesthesia can't be entirely due to a primary sensory deficit. Another interesting evidence in this direction is that in right brain damaged patients, the degree of contralesional somatosensory deficits may be modulated by changing the position of body parts respect to the body midline (Smania & Aglioti 1995). In particular, when the left hand is placed in the right unaffected side of the space the detection of left tactile stimuli significantly improves, suggesting that tactile stimuli are also spatially coded.

It has also been shown that even in the presence of extensive right hemispheric lesion in the primary somatosensory cortex, (SI) cold left CVS may induces a clear cut transient remission of left hemianesthesia activating a neural network (insula, putamen, inferior frontal gyrus in the premotor cortex) in the right hemisphere, suggesting that compensatory mechanisms to recover tactile imperception and somatosensory awareness still rely in the right hemisphere although it has been largely damaged (Bottini et al. 1995). This functional asymmetry is also corroborated by evidence in normal subjects who show bilateral cortical activation more extensive in the right hemisphere during left cold CVS compared with the opposite stimulation (Bottini et al. 2001; Bottini et al. 1994). Recently, in order to better clarify these evidences, it has been systematically explored the effect of CVS differently lateralized in hemianesthetic, right and left brain damaged patients, whose anatomical lesions were mapped to exclude any volumetric difference in the somatosensory areas which might provoke a bias in the behavioural effect of CVS (Bottini et al. 2005). The expected remission of left hemianesthesia during left cold CVS was confirmed compared with no reaction in case of right CVS on right brain damaged subjects. Of more interest, and completely new, was the result on the left damaged population, as, a part the expected inefficacy of right cold CVS, the same kind of manipulation ***to the left*** induced a temporary remission of right hemianesthesia. These behavioural data on patients were combined with

neuroimaging observation in normal subjects and in one left brain damaged patient. Normal subjects underwent tactile stimulation to the right and the left hand during fMRI to identify the somatosensory areas involved by this stimulation of the same kind of which performed on patients before and after CVS. This part of experiment demonstrated a pattern of activation of the contralateral nucleus of the thalamus, of somatosensory SI area and the supplementary motor area, and Secondary Somatosensory Cortex, SII bilaterally. A significantly greater activation for ispilateral hand stimuli has been found in the right hemisphere compared with the left in the parietal operculum (SII area). The right hemianaesthetic patient with an extensive left hemisphere lesion involving left SII, the postcentral gyrus, the posterior limb of the internal capsule and a large portion of the thalamus with a complete destruction of the ventroposterior somatosensory nuclei was also submitted to fMRI during tactile stimulation before and after having left cold CVS. In this patient the areas modulated by CVS involved the right temporoparietal junction including area SII and the supramarginal gyrus which were significantly activated after left CVS and touches delivered to the right hand with a significant *touch-by CVS-by hand* interaction effect.

This right hemisphere effect contributes to better clarify the right hemispheric specialization in body representation (in particular in hand representation). The fact that in the patient with an extensive left hemispheric lesion starting from the thalamus to the cortical somatosensory cortices, touches on the ipsilesional hand, induce activation in SII in the right hemisphere, demonstrates that neurons in this region, have ipsilateral receptive fields. This is a convincing evidence that the right hemisphere contains a more complete representation of the whole body space compared whit the left hemisphere.

## Concluding remarks

Behavioural and neuroimaging data support the hypothesis that body schema results from the integration of different signals. In the body representation processes it is possible to identify progressive hierarchical levels of analysis, from elementary operation, such as somatosensory processing to more complex computation, such as the construction of the feeling of ownership of body parts. However, the boundary between these processes is sometimes fuzzy. For example, the possibility of modulating apparently elementary neurological deficits, such as tactile imperception, through physiological stimulations that allow transient conscious perception of the tactile stimuli, suggests that even low level deficits contain a not obvious higher component. Some aspects of the mutual interaction between the different levels that construct the feeling of having a body acting in the space is starting to become clearer due to the progress in identifying the neurophysiological correlates of the different levels of body representation in normal subjects and in patients with different body representation disorders. The neural correlates of some aspects of pathological behaviours (such as somatoparaphrenia) are still unclear although clinical and neurophysiological findings seem to

suggest that at least in part hemianestesia, deficits of the sense of ownership and related disorders, may share some common mechanisms of spatial representation.

## References


Babinski, J. (1914). Contribution à l'étude des troubles mentaux dans l'hémiplégie organique cérébrale (anosognosie). *Revue Neurologique, 27*, 845–848.

Berti, A. (2001). Neuropsychological syndromes and structure of conscious processes. In *The emergence of the mind* (pp. 65–71). Proceedings of the International Symposium, Fondazione Carlo Erba.

Berti, A., Bottini, G., Gandola, M., Pia, L., Smania, N., & Stracciari, A. et al. (2005). Shared cortical anatomy for motor awareness and motor control. *Science, 309* (5733), 488–491.

Berti, A., & Frassinetti, F. (2000). When far becomes near: Remapping of space by tool use. *Journal of cognitive neuroscience, 12* (3), 415–420.

Berti, A., Làdavas, E., & Della Corte, M. (1996). Anosognosia for hemiplegia, neglect dyslexia, and drawing neglect: Clinical findings and theoretical considerations. *Journal of the International Neuropsychological Society: JINS, 2* (5), 426–440.

Berti, A., Làdavas, E., Stracciari, A., Giannarelli, C., & Ossola, A. (1998). Anosognosia for motor impairment and dissociations with patient's evaluation of the disorders: Theoretical considerations. *Cognitive Neuropsychiatry, 3*, 21–44.

Beschin, N., & Robertson, I. H. (1997). Personal versus extrapersonal neglect: A group study of their dissociation using a reliable clinical test. *Cortex, 33* (2), 379–384.

Bisiach, E. (1995). Unawareness of unilateral neurological impairment and disordered representation of one side of the body. *Higher Brain Function Research, 15* (2), 113–140.

Bisiach, E., & Berti, A. (1987). Dyschiria: An attempt at its systemic explanation. In M. Jeannerod (Ed.), *Neurophysiological and neuropsychological aspects of spatial neglect* (pp. 183–201). Amsterdam: Elsevier.

Bisiach, E., & Berti, A. (1995). Consciousness in dyschiria. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 1331–1340). Cambridge, MA: MIT Press.

Bisiach, E., & Geminiani, A. (1991). Anosognosia related to hemiplegia and hemianopia. In G. P. Prigatano & D. L. Schacter (Eds.), *Awareness of deficit after brain injury*. Oxford, UK: Oxford University Press.

Bisiach, E., Perani, D., Vallar, G., & Berti, A. (1986). Unilateral neglect: Personal and extra-personal. *Neuropsychologia, 24* (6), 759–767.

Bisiach, E., Rusconi, M. L., & Vallar, G. (1991). Remission of somatoparaphrenic delusion through vestibular stimulation. *Neuropsychologia, 29* (10), 1029–1031.

Bottini, G., Bisiach, E., Sterzi, R., & Vallar, G. (2002). Feeling touches in someone else's hand. *Neuroreport, 13* (2), 249–252.

Bottini, G., Karnath, H. O., Vallar, G., Sterzi, R., Frith, C. D., & Frackowiak, R. S. et al. (2001). Cerebral representations for egocentric space: Functional-anatomical evidence from caloric vestibular stimulation and neck vibration. *Brain, 124*, 1182–1196.

Bottini, G., Paulesu, E., Gandola, M., Loffredo, S., Scarpa, P., & Sterzi, R. et al. (2005). Left caloric vestibular stimulation ameliorates right hemianesthesia. *Neurology, 65* (8), 1278–1283.

Bottini, G., Paulesu, E., Sterzi, R., Warburton, E., Wise, R. J., & Vallar, G. et al. (1995). Modulation of conscious experience by peripheral sensory stimuli. *Nature, 376* (6543), 778–781.

Bottini, G., Sterzi, R., Paulesu, E., Vallar, G., Cappa, S. F., & Erminio, F. et al. (1994). Identification of the central vestibular projections in man: A positron emission tomography activation study. *Experimental brain research, 99* (1), 164–169.

Buxbaum, L. J., & Coslett, H. B. (2001). Specialized structural descriptions for human body parts: Evidence from autotopagnosia. *Cognitive Neuropsychology, 18*, 289–306.

Coslett, H. B., Saffran, E. M., & Schwoebel, J. (2002). Knowledge of the human body: A distinct semantic domain. *Neurology, 59* (3), 357–363.

Cowey, A., Small, M., & Ellis, S. (1994). Left visuo-spatial neglect can be worse in far than in near space. *Neuropsychologia, 32* (9), 1059–1066.

Critchley, M. (1953). *The parietal lobe*. New York: Hafner.

De Renzi, E., & Faglioni, P. (1963). L'autotopoagnosia. *Archivio di Psicologia, Neurologia e Psichiatria, 24*, 289–319.

De Renzi, E., & Scotti, G. (1970). Autotopagnosia: Fiction or reality? Report of a case. *Archives of neurology, 23* (3), 221–227.

Denes, G. (1989). Disorders of body awareness and body knowledge. In F. Boller & J. Grafman (Eds.), *Handbook of neuropsychology* (Vol. 2, pp. 207–227). Amsterdam: Elsevier.

Denes, G., Cappelletti, J. Y., Zilli, T., Dalla Porta, F., & Gallana, A. (2000). A category-specific deficit of spatial representation: The case of autotopagnosia. *Neuropsychologia, 38* (4), 345–350.

Geminiani, G., & Bottini, G. (1992). Mental representation and temporary recovery from unilateral neglect after vestibular stimulation. *Journal of neurology, neurosurgery, and psychiatry, 55* (4), 332–333.

Gerstmann, J. (1924). Fingeragnosie: Eine umschreibene storung der orientierung am eigenen korper. *Wein Klinische Wochenschrift, 37*, 1010–1012.

Gerstmann, J. (1942). Problem of imperception of disease and of impaired body territories with organic lesions. Relation to body schema and its disorders. *Archives of Neurology and Psychiatry, 48*, 890–913.

Gialanella, B., & Mattioli, F. (1992). Anosognosia and extrapersonal neglect as predictors of functional recovery following right hemisphere stroke. *Neuropsychological Rehabilitation, 2*, 169–178.

Guariglia, C., & Antonucci, G. (1992). Personal and extrapersonal space: A case of neglect dissociation. *Neuropsychologia, 30* (11), 1001–1009.

Guariglia, C., Piccardi, L., Puglisi Allegra, M. C., & Traballesi, M. (2002). Is autotopoagnosia real? Ec says yes. A case study. *Neuropsychologia, 40* (10), 1744–1749.

Halligan, P. W., & Marshall, J. C. (1991). Left neglect for near but not far space in man. *Nature, 350* (6318), 498–500.

Halligan, P. W., Marshall, J. C., & Wade, D. T. (1995). Unilateral somatoparaphrenia after right hemisphere stroke: A case description. *Cortex, 31* (1), 173–182.

Heilman, K. M. (1979). Neglect and related disorders. In K. M. Heilman & E. Valenstein (Eds.), *Clinical neuropsychology* (pp. 268–307). New York: Oxford University Press.

House, A., & Hodges, J. (1988). Persistent denial of handicap after infarction of the right basal ganglia: A case study. *Journal of neurology, neurosurgery, and psychiatry, 51* (1), 112–115.

Jackson, P. L., & Decety, J. (2004). Motor cognition: A new paradigm to study self-other interactions. *Current opinion in neurobiology, 14* (2), 259–263.

Jeannerod, M. (1994). The representing brain: Neural correlates of motor intention and imagery. *Behavioral and Brain Sciences, 17*, 187–245.

Levine, D. N., Calvanio, R., & Rinn, W. E. (1991). The pathogenesis of anosognosia for hemiplegia. *Neurology, 41* (11), 1770–1781.

Marcel, A. J., Tegner, R., & Nimmo-Smith, I. (2004). Anosognosia for plegia: Specificity, extension, partiality and disunity of bodily unawareness. *Cortex, 40* (1) 19–40.

McIntosh, R. D., Brodie, E. E., Beschin, N., & Robertson, I. H. (2000). Improving the clinical diagnosis of personal neglect: A reformulated comb and razor test. *Cortex, 36* (2), 289–292.

Meador, K. J., Loring, D. W., Lee, G. P., Brooks, B. S., Thompson, E. E., & Thompson, W. O. et al. (1988). Right cerebral specialization for tactile attention as evidenced by intracarotid sodium amytal. *Neurology, 38* (11), 1763–1766.

Neilsen, J. M. (1938). Disturbances of the body scheme. *Bulletin of the Los Angeles Neurological Societies, 3*, 127–135.

Obersteiner, H. (1882). On allochiria: A peculiar sensory disorder. *Brain, 4*, 153–163.

Ogden, J. A. (1985). Autotopagnosia. Occurrence in a patient without nominal aphasia and with an intact ability to point to parts of animals and objects. *Brain, 108*, 1009–1022.

Pardo, J. V., Fox, P. T., & Raichle, M. E. (1991). Localization of a human system for sustained attention by positron emission tomography. *Nature, 349* (6304), 61–64.

Paulesu, E., Frackowiak, R. S. J., & Bottini, G. (1997). Maps of somatosensory systems. In R. S. J. Frackowiak (Ed.), *Human brain function* (pp. 183–242). San Diego: Academic Press.

Pause, M., Kunesch, E., Binkofski, F., & Freund, H. J. (1989). Sensorimotor disturbances in patients with lesions of the parietal cortex. *Brain, 112* (Pt 6), 1599–1625.

Peru, A., & Pinna, G. (1997). Right personal neglect following a left hemisphere stroke. A case report. *Cortex, 33* (3), 585–590.

Pia, L., Neppi-Mòdona, M., Ricci, R., & Berti, A. (2004). The anatomy of anosognosia for hemiplegia: A meta-analysis. *Cortex, 40* (2), 367–377.

Pick, A. (1908). *Über störungen der orientierung am eigenen körper. Arbeiten aus der deutschen psychiatrischen universitäts-klinik in prag*. Berlin: Karger.

Pick, A. (1915). Zur pathologie des bewußtseins vom eigenen körper. *Neurologisches Centralblatt, 34*, 257–265.

Pick, A. (1922). Störung der orientierung am eigenen körper. Beitrag zur lehre vom bewußtsein des eigenen körpers. *Psychologische Forschung, 1*, 303–318.

Pizzamiglio, L., Antonucci, G., Judica, A., Montenero, P., Razzano, C., & Zoccolotti, P. (1992). Cognitive rehabilitation of the hemineglect disorder in chronic patients with unilateral right brain damage. *Journal of clinical and experimental neuropsychology: Official journal of the International Neuropsychological Society, 14* (6), 901–923.

Poeck, K., & Orgass, B. (1971). The concept of the body schema: A critical review and some experimental results. *Cortex, 7* (3), 254–277.

Prigatano, G. P., & Schacter, D. L. (1991). *Awareness of deficit after brain injury: Theoretical and clinical aspects*. New York: Oxford University Press.

Reed, C. L., & Farah, M. J. (1995). The psychological reality of the body schema: A test with normal partecipants. *Journal of Experimental Psychology: Human Perception and Performance, 21* (2), 334–343.

Rizzolatti, G., Berti, A., & Gallese, V. (2000). Spatial neglect: Neurophysiological bases, cortical circuits and theories. In F. Boller, J. Grafman, & G. Rizzolatti (Eds.), *Handbook of neuropsychology* (2nd ed., Vol. 1, pp. 503–537). Amsterdam: Elsevier Science B.V.

Rizzolatti, G., & Camarda, R. (1987). Neural circuits for spatial attention and unilateral neglect. In M. Jeannerod (Ed.), *Neurophysiological and neuropsychological aspects of spatial neglect* (pp. 289–313). Amsterdam: Elsevier.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annu Rev Neurosci, 27*, 169–192.

Rizzolatti, G., Luppino, G., & Matelli, M. (1998). The organization of the cortical motor system: New concepts. *Electroencephalography and clinical neurophysiology, 106* (4), 283–296.

Rizzolatti, G., Matelli, M., & Pavesi, G. (1983). Deficits in attention and movement following the removal of postarcuate (area 6) and prearcuate (area 8) cortex in macaque monkeys. *Brain, 106* (Pt 3), 655–673.

Roland, P. E. (1987). Somatosensory detection in patients with circumscribed lesions of the brain. *Experimental brain research, 66* (2), 303–317.

Rorden, C., & Karnath, H. O. (2004). Using human brain lesions to infer function: A relic from a past era in the fmri age? *Nature reviews. Neuroscience, 5* (10), 813–819.

Roth, M., Decety, J., Raybaudi, M., Massarelli, R., Delon-Martin, C., & Segebarth, C. et al. (1996). Possible involvement of primary motor cortex in mentally simulated movement: A functional magnetic resonance imaging study. *Neuroreport, 7* (7), 1280–1284.

Schwoebel, J., & Coslett, H. B. (2005). Evidence for multiple, distinct representations of the human body. *Journal of cognitive neuroscience, 17* (4), 543–553.

Schwoebel, J., Coslett, H. B., & Buxbaum, L. J. (2001). Compensatory coding of body part location in autotopagnosia: Evidence for extrinsic egocentric coding. *Cognitive Neuropsychology, 18*, 363–381.

Semenza, C. (1988). Impairment in localization of body parts following brain damage. *Cortex, 24* (3), 443–449.

Semenza, C., & Goodglass, H. (1985). Localization of body parts in brain injured subjects. *Neuropsychologia, 23* (2), 161–175.

Sirigu, A., Grafman, J., Bressler, K., & Sunderland, T. (1991). Multiple representations contribute to body knowledge processing. Evidence from a case of autotopagnosia. *Brain, 114*, 629–642.

Small, M., & Ellis, S. (1996). Denial of hemiplegia: An investigation into the theories of causation. *European neurology, 36* (6), 353–363.

Smania, N., & Aglioti, S. (1995). Sensory and spatial components of somaesthetic deficits following right brain damage. *Neurology, 45* (9), 1725–1730.

Sterzi, R., Bottini, G., Celani, M. G., Righetti, E., Lamassa, M., Ricci, S., et al. (1993). Hemianopia, hemianaesthesia, and hemiplegia after right and left hemisphere damage. A hemispheric difference. *Journal of neurology, neurosurgery, and psychiatry, 56* (3), 308–310.

Tanji, J. (1996). New concepts of the supplementary motor area. *Current opinion in neurobiology, 6* (6), 782–787.

Vallar, G. (1988). Spatial hemineglect in humans. *Trends in cognitive sciences, 2* (3), 87–97.

Vallar, G. (1997). Spatial frames of reference and somatosensory processing: A neuropsychological perspective. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences B, 352*, 1401–1409.

Vallar, G., Bottini, G., & Paulesu, E. (2003). Neglect syndromes: The role of the parietal cortex. *Advances in neurology, 93*, 293–319.

Vallar, G., Bottini, G., Rusconi, M. L., & Sterzi, R. (1993). Exploring somatosensory hemineglect by vestibular stimulation. *Brain, 116*, 71–86.

Vallar, G., Bottini, G., Sterzi, R., Passerini, D., & Rusconi, M. L. (1991). Hemianesthesia, sensory neglect, and defective access to conscious experience. *Neurology, 41* (5), 650–652.

Vallar, G., Rusconi, M. L., & Bernardini, B. (1996). Modulation of neglect hemianesthesia by transcutaneous electrical stimulation. *Journal of the International Neuropsychological Society: JINS, 2* (5), 452–459.

Vallar, G., Sandroni, P., Rusconi, M. L., & Barbieri, S. (1991). Hemianopia, hemianesthesia, and spatial neglect: A study with evoked potentials. *Neurology, 41* (12) 1918–1922.

Vallar, G., Sterzi, R., Bottini, G., Cappa, S., & Rusconi, M. L. (1990). Temporary remission of left hemianesthesia after vestibular stimulation. A sensory neglect phenomenon. *Cortex, 26* (1), 123–131.

Zingerle, H. (1913). Über störunger der wahrnemung des eigenen korpes bei organischen gehimerkrankungen. *Monatschrift für Psychiatrie und Neurologie, 34*, 13–36.

Zoccolotti, P., & Judica, A. (1991). Functional evaluation of hemineglect by means of a semistructured scale: Personal and extrapersonal differentiation. *Neuropsychological Rehabilitation, 1*, 33–44.

CHAPTER 4.6

# Simulating object-centred neglect with head-centred coding of space based on non-linear gaze-dependent units

Massimo Silvetti, Fabrizio Doricchi, and Eliano Pessa

## Introduction

The neglect syndrome is a frequent consequence of right parietal-frontal cortical-subcortical brain damage (Gaffan & Hornak 1997; Leibovitch et al. 1998; Mort et al. 2003; Doricchi & Tomaiuolo 2003) causing unawareness of the left side of space (both personal and extrapersonal), objects and mental images (Bartolomeo & Chokron 2002). This syndrome can affect different spatial reference frames simultaneously or separately. Most frequently, neglect patients have problems in processing objects placed to the left of the head-body midline, but not for those placed to the right of the body midline (i.e., egocentric or body-centred neglect: Walker 1995, 1996). More rarely some patients are able to detect all of the objects around them but systematically neglect the left side of the same objects. This form of neglect is now commonly called "object-based" neglect. As Olson described (2003), object-based form of neglect can affect two different frames of reference: a) an "object aligned" frame such that the left side of objects with canonical horizontal orientation (i.e., letters and words) or with gravitationally defined left and right sides is neglected regardless of canonical (i.e., "B"), or mirror-reversed presentation ("ꓭ"), and regardless of changes in object position due to rotations on the frontal parallel plane (Driver, et al. 1994; Driver & Halligan 1991; Behrmann & Moscovich 1994; Tipper & Behrmann 1996); b) an "object centred" frame, such that the left side of objects without canonical left-right orientation is neglected independently of their lateral egocentric spatial position as, for example, typically observed in patients' copies of multi-item line drawings (Gainotti & Tiacci 1970; Marshall & Halligan 1993; Doricchi & Galati 2000).

These clinical findings pose interesting challenges about space representation through human brain circuits. An important problem is if the presence of different reference frame impairment is due to damages involving circuits with different computational roles, or if there is only a unique neural population devoted to visual space representation and, if damaged, it is at the base of all the different impaired perfor-

mances. Moreover it is necessary to develop explicit and formal computational theories, which absolve a gate-like role between neurobiological and neuropsychological knowledges.

Solution attempts to these problems brought to the realization of some neural theories about the space computation in different frame of reference. Deneve and Pouget (2003) developed one of these attempts. They simulated "object aligned" neglect satisfactorily by a network implementing gain-field units with retinal response modulated by rotation of the object on the fronto-parallel plane (similar to the LIP neurons described by Sabes and co-workers 2002). Driver and Pouget (2000), instead, examined if there is the necessity of postulating the existence of brain mechanisms devoted to the "object-centred" coding of space. They observed that an egocentric gradient of horizontal space representation endowed with monotonic right to left decline of representational salience satisfactorily explains object-centred neglect, because at any point of the gradient (i.e., irrespective of egocentric position) the left side of an object is always under-represented compared to its right side. According to this hypothesis, object-centred neglect is interpreted in terms of relative egocentric neglect. These ideas were implemented in a neural model realized by Pouget and Sejnowski (1997, 2001) and Pouget and co-workers (1999). Two bi-dimensional matrices of neural units, one for each cerebral hemisphere, constitute the core of this model. In each matrix, retinal and eye position signals are integrated by gaze-dependent units endowed with functional properties that correspond to those of neurons found by Andersen and co-workers (1985) in area 7a of the monkey brain, in the majority of these neurons, defined gaze-dependent, retinotopic coding of space is linearly modulated by eye position. In both the matrices contralateral side of space is over-represented so that, for example, in the network simulating the left hemisphere the majority of units code for right retinal and right eye positions. In the model, gaze-dependent units are called "basis function" (BF). This term is derived from linear algebra to indicate that the linear combination of their output functions, determined by the convergence of retinotopic and eye position signals, is equivalent to an approximation of a non-linear coordinate transformation allowing for head-centred coding of space. This kind of network is able to code multiple frames of reference simultaneously and a damage to the right side of their network produces deficits of left space representation simultaneously in both eye- and head-centred co-ordinates. This result does not fit satisfactorily with clinical data, that show the presence of some performances where the head-centred reference frame is intact, while the eye-centred one is damaged, and some others where the deficit pattern is inverted.

Here we introduce a new artificial neural network based on BF neurons and demonstrate that "object- centred" neglect is effectively simulated if the head centred position of objects in space is coded by units in which response amplitude is not linearly modulated by gaze position. These functional and computational properties were found in head-centred neurons located in the occipital parietal cortex ("real position" neurons of V6A, Galletti, Battaglini & Fattori 1993) and in the ventral intra-parietal area (VIP, Duhamel, Bremmer & Graf 1997) of the monkey brain.

The second aim of this study is to detail, test and compare a classic BF model (Pouget, et al. 2002) and the new model implementing "real-position like" head-centred coding of space. We kept the architectural-functional properties of this new model close to available neurophysiological data. Both of these models were tested in a simplified version of the multi-item copy drawing task used in the diagnosis of object-centred neglect.

## Neural-computational simulation of object-centred neglect with a basis function (BF) network

In order to test if the neural system realized by Pouget and co-workers could effectively simulate the performance of patients with object-centred neglect, we simulated the consequences of right brain damage by implementing the left side of a BF model, and tested it by a multi item detection task having structural features similar to the multi item copy test used in clinical practice. The architecture of a BF network consists of a matrix of basis function neurons receiving input from retinal position and eye position units. Both types of units have a gaussian output function (Pouget et al. 2002). These units have functional properties similar to those found in part of the population of gaze-dependent neurons located in area 7A (Andersen et al. 1985). The distribution of input layer units was set to obtain a linear gradient of space representation (equation (1)), with over-representation of the right side of space (Pouget et al. 1997, 1999, 2001), such that the majority of units responded to right retinal and eye positions (Fig. 1)

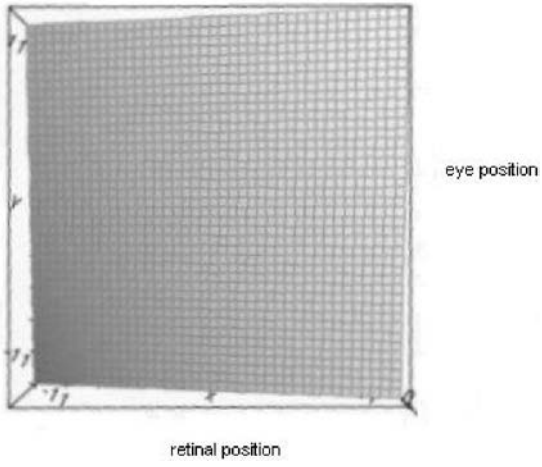



**Figure 1.** Neuronal gradient in BF map representing the left hemisphere. Lighter grey indicates a higher concentration of units coding for contralateral right retinal and right eye positions.

The output of BF matrix was given:

(1) $o_{ij} = e_i r_j$

where $e_i$ is the output of an eye-position unit with peak activity centred on craniotopic position $i$, $r_j$ the output of a retinal position unit, belonging to the one-dimensional retina, with peak activity centred on retinal position $j$, and $o_{ij}$ is the output of a BF neuron, obtained through the product of retinal and eye-position output functions (Pouget & Sejnowski 1997). In this work, it was assumed that eye-position units have a "peak-like" activity (Pouget et al. 2002). The receptive field width of each retinal and eye-position unit was conventionally considered to be 2°.

The number of BF units having the i-j$^{TH}$ position in the BF matrix ($N_{ij}$) was given by:

(2) $N_{ij} = \lambda_1 \overline{r_j} + \lambda_2 \overline{e_i} + \varepsilon$

Where $\overline{r_j}$ and $\overline{e_i}$ are the peak positions of the retinal receptive field and of the function of eye position (Pouget & Sejnowski 2001); λ and ε are parameter.

The model is also endowed with a head-centred units layer, receiving input from the BF matrix. Each head-centred unit (output layer) receives input from all the BF coding for its corresponding head-centred co-ordinate, all connections have a weight equal to 0.1.

The network was tested in the detection of two visual patterns comprised of four contiguous stimuli each (with each stimulus considered as a different sector of the same object, and each pattern a single object). The two objects were in two different head-centred positions: one 6° to the right of the head midsagittal plane and the other 6° to the left of the same plane; see Fig. 2. We simulated gaze shifts toward identical object-centred positions of objects located to the left and to the right of the head midsagittal plane. We made reference to the concept of "stimulus salience" defined in Pouget and Sejnowski (2001), in order to calculate the probability of selecting a specific sector of each object. In our implementation, stimulus salience values are equivalent to the discharge level of units belonging to the head-centred layer. Salience values of




**Figure 2.** Stimuli used for BF and RP simulations of object-centred neglect, consisting of two groups of four points each, situated respectively on the right (6°) and on the left (–6°). Each grey circle represents an object sector aligned to the centre of the receptive field of four corresponding visual units belonging to the first layer (i.e., input layer).

the different object sectors were submitted to a selection algorithm taken from Pouget and Sejnowski (2001), which involves three phases:

1) winner-takes-all: the stimulus with the highest salience is selected;
2) inhibition of return: the activity of the selected stimulus was set at zero;
3) recovery: the salience over time for stimulus $i$ (previously selected), $s_i(t)$, is updated according to

$$(3) \quad S_i(t+1) = S_i(t) + \delta(S_i(t_0) - S_i(t)) + n(t).$$

where $S_i(t_0)$ is the salience of stimulus $i$ at time $t_0$, i.e., the first time it is selected, $\delta$ is the recovery rate, and $n$ is a white noise process with normal distribution. The parameters were set to obtain the best result for both models. The probability of selecting a stimulus $i$ ($\mathrm{Pr}_i$) was computed as follows:

$$(4) \quad \mathrm{Pr}_i = N_i/T$$

where $N_i$ is the number of times $i$ was selected, and $T$ the number of trials.

The second algorithm differs from the first only for the adding of:

$$(5) \quad \mathrm{Pr}^*_i = \mathrm{Pr}_i \pi_i$$

Where $\mathrm{Pr}_i$ is from equation (4), and:

$$(6) \quad \pi_i = \frac{1}{1 + \exp\left(-(S_i - \alpha)/\beta\right)}$$

which express the probability of detecting a stimulus by the signal-detection theory. In earlier works on BF, this formula was used to calculate the probability of detecting single stimuli (Pouget et al. 1999). Equation (5) expresses the probability of selecting a stimulus as the composite likelihood of detection and competitive selection. Figure 3 shows the output of the head-centered units coding each of the four object sectors. The upper row shows the simulation results obtained by using the original selection algorithm (Pouget & Sejnowski 2001), while the lower row shows the results obtained by using the algorithm endowed whith Equation 5.

In this last case, where the signal-to-noise ratio plays a stronger role compared to the algorithm proposed by Pouget and Sejnowski (2001), the combination of eye- and head-centred impairments is even more evident.

In conclusion, this model computes multiple reference frames by using a unique neural population (the BF matrix), and a damage of one network generates a space coding impairment contemporarily in multiple frames of reference belonging to the contralateral space. This result is caused by the dependence of object sector salience on two factors:

a) the stimulated sector of the visual field (stimuli on the left side of the eye-centred frame evoke weaker responses);
b) the position of the eye in the orbit (progressive leftward gaze deviation evokes progressively weaker responses to stimuli presented at an identical retinal position).

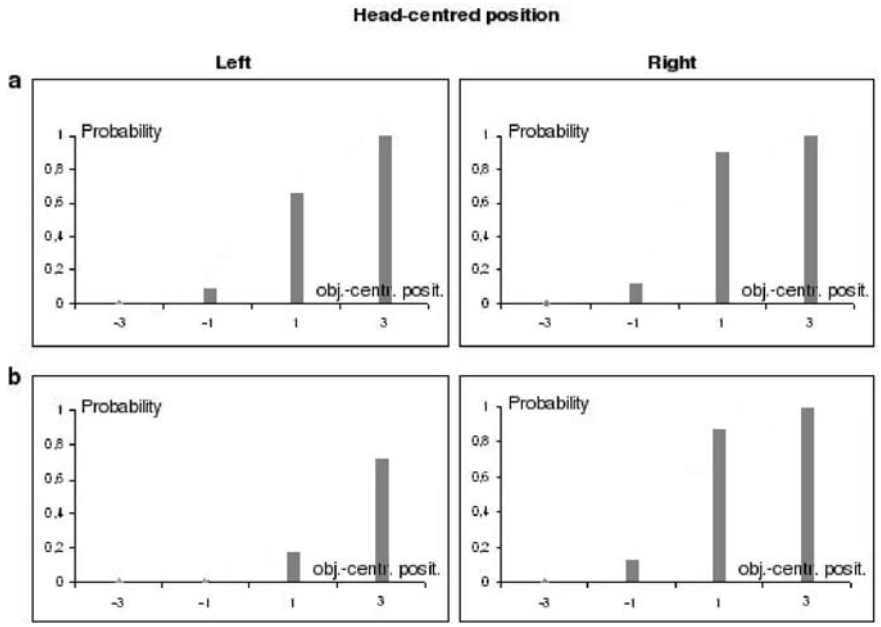



**Figure 3.** Results of simulations through BF network. Probability selection (ordinate) of each of the four object sectors centred at –3, –1, 1 and 3 degrees from fixation aligned to the centre of the object, in the left and right egocentric space. a: results obtained using Pouget and Sejnowsky's (Pouget & Sejnowsky 2001) original selection algorithm. b: results obtained using a modified algorithm taking into account the signal detection probability. It is evident that in both cases visual neglect emerges either in the eye-centred co-ordinate (the left part of each object is neglected) or in the head-centred co-ordinate (i.e., the system that is less effective in the detection of objects located in the left egocentric space).

### Simulations by Real-Position (RP) network

As anticipated in the introduction, a selective impairment of a reference frame with sparing of the other one could be obtained by a neural system in which stimuli salience is not modulated by eye position: a feature proper of head-centred neurons of V6A and VIP areas. In this paragraph we tested an artificial system based on neurophysiological data found in those areas of the dorsal visual system of monkey brain. The artificial neural system was tested on the same task used to test the BF network.

The entire system is composed of two networks, one for each hemisphere. Here, in order to simulate right brain damage we tested only the left hemisphere network. The general scheme of the network is displayed in Fig. 4. It is a five-layered feed-forward network, and it was trained by a two-step learning algorithm, of which the first phase was unsupervised and the second was supervised. The mathematical explanation of the learning phase is not relevant for the matter treated in this chapter, so it will not be exposed.

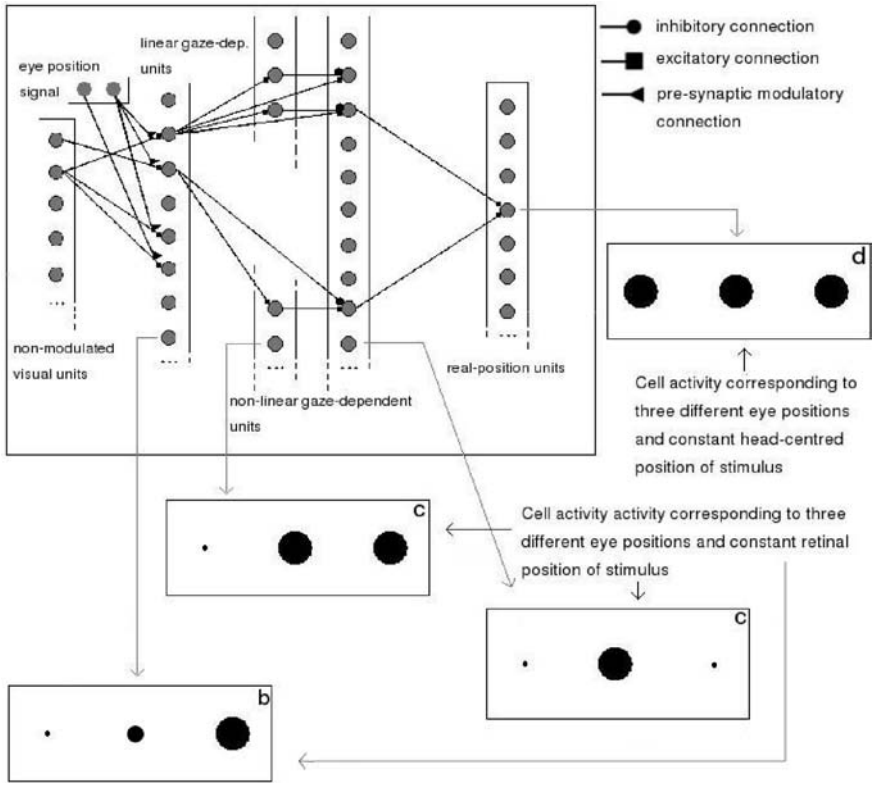



**Figure 4.** General scheme of the real-position network. The dimension of black circles is proportional to discharge rate.

The first layer consists of neurons with retinal RF not modulated by gaze position (i.e., striate cortex neurons). The left half of the layer codes for the left hemifield and the right half for the right one. The activity of first layer units peaks when the stimulus is aligned to the centre of the RF, showing a very steep response decay as the stimulus shifts from the centre (i.e., bell-shaped response).

The second layer consists of units with gaze-dependent behaviour. They receive visual signals from the first layer and eye position signals, set by the modeller, as a linear function of eye position in the orbit (Schlag-Rey & Schalg 1984). These units show a linear modulation of visual input by gaze direction (Andersen et al. 1985; Galletti et al. 1989), with 90% of them being facilitated by contralateral gaze shift (Galletti & Battaglini 1989).

The units belonging to the third layer have a non-linear gaze-dependent behaviour (V6-V6A; Galletti et al. 1995). They receive connections from the second layer and show a steep discharge increase as far as they reach their threshold of activation.

The fourth layer consists of non-linear gaze-dependent units with a peak-shaped discharge modulation by gaze (V6-V6A), with the peak corresponding to a specific

gaze position (Galletti et al. 1995). They receive inputs from the second (excitatory) and the third layer (inhibitory). The combined activity of these two signals shapes the "peak" response of these units.

Finally, the neurons in the fifth layer simulate the activity of Real-Position cells in V6A. The head-centred properties of fifth layer units emerge from the linear combination of the response of fourth layer units coding the same head-centred co-ordinate in different retinal positions (Galletti et al. 1993, 1995; Galletti, et al. 2003).

RFs in layers two, three and four are biased toward the contralateral visual field, with a non-linear representational gradient. Although unit discharge is facilitated by contralateral gaze shift in the second layer, in the fourth layer the peak of activity of non-linear gaze-dependent units is uniformly distributed along the head-centred space, with no lateral representational gradient, as found in the monkey brain (Galletti et al. 1995). This is at variance with equivalent units in BF models, where an eye position gradient is present. Therefore, in our model the majority of non-linear gaze-dependent units are biased toward contralateral retinal positions without being biased by eye position. This latter feature makes the response magnitude of units in the real-position layer independent from gaze shifts. In this network, the salience of the different object sectors corresponds to the response level of different real-position units. Follow the mathematical form of computational features of the network layers.

This is the post-synaptic potential function of the first layer modules:

$$(7) \quad p_i = \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(z-m_i)^2}{2\sigma^2}\right)$$

A gaussian function, where $p_i$ is the potential of the $i^{\text{th}}$ cell, $z$ the retinal position of the stimulus, $m_i$ the retinal position of the receptive field centre of the $i^{\text{th}}$ cell, and $\sigma$ is the standard deviation. The output $u_i$ of the $i^{\text{th}}$ unit is computed as a function of potential:

$$(8) \quad u_i = \tanh(p_i)$$

That is a hyperbolic tangent function.

Post-synaptic potential of neural units belonging to layers following the first, is computed by:

$$(9) \quad P_i^* = \sum_{j=1}^{n} w_{ij} u_j$$

where $n$ is the total number of afferent units to the $i^{\text{th}}$ neuron, $w_{ij}$ is the "weight", that is the efficacy, of the connection between the $j^{\text{th}}$ neuron (pre-synaptic) and the $i^{\text{th}}$ neuron (post-synaptic), and $u_j$ represents the output of the $j^{\text{th}}$ neuron. Obviously, the $w$ value can be either positive (excitatory synapses) or negative (inhibitory synapses). Then, it is simple to demonstrate that, at least when this rule is used, gaze-dependent behaviour cannot be generated by a post-synaptic modulation. In fact, in this case the rule is:

$$(10) \quad P^* = \sum_{j=1}^{n} W_{ij} u_j + w'_{ij} u'_j$$

that is, mathematically equivalent to Equation (9), but in this one it is possible to distinguish between the contribution of non-modulated visual cells [$wu$] and eye position cells [$w'u'$]. Because $u_j$ is defined by Equation (8), and $u'_j$ is defined by a linear function, since this is the eye-position output, it is inferred that the potential should be a weighted sum of the two functions, and not their product. Instead, when a pre-synaptic modulation is supposed, it is possible to obtain results in agreement with neurophysiological data.

Consistent with the view represented by Equation (9), a pre-synaptic modulation would be a transient variation of $w_{ij}$ expressible in the case of only one modulated synapse for each gaze-dependent unit (corresponding to the architecture of this model), by the following:

$$(11) \quad P_i^* = \left(w_{ij} + w'_{ij} u_k\right) \cdot u_j$$

where $P_i^*$ is the potential of the $i^{\text{th}}$ neuron, $u_j$ the output of the pre-synaptic neuron, $w$ the value of the "static" part of the connection between $i$ and $j$, $u_{\text{k}}$ the output of the $k^{\text{th}}$ modulating neuron, and, finally, $w'$ the weight of the connection between $k$ and the connection $i - j$. In conclusion, $P^*$ is obtained by the product of the function expressed by Equation (8) and the linear function expressing the degrees of gaze deviation (output of eye-position cells), whose value is $u_{\text{k}}$.

The output function of linear gaze-dependent cells is the following:

$$(12) \quad u_i^* = \eta P_i^*$$

a linear function. The representation of discharge activity of this kind of cell is shown in Figure 4b.

The post-synaptic potential of units belonging to the third and the fourth layers is computed by Equation (9), while their output is calculated by:

$$(13) \quad u_i^{**} = \begin{cases} \dfrac{1}{1 + e^{-[p-s]}} & \text{if } P_i^{**} > 0 \\ 0 & \text{if } P_i^{**} \leq 0 \end{cases}$$

where $s$ is the threshold of the $i^{\text{th}}$ neuron.

Figure 5 shows the results of simulations. These show that the left side of the object is similarly and completely neglected in both of the head-centred positions, i.e. with no influence from eye position. The results are identical with both selection algorithms. Therefore, the system performance shows a concomitant unilaterally defective eye-centred frame of reference (the left side of each object is neglected) and intact head-centred frame (the right side of the objects is equally represented despite their different head-centred positions).

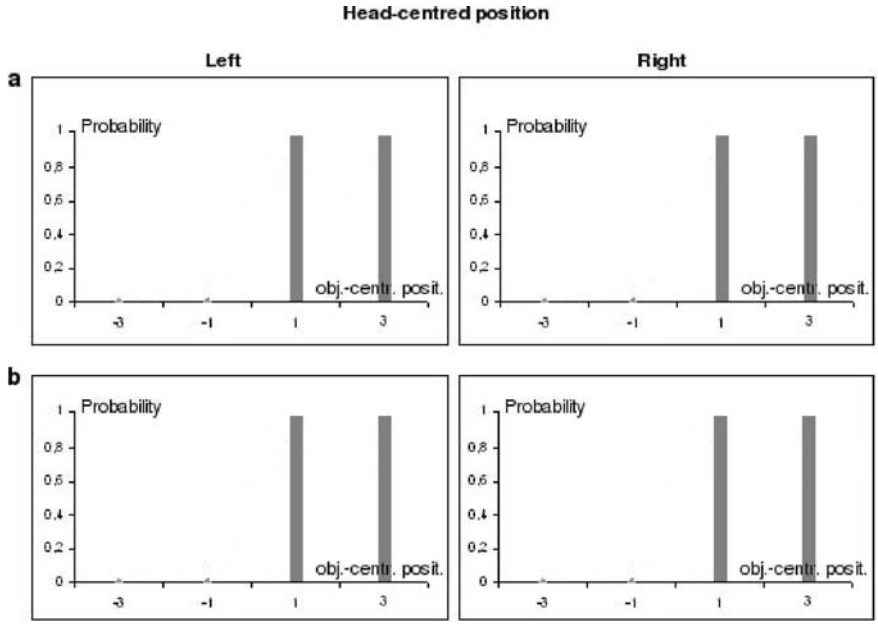



**Figure 5.** Results of simulations through Real-position network. Probability selection (ordinate) of each of the four object sectors centred at –3, –1, 1 and 3 degrees from fixation aligned to the centre of the object, in the left and right egocentric space. a: results obtained using Pouget and Sejnowsky's (Pouget & Sejnowsky 2001) original selection algorithm. b: results obtained using a modified algorithm taking into account the signal detection probability. In both simulations neglect is purely anchored to eye-centred co-ordinates (i.e. the left part of each object is neglected independently of its head-centred position).

## Conclusions

Even if the existence of pure object-centred is well documented, a mixed form of impairment, involving different frame of reference simultaneously, is surely more frequent in clinical reports. This is probably linked to the fact that the most enduring and severe forms of neglect are caused by extended damage of parietal frontal areas irrigated by the middle cerebral artery.

This type of damage can functionally disrupt different but anatomically close circuits (Husain & Kennard 1996; Leibovitch et al. 1998; Mort et al. 2002; Doricchi & Tomaiuolo 2003) and cause massive disconnection of white matter fibres (i.e., superior longitudinal fasciculus) linking different sectors of the parietal lobe to the frontal lobe (Gaffan & Hornak 1997; Leibovitch et al. 1998; Doricchi & Tomaiuolo 2003).

Here we showed that neglect selectively affecting object-centred co-ordinates is well simulated by neural networks head-centred "real-position like" units, whose activity is determined by gaze-dependent units with both of the two following features: a) no lateralized gradient of preferred eye positions along the horizontal egocentric

space (Andersen et al. 1985; Galletti et al. 1995, 2003); b) non-linear modulation by eye position signals.

Real position neurons in V6A are critically involved in reaching and grasping behaviours (Battaglini et al. 2002; Galletti et al. 2003) and, interestingly, selective ablation of V6A does not produce egocentric neglect though the association between disruption of the V6A-VIP-SEF (Supplementary Eye Fields) network, and object-centred neglect has never been investigated directly.

Nonetheless cues about the anatomical correlates of object-centred coding can be gathered from clinical and brain imaging studies in humans. Marshall and Halligan (1993) examined six patients and found that the only one suffering from object-centred neglect had brain damage localised in the occipital-parietal area. Doricchi and Galati (2000) documented a similar localisation of the lesion in a patient with object-centred neglect. Finally, Ota et al. (Ota et al. 2001) described two right brain damaged patients, one with egocentric and the other with object-centred neglect. In the first patient, the lesion involved the putamen, the insula, the anterior superior temporal gyrus and the posterior inferior frontal gyrus, instead, in the second patient, object-centred neglect was linked to more posterior and dorsal damage, extending up to the superior parietal lobule and the white matter close to the parietal-occipital junction.

Even if clinical evidence is quite scattered, it has interesting analogies with the results of brain imaging studies. All of these investigations demonstrate the specific involvement of the dorsal parietal-occipital junction, the superior parietal lobule (Fink et al. 1997; Honda et al. 1998) and frontal areas Ba 6 and 46 (Honda et al. 1998) in object-centred coding of space. Moreover, in the monkey the role of SEF (located in the dorsal part of area 6) in the object-centred programming of saccadic vectors (Olson 1995) is well documented, while evidence of the involvement of the lateral intraparietal area (LIP) in the object-centred coding of space is still being debated (Sabes et al. 2002; Olson 2003). Altogether, these findings suggest that in primate mammals a network including the dorsal sectors of the occipital-parietal area, the VIP and the SEF may be quite involved in the object-centred coding of space.

Based on the results of simulations and the review of electrophysiological, clinical and imaging data, some detailed anatomical and functional hypotheses can be formulated. Anatomical studies of the macaque brain do not show a direct stream between the V6A area and the SEF, which receives most of its afferents from the granular prefrontal cortex and the dorsal premotor cortex (Shipp et al. 1998; Luppino, et al. 2003). However, Marconi and co-workers (Marconi et al. 2001) and Luppino and co-workers (Luppino et al. 2003) showed that about half of the SEF afferents arrive from the F7-non SEF area, which, in turn, is the major target of frontal V6A projections (Shipp et al. 1998; Galletti et al. 2001; Matelli et al. 1998). In light of these data, it is possible to hypothesise that the F7-non SEF area is a relay between V6A and SEF. Considering the relevance of V6A in reaching and grasping, it can be further argued the V6A-F7-SEF circuit provides object-centred computations supporting reaching and grasping. Interruption of V6A-SEF connections, with concomitant sparing of egocentric coding of space found in other sectors of the parietal-frontal system (Mesulam

1981; Vallar et al. 1999; Doricchi & Tomaiuolo 2003), could generate a pathological ipsilesionally biased eye-centred gradient with defective object-centred planning of compensatory eye movement in the contralesional direction. Notably, Walker and co-workers (Walker et al. 1996) documented this type of deficit in a patient suffering from object-centred neglect.

In conclusion, in this chapter it was supported the theoretical position in which neglect is a multi-componential syndrome, involving many neural circuits with different computational roles, and that the frequent association of different space representation impairment, emerging from clinical studies, is due merely to the vascular structure and anatomical circuits closeness of human brain, and not to the damage of a unique neural population with very wide computational functions. Moreover, it was underlined the efficacy of utilizing the formal rigor of neural networks modelling to generate an anatomo-functional hypothesis about the causes of object-centred neglect, and its possible link with circuits dedicated to reaching behaviour.

## References

Andersen, R. A., Essik, G. K. & Siegel, R. M. (1985). Encoding of spatial location by posterior parietal neurons. *Science, 230*, 456–458.

Bartolomeo, P., & Chokron S. (2002). Orienting of attention in left unilateral neglect. *Neuroscience and biobehavioural reviews, 26*, 217–234.

Battaglini, P. P., Muzur, A., Galletti, C., Skrap, M., Brovelli, A., & Fattori, P. (2002). Effects of lesions to area V6A in monkeys. *Experimental Brain Research, 144*, 419–422.

Behrmann, M., & Moscovich, M. (1994). Object-centred neglect in patients with unilateral neglect: Effect of left-right coordinates of objects. *Journal of cognitive neuroscience, 6*, 151–155.

Doricchi, F., & Galati, G. (2000). Implicit semantic evaluation of object symmetry and controlesional object denial in a case of left unilateral neglect with damage of dorsal paraventricular white matter. *Cortex, 36*, 337–350.

Doricchi, F., & Tomaiuolo, F. (2003). The anatomy of neglect without hemianopia: A key role of parietal-frontal disconnection? *NeuroReport, 14*, 2239–2243.

Driver, J., & Halligan, P. W. (1991). Can visual neglect operate in object-centred coordinates? An affirmative single case study. *Cognitive Neuropsychology, 18*, 475–496.

Driver, J., Baylis, G. C., Goodrich, S. J., & Rafal, R. D. (1994). Axis-based neglect of visual shapes. *Neuropsychologia, 32*, 1353–1365.

Driver, J., & Pouget, A. (2000). Object-centred visual neglect, or relative egocentric neglect? *Journal of cognitive neuroscience, 12*, 542–545.

Duhamel, J. R, Bremmer, F., BenHamed, & Graf, W. (1997). Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature, 389*, 845–848.

Fink, G., R., Dolan, R. J., Halligan, P. W., Marshall, J. C. & Frith, C. D. (1997). Space-based and object-based visual attention: Shared and specific neural domains. *Brain, 120*, 2013–2028.

Gaffan, D., & Hornak, J. (1997). Visual neglect in the monkey. Representation and disconnection. *Brain, 120*, 1647–1657.

Gainotti, G., & Tiacci, C. (1970). Patterns of drawing disability in right and left hemispheric patients. *Neuropsychologia, 8*, 379–384.

Galletti, C., & Battaglini, P. P. (1989). Gaze-dependent visual neurons in area V3a of monkey prestriate cortex. *Journal of Neuroscience, 9*, 1112–1125.

Galletti, C., Battaglini, P. P., & Fattori, P. (1995). Eye position influence on parieto-occipital area PO (V6) of the macaque monkey. *European journal of Neuroscience, 7*, 2486–2501.

Galletti, C., Battaglini, P. P., & Fattori, P. (1993). Parietal neurons encoding spatial locations in craniotopic coordinates. *Experimental Brain Research, 96*, 221–229.

Galletti, C., Gamberini, M., Kutz, D. F., Fattori, P., Luppino, G., & Matelli, M. (2001). The cortical connections of area V6: An occipito-parietal network processing visual information. *European journal of Neuroscience, 13*, 1572–1588.

Galletti, C., Kutz, D. F., Gamberini, M. Breveglieri, R., & Fattori, P. (2003). Role of the medial parieto-occipital cortex in the control of reaching and grasping movements. *Experimental Brain Research, 153*, 158–170.

Galletti, C., & Fattori, P. (2003). Neuronal mechanisms for detection of motion in the field of view. *Neuropsychologia, 41*, 1717–1727.

Honda, M., Wise, S. P., Weeks, R. A., Deiber M. P., & Hallett, M. (1998). Cortical areas with enhanced activation during object-centred spatial information processing. A PET study. *Brain, 121*, 2145–2158.

Husain, M., & Kennard, C. (1998). Visual neglect associated with frontal lobe infarction. *Journal of Neurology, 243*, 652–657.

Leibovitch, F. S., Black, S. E., Caldwell, C. B., Ebert, P. L., Ehrlich, L. E., & Szalai, J. P. (1998). Brain-behavior correlations in hemispatial neglect using CT and SPECT: The Sunnybrook Stroke Study. *Neurology, 50*, 901–908.

Luppino, G., Rozzi, S., Calzavara, R., & Matelli, M. (2003). Prefrontal and agranular cingulate projections to the dorsal premotor areas $F_2$ and $F_7$ in the macaque monkey. *European Journal of Neuroscience, 17*, 559–578.

Marconi, B., Genovesio, A., Battaglia-Mayer, A., Ferraina, S., Squatrito, S., Molinari, M., Lacquaniti, F., & Caminiti, R. Eye-hand coordination during reaching. I. (2001). Anatomical relationships between parietal and frontal cortex. *Cerebral Cortex, 11*, 513–527.

Marshall, J. C., & Halligan, P. W. (1993). Visuo-spatial neglect: A new coping test to assess perceptual parsing. *Journal of neurology, 240*, 37–40.

Matelli, M., Govoni, P., Galletti, C., Kutz, D. F., & Luppino, G. (1998). Superior area 6 afferents from the superior parietal lobule in the macaque monkey. *The Journal of comparative neurology, 402*, 327–352.

Mesulam, M. M. (1981). A cortical network for directed attention and unilateral neglect. *Annals of neurology, 10*, 309–325.

Mort, D. J., Malhotra, P., Mannan, S. K., Rorden, C., Pambakian, A., Kennard, C., & Husain, M. (2003). The anatomy of visual neglect. *Brain, 126*, 1–12.

Olson, C. R., & Gettner, S. N., (1995). Object-centered direction selectivity in the supplementary eye field of the macaque monkey. *Science, 269*, 985–988.

Olson, C. R. (2003). Brain representation of object-centred space in monkeys and humans. *Annual review of neuroscience, 26*, 331–354.

Ota, H., Fujii, T., Suzuki, K., Fukatsu, R., & Yamadori, A. (2001). Dissociation of body-centered and stimulus-centered representations in unilateral neglect. *Neurology, 57*, 2064–2069.

Pouget, A., & Sejnowki, T. J. (2001). Simulating a lesion in a basis function model of spatial representations: Comparison with hemineglect. *Psychological Review, 108*, 653–673.

Pouget, A., & Sejnowski, T. J. (1997). Spatial transformations in the parietal cortex using basis functions. *Journal of cognitive neuroscience, 9*, 222–237.

Pouget, A., Deneve, S., & Duhamel, J. R. (2002). A computational perspective on the neural basis of multisensory spatial representations. *Nature reviews. Neuroscience, 3*, 741–747.

Pouget, A., Deneve, S., & Sejnowski, T. J. (1999). Frames of reference in hemineglect: A computational approach. *Progress in brain research, 121*, 81–97.

Sabes, P. N., Breznen, B., & Andersen, R. A. (2002). Parietal representation of object-based saccades. *Journal of neurophysiology, 88*, 1815–1829.

Schlag-Rey, M., & Schlag, J. (1984). Visuomotor functions of central thalamus in monkey. I. Unit activity related to spontaneous eye movements. *Journal of neurophysiology, 51*, 1149–1174.

Shipp, S., Blanton, M., & Zeki, S. (1998). A visuo-somatomotor pathway through superior parietal cortex in the macaque monkey: Cortical connections of areas V6 and V6a. *European Journal of Neuroscience, 10*, 3171–3193.

Tipper, S. P., & Behrmann, M. (1996). Object-centred not scene based visual neglect. *J. Exp. Psychol. Hum. Percept Perform., 22*, 1261–1278.

Vallar, G., Lobel, E., Galati, G., Berthoz, A., Pizzamiglio, L., & Le Bihan, D. (1999). A fronto-parietal system for computing the egocentric spatial frame of reference in humans. *Experimental Brain Research, 124,* 281–286.

Walker, R. (1995). Spatial and object based neglect. *Neurocase, 1*, 371–383.

Walker, R., Findlay, J. M., Young, A. W., & Lincoln, N. B. (1996). Saccadic eye movements in object-based neglect. *Cognitive Neuropsychology, 13*, 569–615.

CHAPTER 4.7

# Omission vs. shift of details in spatial representations

Alessio Toraldo and Gabriella Bottini

## Introduction

There are (at least) two mistakes one can make while drawing a map. One is to leave out a relevant detail, the other is to draw a detail in the wrong place. We will refer to the former error by using the term "omission"; the latter concept will be referred to as a "shift" of the detail from its correct position in the map. This very broad distinction might apply to errors made while building up any kind of analogical map, including representations of space in the human cognitive system.

In this Chapter, we will discuss a number of results collected in cognitive neuropsychological research suggesting that errors of both types, i.e. omissions and shifts of relevant details, are made while building up internal representations. In particular, we will analyse examples from the immense corpus of research concerning unilateral neglect, and propose a broad re-classification of part of the neglect-related phenomena in terms of the omission/shift dichotomy.

Before that, we will briefly discuss a distinction that has long been investigated in the classical neuropsychological literature, and which conceptually overlaps the proposed dichotomy of omission vs. shift.

## "Detection" vs. "Localization" in common sense and in the classical literature

Since the early days of psychophysics, "detection" – the *task* of reporting the presence vs. absence of a stimulus, and "localization" – the *task* of reporting the position of a stimulus, have been investigated. Common sense would suggest that localization logically implies detection, while the reverse does not hold. If one knows where an object is, it seems mandatory to assume that s/he has detected it; conversely, if one knows that an object is present, it is far from certain that s/he also knows its position. For instance, in the memory domain, it is not uncommon that one is absolutely certain to have seen a given object without being able to recall where the object is. In spite of the vagueness of this proto-cognitive theory, the straightforward prediction is that it should be im-

possible to find a subject who can localize an object, while at the same time failing to detect it. The most dramatic falsification of this apparently trivial prediction has been first described by Weiskrantz (1974), who studied patients with hemianopia. Some of these patients, although (by definition) unable to detect stimuli presented in their blind hemifield, were nonetheless able to localize them – an instance of "blindsight". In typical paradigms, the patient is asked to guess whether the stimulus appeared in the upper or lower quadrant of the blind hemifield, or to point at the missed target; although such patients perceive the tasks as utterly meaningless, their performance is significantly above chance, up to ceiling (normal) performance. Whilst many of the reported blindsight phenomena might be ascribed to methodological artefacts, at least some of them seem genuine (see Azzopardi & Cowey 1997, 1998; Harris et al. 2004, for discussion).

Therefore, the common-sense theory is false – it is *not* true that detection is necessary for localization to occur, at least in the visual modality (see Harris et al. 2004, for an opposite view regarding the tactile modality). In a cognitive framework, it is *not* possible that the process subserving localization is serially connected to (and downstream from) the process subserving detection (see Fig. 1A). The assumption seems necessary that the information underlying the two tasks, localization and detection, travels *in parallel* at some point of the architecture (Fig. 1B). In other words, there would be a representation (1) of the stimulus pattern providing input to a system that generates detection judgements, and another representation (2) doing so for a system generating localization judgements; selective damage to representation (1) would generate the puzzling phenomenon of "blind-localization"; selective damage to representation (2) would predict the converse pattern, intact detection with defective localization. Instances of this latter profile are classical, both in the visual *perceptual* domain (e.g. Faglioni et al. 1971) and in the visuo-*motor* domain (optic ataxia, see e.g. Milner & Harvey, this volume).

## "Shifts" vs. "omissions" in (perceptual) spatial tasks

In the blindsight literature alluded above, detection and localization tasks have been investigated in the tradition of psychophysics, i.e. by measuring the *sensitivity* of subjects in forced-choice paradigms. Thus subjects were forced to say whether or not they detected a stimulus, and in which of (e.g.) two pre-defined positions the stimulus was presented. While having a number of advantages, mostly related to the well-developed underlying psychometric theory, forced-choice paradigms lose much of the information potentially available in subjects' behaviour. As an example regarding localization, further insight into its underlying mechanisms might be provided by analysing the *type* and *spatial distribution* of errors. By asking the subject to report the subjective position of a stimulus, information would be available that distinguishes the effect of "noise", uncertainty by the subject (variable error), from systematic misperceptions of position (constant errors; in the present terminology, "shifts" within some internal spatial

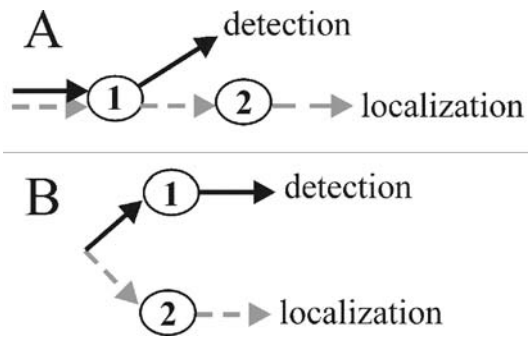



**Figure 1.** Two general models of information processing involved in detection and localization tasks (modified from Harris et al. 2004, Fig. 5). Solid black arrows show the path followed by information used in the detection task; dashed grey arrows show the same for the localization task. **A**, The "serial" model supported by empirical evidence in the tactile modality (Harris et al. 2004); **B**, The "parallel" model, more plausible for the visual modality.

representation). Sensitivity measures do not allow this distinction. For instance, a patient who is very uncertain about stimulus location (but, on average, correct), might obtain the same (low) *d'* score as a subject who is entirely certain about a *wrong* position – a dissociation underlying (presumably) separate components, which would go unnoticed.

Although in a completely different context with respect to blindsight studies, the task of reporting the (relative) position of a stimulus has been administered in a number of different ways to neglect patients (see Toraldo 2003, for review). It is to this literature that we now turn, in order to analyse the relationship between "shifts" and "omissions".[1]

*A misleading paradox?*

By definition "neglect patients" are subjects with a detection deficit ("neglect" is essentially the negation of "detection").[2] More precisely, by using the term (visual) "neglect", one refers to a patient who *omits* a number of targets in visual search tasks, with omission frequency typically increasing from the ipsilesional to the contralesional side (Halligan et al. 1992). In the last decade a number of theories have been proposed to explain some puzzling behaviours shown by neglect patients. Such models emerged after a very counterintuitive phenomenon first described by Bisiach et al. (1994). These authors reported data from two patients who, in spite of left neglect, *over*-explored the left (contralesional) side when required to set the endpoints of an imaginery horizontal line given its midpoint alone. The patients set the left endpoint farther from the midpoint than the right endpoint (relative contralesional overextension, rCO). This behaviour was interesting in that it could shed light on the mechanisms involved in metric processing – in the present terminology, it suggests a form of "shift" of details

within some spatial representation. Nevertheless, the authors focused all of their attention to the relationship of the rCO phenomenon with "neglect" (in the sense of the *empirical* omission of contralesional targets in visual search), presumably because of the puzzling paradox – how can a patient who is relatively incapable of reaching out towards contralesional space show an "overshoot" towards that side? This paradox so captured the interest of the neuropsychological community (including one of us, see Toraldo 1996) that Shallice's (1988) methodological caveat about the theoretical insignificance of an association of symptoms (in this case, the strange behaviour of "contralesional overextension" in the Endpoints Task, and the omission of targets on the contralesional side of a display) was "neglected". Thus two years later, Bisiach et al. (1996) proposed a hypothesis accounting for the paradox, that explicitly assumed a common functional origin for the two key symptoms. Bisiach et al. (1996) proposed that an "anisometry" of space representation caused both the rCO on the Endpoint Task and contralesional omissions in visual search. Anisometry refers to a lack of correspondence between the metrics in the physical world and the metrics within the mental representation of space. Thus, for example, two segments of equal physical length would have different apparent lengths and, more precisely, the more contralesional segment would appear shorter (a prediction that was demonstrated empirically by Milner et al. 1993, with their well-known "Landmark-Task"). This "distortion" of the representational medium would be so severe in its far contralesional sector that conscious perception of stimuli presented in that region would be prevented, thus producing their omission in overt behaviour.

While perhaps speculative, Bisiach et al.'s proposal had the merit of being testable. The basic notion of their hypothesis is that the same spatial representation should serve as input to two separate processes, one for estimation of relative metrics and the other for detection of items in visual search. Damage to the spatial representation would cause *both* underestimation of contralesional with respect to ipsilesional spatial extents, and omission of contralesional targets in visual search. The theory, in this clear-cut formulation, forbids double dissociations between the two symptoms, i.e., contralesional neglect and contralesional relative underestimation. Toraldo (2003) reported a series of five patients, all of whom presented with profound neglect on visual search. In spite of this, two of them (BC and MN) showed normal performance on a highly specific test of horizontal extents estimation (Distance Judgment Task, DJT). In this psychophysical task, patients were given two fixed lateral landmarks (anchors), defining an empty reference space; inside this space, a stimulus (target) was presented in various positions (24 equispaced positions along the reference space were used). Subjects were asked to judge the position of the target numerically, by using numbers from 0 to 100; thus, 50 was the appropriate response if the target looked exactly halfway along the reference space. The psychophysical functions of both BC (left neglect on visual search) and MN (right neglect) failed to show significant lateral biases. The opposite dissociation (contralesional relative underestimation without neglect) can also be found in the literature. Ironically, Bisiach et al.'s (1996) patient #19, and a further nine patients described by Bisiach et al. (1998; the "G-9" group),

as well as five patients in Ferber and Karnath's (2001) study, showed reliable relative underestimation of contralesional spatial extents on a number of metric estimation tasks, without neglecting contralesional targets in visual search (but see comments by Doricchi et al. 2002b, about Ferber & Karnath's patients). This remarkable (multiple) double-dissociation shifts the weight of empirical evidence against Bisiach et al.'s (1996) hypothesis. It is our opinion that a strong functional link between the cause of the exploratory impairment and the cause of the failure on "metric" tasks is untenable, also on purely theoretical grounds (see Toraldo 2003: 596–597). In an extreme interpretation, the association between neglect and contralesional overextension on the Endpoints Task (Bisiach et al. 1994), which puzzled part of the neglect community so deeply, might really have been illusory – an (at most) statistical association of two entirely unrelated symptoms, possibly due to anatomical contiguity of the two relevant neural substrates (see also Ferber & Karnath 2001). It should be noticed, after all, that the computational requirements of the two mental operations, visual search and metrics estimation, are so profoundly different that a functional separation between them should not be surprising. The neglect community has nonetheless tried to clarify the relationship between visual search and metric estimation impairments, without converging on any convincing account. In an overwhelmingly complex picture, different authors have used a wide variety of different tasks (see Toraldo 2003, for a comparative analysis of some of these methods); task differences are quite likely to have increased confusion and discrepancies across studies. Nonetheless, one remarkable (and stable) result has been convincingly brought to the fore. In a sound research programme, Doricchi and his colleagues (Doricchi & Angelelli 1999; Doricchi et al. 2002a, 2002b) showed that contralesional relative underestimation is typically found in patients with both neglect and *hemianopia*; patients with neglect but without hemianopia show, on average, minor left-right asymmetries in metric estimation tasks. Moreover, patients with hemianopia but without neglect tend to show the paradoxical pattern of contralesional relative *over*estimation.

*Another paradox*

The complexity of neglect patients' behaviour on this type of tasks goes even further. Recently Toraldo and Reverberi (2004) reported the case of a left neglect patient with hemianopia (GL) who was administered with three tasks involving metric estimation (see Fig. 2). On the Endpoints task, GL showed the classical pattern, rCO, suggesting contralesional *under*estimation of spatial extents (see Fig. 2A). On the Distance Judgment Task (DJT, Toraldo 2003), in which she had to report verbally the position of a stimulus within a reference horizontal space, GL showed contralesional *over*estimation (Fig. 2B). This latter pattern was also found in two out of a further 10 neglect patients (#4 and #8) and could be replicated (twice) in GL by means of a slightly different technique, the Length Judgment Task (LJT, Toraldo & Reverberi 2004; see Fig. 2C). A contradiction is evident: GL showed contralesional *under*estimation on one task, and contralesional *over*estimation on another two. Clearly, Bisiach et al.'s (1996) "anisometry" hypothesis cannot explain such a pattern.

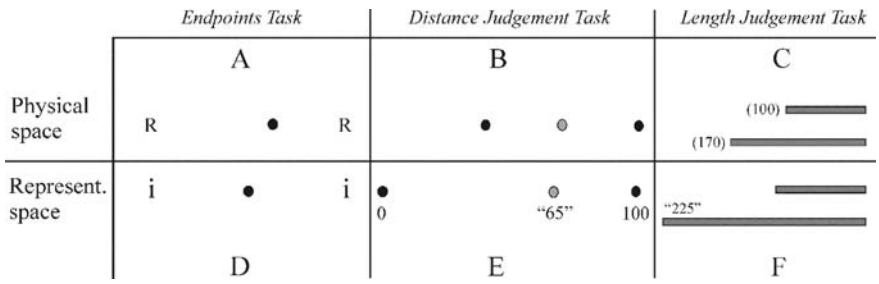



**Figure 2.** GL's performance on three tasks (Toraldo and Reverberi 2004). **A**, **B**, **C**: physical space; **D**, **E**, **F**: interpretation in terms of leftward shift of visual features (either dots or line Endpoints) within GL's spatial representation (Represent. = Representational). **A**, **D**: Endpoints Task. Black dot: midpoint (the stimulus); "i": imaginery endpoints set by GL equidistantly from the midpoint in her mental representation; "R": Real marks drawn by the patient in physical space. **B**, **E:** Distance Judgement Task. Black dots: lateral (fixed) anchors; grey dot: target (varying) stimulus – in this example, at the physical midpoint of the reference space. In GL's representational space (E), the target appeared 65% of the distance from the left to the right anchor. **C**, **F**, Length Judgement Task (LJT). In LJT, subjects are presented with two horizontal lines, one 50 mm above the other, and whose right endpoints are vertically aligned. The upper line is always 100 mm long, and serves as the "sample". The lower line's left endpoint varies across trials, with the line length varying in the range from 30 to 170 mm. The task is to say how long the lower line is given that the upper line's length equals "100". In the example, the lower line is the 170-mm stimulus; in GL's representation (F), its length was (on average) 225.

*The "shift" (or "misprojection") model*

Toraldo and Reverberi (2004) proposed an interpretation for GL's behaviour in terms of a qualitatively different deficit. The basic idea is that visual stimuli are placed in wrong locations within an allocentric spatial representation, and more precisely, "shifted" ("misprojected" in the original article) contralesionally from their correct locations. These shifts would be minor, or absent, for stimuli on the ipsilesional side, and increasingly severe the more contralesional are the stimuli. Thus for instance, if the patient had been presented with three dots, one on the left, one at the centre, and one on the right of an A4 sheet, in the allocentric representation of the sheet the right dot would be shifted leftwards by (say) 1 cm, the central dot by 2 cm, the left dot by 5 cm, etc.[3] This pattern of shifts would induce a subject to make the errors shown by GL on the DJT and the LJT (see Figs. 2B, 2C). Consider the DJT's simplest item (Fig. 2B), with the target stimulus physically equidistant from the two lateral anchors. In the defective representation of GL, the left lateral anchor would be shifted to the left, while smaller shifts would affect the target and the right anchor (Fig. 2E). As a consequence, the gap between left anchor and target would look larger than the complementary gap, thus leading the patient to relatively overestimate it in her numerical judgements. Similar reasoning would apply to the LJT (see Figs. 2C, 2F), if one considers the line

endpoints as landmarks that "shift" following a similar law as that obeyed by isolated stimuli (as the anchors and the target in the DJT; see also McIntosh et al. 2004).

The shift (or "misprojection") of visual features in the allocentric representation predicted GL's performance on the Endpoints Task with remarkable accuracy (see Figs. 2D, 2E in Toraldo & Reverberi 2004). On this task, only one visual stimulus is provided, i.e. the centre of the virtual line. According to the theory, this dot was slightly shifted to the left in the representation. When asked to set two marks equidistant from the central dot on either side, GL referred to the *illusory* dot (Fig. 2D), which was some distance to the left of the physical one (Fig. 2A). The consequence was a leftward imbalance of the two physical marks around the *physical* central dot, as shown in Figure 2A.

Toraldo and Reverberi (2004) conjectured that the shift of visual features might be related to hemianopia. If one visual hemifield is blind, every higher-level spatial representation is deprived of visual input from that hemifield. The contralesional side of the spatial representation is more often deprived than the ipsilesional side, with a gradient going from a maximum deprivation at the contralesional extreme to a minimum deprivation at the opposite extreme. While patients with pure hemianopia can reduce this deprivation by moving their gaze towards the contralesional side, thereby "feeding" the spatial representation's contralesional side with their seeing hemifield, patients (like GL) with hemianopia and neglect do not move their eyes to that side, thus failing to counteract the effects of deprivation. As argued by Lebedev et al. (2000) in the domain of whiskers-mediated perception in the rat, a deprived neural region can become "hyper-excitable" and "steal" stimuli delivered to the neighbouring non-deprived (or less deprived) region (see Fig. 3 for details). In a (partial) analogy, this putative phenomenon recalls the well-known misperception experienced by amputees who, when receiving a stimulus in somatic regions close to an amputated limb, feel a supplementary touch over the phantom limb (see e.g. Hunter et al. 2003).

This hypothesis of a contralesional shift of perceptual features (Toraldo & Reverberi 2004) allowed us to derive a number of predictions.

(1) Hemianopes (without neglect) should misbisect horizontal lines towards the contralesional side, because the contralesional endpoint should "shift" perceptually some distance to the left in their representation. However, the magnitude of the shift should be relatively small as the sensory deprivation inducing the shift would be reduced by compensatory contralesional eye movements in these patients. This prediction is largely confirmed in the literature, since slight contralesional bisection errors in patients with pure hemianopia is a well-established phenomenon.

(2) Hemianopes (without neglect) should perceive the ipsilesional half of a correctly bisected line as shorter. This prediction is confirmed by empirical data (see e.g. Doricchi et al. 2002b, Table 1, Landmark Task).

(3) Hemianopes (without neglect) should show (small) ipsilesional relative overextension on Doricchi et al.'s (2002b) Gap Matching Task (see Fig. 2F in Toraldo & Reverberi 2004, for explanation). Doricchi et al.'s (2002b) results were consistent with this prediction.

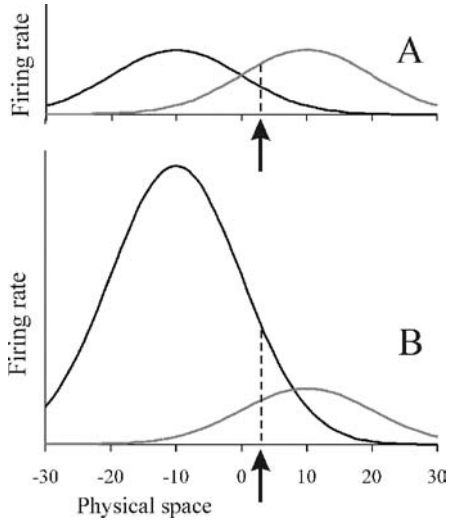



**Figure 3.** Horizontal axis: position of a stimulus (e.g. a spot of light) along the horizontal dimension of physical space. Vertical axis: firing rate of neurones belonging to a high-level allocentric spatial representation of visual space. The tuning curves of two neurones are shown whose maximum discharge is for spotlight position –10 (black curve) and +10 (grey curve). Consider a spotlight presented at position +3 (black arrow). **A**: normal subject. Since the firing rate of the "right" neuron is higher than that of the "left" neuron (dashed line), the subject will perceive the spotlight as closer to +10 than to –10. **B**: patient with left neglect and left hemianopia. The "left" neuron is often deprived of visual input because stimuli in its preferred spatial locations often fall in the blind hemifield; the neuron thus becomes hyper-excitable, i.e. its firing rate curve is abnormally high. The spotlight presented at +3 activates more the "left" than the "right" neuron (dashed line), thus inducing a misperception of the spotlight as closer to –10 than to +10. Toraldo and Reverberi (2004) proposed this mechanisms for ventral-stream (allocentric) spatial representations; thus such mislocalizations would affect perceptual judgements, and not visuo-motor control (dorsal stream processing, Milner & Goodale 1995).

(4) Another prediction regards the bisection performance of patients with both hemianopia and neglect. Consider a patient with left neglect and left hemianopia. If the line to be bisected is explored in its full extent with the good (right) hemifield, the left endpoint, a relevant visual landmark, should be "shifted" contralesionally in the representation, thus leading to leftward bisection error. Conversely, if the line has not been explored entirely with the good hemifield, the spatial representation should receive only the explored part, an "amputated" line. In this case, what would be shifted leftwards is the left edge of the amputated line, i.e., the "cut" end of the line. Figure 4 shows what should happen if lines of different lengths were presented. With short lines, patients would succeed in exploring with their good hemifield most or all of the line's extension (Fig. 4A). With long lines, the pathological "attentional attraction" ex-

erted by the right endpoint (typical in neglect patients) would prevent fixation from reaching the left endpoint, so that just a small portion of the line will fall in the seeing hemifield and enter the spatial representation (Fig. 4B). The prediction then is a leftward bisection error for short lines, and a rightward bisection error for long lines. This pattern is the well-known "cross-over" effect in bisection performance in neglect patients (Halligan & Marshall 1989). Most crucially, the cross-over pattern should only appear when neglect is accompanied by hemianopia. Indeed, neglect patients *without* hemianopia would not suffer from the visual input deprivation that induces the representational "shift" of features (be they endpoints or "cut" points); therefore leftward bisection error on short lines would not be possible. This prediction has been fully confirmed in a study by Doricchi et al. (2005): only patients with both neglect and hemianopia showed the classical contralesional error on short lines, with "pure" neglect patients failing to show such an effect (however, notice that Doricchi et al. 2005, interpreted these results in different terms).

(5) As shown in Figure 4B, another prediction is that patient with both left neglect and left hemianopia should place the bisection point in the left half of the part of line they have explored with their seeing hemifield (i.e. the grey portion in Fig. 4B). Ishiai et al. (1989) found that this is the case: by recording the eye movements of a set of left neglect patients, they could show that the bisection mark was placed in the vicinity of the "visual cut" point (black arrow in Fig. 4B), i.e., the leftmost point of the line that fell within the seeing hemifield during stimulus inspection.

Although the amount of empirical evidence in favour of the "shift" model looks promising, it is obvious that it cannot account for all possible patterns of performance. Several studies have addressed distance perception in neglect and hemianopia, leading to a host of contradictory results – it is only the tip of the iceberg that seems explainable by the representational shift theory. For instance, this hypothesis cannot explain cases where the Judgement Tasks (DJT and LJT, Toraldo & Reverberi 2004) and the Endpoints Task give *consistent* results, i.e., contralesional relative underestimation on both task types. Case AL (Toraldo 1996, 2003; Toraldo & Reverberi 2004, Table 1, #10) showed this type of consistency. AL produced the classical pattern of left relative underestimation on the Endpoints task (left endpoint placed farther than right Endpoints from the central dot), and a left relative underestimation on both the DJT and the LJT. Neither can the representational shift hypothesis explain why patients with both neglect and hemianopia show contralesional overextension on tasks like Doricchi et al.'s (2002a) "(*single*) Endpoint Task". One possible suggestion is that "anisometry" (Bisiach et al. 1996) exists as an independent deficit, which may appear in isolation or in addition to the effects of "representational shifts". As Toraldo and Reverberi (2004) argued, anisometry might reflect a radically different impairment from that inducing representational shifts, e.g., a deficit of abstract quantification of the size of an object or gap, possibly carried out by the ventral stream. In this view, GL would be a (relatively rare) case of hemianopia with a concomitant attentional/premotor deficit (a

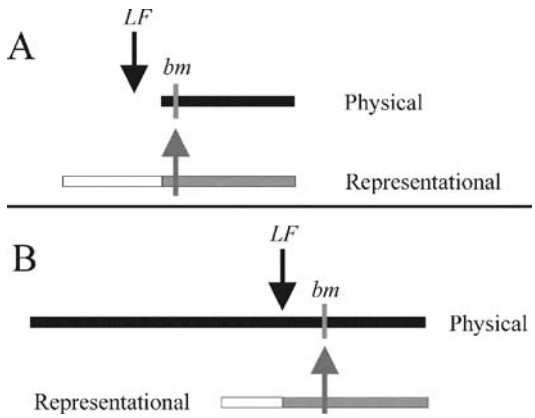



**Figure 4.** Performance of a putative patient with left neglect and left hemianopia on line bisection with lines of different length (**A**: short line; **B**: long line), as predicted by the "representational shifts" hypothesis. Physical lines are shown in *black*. *Grey* sections of representational lines: parts that have been "seen" through the good (right) visual hemifield, i.e., parts that lie to the right of the leftmost fixation point (*LF*, shown as a downward black arrow). *White* sections of representational lines: "hallucinatory" parts of line generated by the leftward "shifts" of the left endpoints of the "seen" lines (in grey). Upward grey arrows: representational (subjective) midpoints generating bisection marks (*bm*) over the physical lines. Note that the grey portions are assumed to have access to both processing streams (dorsal visuo-motor and ventral "perceptual", see Milner & Goodale 1995), while white portions are assumed to be generated within the ventral stream. Thus, if the patient is required to point to the left endpoint of the line, s/he should reach out towards the end of the *grey* line, i.e. the only feature "visible" to the dorsal stream which is automatically recruited by this kind of direct visuo-motor tasks.

combination leading to severe representational shifts) *without* size-estimation deficit ("anisometry").[4]

As an alternative view for explaining this complex pattern of results, the interested reader should consider Doricchi et al.'s (2002a, 2002b, 2005) general model, which calls into play reflexive contralesional gaze shift in hemianopia.

*"Shift" vs. "Omission"*

In the above sections we showed how the representational shift theory ("misprojection" in Toraldo & Reverberi 2004) can account for a number of results in the neglect literature. Crucially, the necessary condition for representational shifts to appear is the loss of visual input – hemianopia. The attentional/premotor disorder causing neglect has only an indirect role in the genesis of representational shifts; the attentional/premotor disorder would simply amplify visual input loss by preventing compensatory contralesional eye movements, with the final effect of increasing the amplitude of representational shifts. The "amplification" effect is clear when comparing

the performance of a typical patient with pure hemianopia (see Doricchi et al. 2002a, 2002b) with that of GL (hemianopia with neglect; Toraldo & Reverberi 2004). GL and patients with pure hemianopia show qualitatively similar performance; the only difference is in the size of the deficit – while pure hemianopes show slight overestimation of contralesional extents, GL showed a massive effect of the same type.

In this view, *shifts* of visual features in a spatial representation are functionally independent of *omissions* of visual features. The impairment causing contralesional omissions would reside in very different cognitive loci (e.g. visual attention processing, Posner et al. 1984) from those involved in allocentric spatial localization, whose disruption would cause illusory shifts.

In the following sections, we propose to apply the very general idea of functionally separate mechanisms leading to omissions vs. shifts, to other fields of neglect-related research. In one area, regarding the auditory modality, the omissions vs. shifts dichotomy has already received empirical confirmation; in another area, regarding motor programming, evidence (to our knowledge) has not yet been collected.

## "Shifts" vs. "omissions" in the auditory modality

"Omission" and "shift" errors could convincingly be distinguished also in the domain of lateralized impairments of auditory perception. It is not uncommon to find patients who, soon after a right hemisphere stroke, do not respond to noises or voices coming from their contralesional side (Heilman & Valenstein 1972). Unfortunately, these genuine "omission" errors (the only phenomenon for which, in our opinion, the label "auditory *neglect*" is appropriate[5]) are not easy to study precisely because they occur in a phase where patients cannot participate in demanding experimental designs. In later (post-acute) phases, omission of unilateral stimuli are comparatively much rarer, whereas "auditory *extinction*" is reasonably easy to find (i.e. patients who fail to respond to contralesional auditory stimuli only when these are coupled with different ipsilesional stimuli, a form of "dichotic" listening task). Thus for instance, if simultaneously presented with the sound "ba" at the left ear and "ra" at the right ear, a right hemisphere patient would often report only the latter. Another set of observations regards the mislocalization of sounds (see e.g. Bisiach et al. 1984), i.e. the tendency by right hemisphere patients to misperceive a sound as coming from a position shifted ipsilesionally with respect to the correct sound source. In an elegant study, Bellmann et al. (2001) administered right hemisphere patients with both a sound localization task and a *diotic* listening task. A diotic listening task is an analogue of the classical dichotic listening task, with the crucial difference that the apparent position of the two sounds is not encoded on grounds of interaural intensity differences, but rather, relying of interaural *time* differences (ITD), thus eliminating a series of theoretical confounds. A clear-cut double dissociation was found between two patients showing a deficit of sound localization without auditory extinction on the diotic listening task, and another two patients showing the opposite pattern.[6] This, we think, is empirical grounds

for assuming a functional distinction between omission and shift also in the auditory modality, although the two processes involved might be different from those relating to the visual modality. As Bellmann et al. (2001) suggest, the omission of contralesional auditory stimuli (although conditional on the presence of simultaneous ipsilesional stimuli) might be mediated by a deficit of auditory attention. The "representational shift" of sounds which, differently from the shift in the visual modality as inferred by Toraldo and Reverberi (2004), was towards the *ipsi*lesional side and seemed to be constant across stimulus positions, might be interpreted in terms of a shift of the reference frame towards the *contra*lesional side.[7]

## "Shifts" vs. "omissions" in motor programming: Directional hypo*kinesia* vs. directional hypo*metria*?

A considerable amount of work has been carried out in the last three decades concerning the distinction between "perceptual" and "premotor" factors of unilateral neglect. Since Heilman and Valenstein's (1979) seminal paper (see also Heilman et al. 1985), the idea that omission of contralesional details in overt behaviour might derive from missing motor programming rather than from defective "perception" of those same details has enjoyed increasing success, leading especially to several attempts to disentangle the two components (see e.g. Harvey et al. 2002; Adair et al. 1998; Toraldo et al. 2004, for review). While the set of empirical results collected on this putative distinction is extremely rich, little or no work has been devoted to theoretical modeling. In most studies of "perceptual/premotor neglect" the relationship between experiment and underlying cognitive model has been left to vague intuition, quite simply because a cognitive model is entirely missing. This lack of theoretical work has led to a number of consequences. First, since without models no predictions can be derived, no comparison between predictions and empirical evidence can be carried out. Hence, the set of (often brilliant) experiments about perceptual/premotor neglect in the literature lack the indispensable characteristic of speaking in favour, or against, a given theory of the phenomena involved. Second, without a model of the involved cognitive architecture – a model of what one is trying to measure – it is impossible to derive a *theoretically meaningful* measure of the two putative deficits, perceptual and premotor neglect.[8] Due to the lack of a reference functional model, each and every lab invented different means of measuring the two components – again, quite brilliant intuitions, but entirely incomparable to each other: Isolated pieces of evidence swimming in a theoretical vacuum. Without agreement about what is to be measured (which in turn requires at least momentary agreement about how the system works) normally it is of little surprise that the correlation between different techniques of perceptual / premotor disentanglement is essentially zero (Harvey et al. 2002; Harvey & Olk 2004): most likely they are measuring different sets of functions of the cognitive architecture.

Yet well-developed theoretical grounds on which to build a cognitive model of the perceptual/premotor dichotomy are available. For instance, Milner and Goodale's

(1995) "perception/action" general theory can provide a solid reference basis, given that it has been supported and refined by one of the most successful neuropsychological research programmes ever.

Our purpose here is to sketch a model that relies on Milner and Goodale's (1995) general framework and implements perceptual and premotor neglect. Milner and Goodale (1995; see also Milner & Harvey, this volume) proposed that the dorsal (occipito-parietal) pathway processes visual information for direct motor action towards, or away from, objects. The ventral (occipito-temporal) pathway instead subserves "perception", in the sense of every visual computation useful for a delayed response. Thus visual memory, recognition, reading, etc. would all be ventral-stream mediated processing. Crucially, sooner or later both streams should converge towards a system of premotor programming. The reason for assuming this convergence is that the ventral stream *can* guide motor behaviour if task demands "prevent" the dorsal stream from taking control. In a seminal study, Milner et al. (1999, 2001) showed that, consistently with their model, patients with optic ataxia (dorsal stream lesions) could successfully (and counter-intuitively!) point to a visual target, provided that this had *disappeared* at least 2 secs before movement initiation. This puzzling result had been predicted on grounds of the authors' general theory. According to it, the dorsal stream, specialized for online motor control, can only act on visible objects. To "remember" the position of a disappeared object (encoded in allocentric terms with reference to a relevant landmark, e.g., the screen border) is by definition a ventral-stream task. Since the latter stream was spared in optic ataxia patients, the prediction was of paradoxically more accurate pointing when the target had disappeared.

This elegant studied clarified that the ventral stream does have access (by converging with the dorsal stream) to premotor systems.

*The "premotor map"*

We will now specify the nature of some cognitive operations done by the visuo-motor (dorsal) and the perceptual (ventral) streams. For clarity, we will focus on the processing of a simulus's position. The *visuo-motor* stream can be assumed to compute the position of an object in *hand-centred coordinates*, starting from its retinal coordinates, through integration with vestibular and proprioceptive signals about the relative position of head, trunk, and limb. The final output of the dorsal stream processing might thus be a spatial representation in hand-centred co-ordinates ("premotor map"); each point of this map would constitute a potential "motor aim". In other words, a "dot" in the map would correspond to a premotor programme for reaching an object, it would specify the vector that the hand should travel across to reach the object. Suppose (in a simplified two-dimensional case) that the dot is in the position (0, +12) of the premotor map. The simple *presence* of that dot in the map would correspond to a premotor programme for the hand to move 12 units towards the right (see also Khan et al. 2005, "reach space").

Suppose that this premotor map is the locus of convergence between dorsal and ventral stream processing – in other words, the ventral stream could generate, as an

output, a hand-centred encoding of a (remembered, or imagined) object position. An initial prediction of this model would be that damage to a region of the premotor map would cause failure to initiate hand movements towards the corresponding region of physical space, irrespective of whether the task is visuo-motor (involving the dorsal stream) or "perceptual" (involving the ventral steam). Another straightforward consequence of this model is the way of measuring the degree of damage in the map. Since the map is (by assumption) a hand-centred co-ordinate system, local damage to a map region would be measured in terms of the probability that a reaching movement is omitted, or of the latency of performed reaching movements. Suppose also that the map can be "damaged" with a gradient along the horizontal dimension, the degree of damage in this case would be measured as a left-right asymmetry in the latency of reaching movements, according to the starting position of the hand. If the premotor map is damaged on its *left* side, reaching towards a central target would be slower (or performed less often) when the hand starting position is to the *right* of the target than when it is to the left. This asymmetry, we think, might be considered as a theoretically-founded operational definition of "premotor neglect".

The distinction between probability to omit a movement altogether and latency of a movement (see also Mattingley et al. 1998) is also worth discussing. One theoretical possibility is that lesion to some region of the premotor map diminishes the amount of neural activity triggered by a stimulus presented in that region. If the residual activity is below some threshold, no movement would be performed at all; otherwise, it might be performed but with some delay due to the need to "accumulate activation" up to some critical point, as in many connectionist models. The straightforward prediction of such a view is that of a high correlation between omission probability and latency of actually performed movements – an open question.

However, the most interesting consequence of the premotor map model is that in principle, points on the map can be omitted, or *misplaced*. Consistent with the omission/shift dichotomy proposed in this Chapter, it might well be that movements are dropped/slow ("motor aims" are omitted, or diminished in their level of activation in the premotor map), or else misdirected ("motor aims" misplaced in the premotor map). Even though this idea was intrinsic in some early terminology (e.g. hypo*kinesia* vs. hypo*metria*; Meador et al. 1986), the vast literature on "premotor neglect" (or "directional hypokinesia", the most used term) seems to assume that a unique mechanism underlies all phenomena. Yet different labs used different tasks, often appropriate for recording just one of the two possible error types, omission vs. misdirection of reaching movements. For instance, Heilman and Valenstein (1979), like the majority of researchers in the following decades, used the bisection task in which just errors of movement misdirection can be elicited; by contrast, Tegner and Levander (1991), like others, employed a cancellation task in which (mostly) omission errors are elicited. To our knowledge, explicit dissociations between movement misdirection and omission have not yet been described.

If the model of the premotor map were further specified, perhaps by means of explicit connectionist simulations, it would be possible to predict precise patterns

of association/dissociation between movement misdirection and movement omission/delay.[9] Since we are not aware of any such modelling and/or empirical work, we leave these points as open questions.

*The "perceptual map"*
Milner and Goodale's (1995) general framework also contains a suggestion as where in the cognitive system "perceptual neglect" might be located. These authors argued (Section 7.2) that two different, co-ordinated, attentional systems might select information that enters the dorsal (visuo-motor) and the ventral (perceptual) streams respectively. The attentional systems would filter out information that is irrelevant to the task currently carried out. As we have conjectured in the previous Section ("Shifts vs. omissions in (perceptual) spatial tasks"), shifts of visual features within an allocentric map (ventral stream) are likely to be functionally independent of omissions. Our proposal is that *attentional* processes would, when damaged, induce omission of details from downstream spatial representations (and therefore empirically observable "neglect", on e.g. visual search or detection tasks). Shifts within spatial representations might instead be caused by sensory deprivation (hemianopia; see the Section "The shift (or misprojection) model"). Consistent with this view, the purest measures of "perceptual neglect" would be provided by "attentional" tasks such as Posner et al.'s (1984) paradigm.[10]

## Concluding remarks

In this Chapter we presented evidence in favour of the general assumption that processes leading to the detection of stimuli are functionally separate from those leading to their localization. Most parsimoniously and consistent with successful research programmes, we proposed that *omissions* – failure in the detection mechanisms that "draw" the stimulus in some spatial representation – might follow attentional impairment (on the input side) or premotor impairment (on the output side), while representational *shifts* – mislocalization of stimuli – might be the consequence (at least in the visual modality) of sensory deprivation.

*A comment on the line bisection task as a diagnostic tool/selection criterion*
The time-honoured line bisection task is quite obviously influenced both by failure to detect contralesional portions of the line, and by representational shifts of the line's relevant features – its endpoints. Moreover, "anisometry", which we attributed to a perturbation of the ventral stream's size estimation processing, also has a role in bisection as this task requires matching of the perceptual sizes of the two hemi-lines. Bisection is also very sensitive to visual field defects, with hemianopes typically showing contralesional deviations. In an even more complex interaction, (ipsilesional) bisection errors are four times larger in patients with neglect and hemianopia than in patients

with neglect alone (Doricchi & Angelelli 1999). Bisection is also likely to require visual imagery: Subjects might generate an imaginery point and then move it mentally across the line till it splits the line in two parts that, maybe by mental shift of one line part over the other, overlap perfectly. After that, a motor act is to be performed towards the stopped imaginery point, thus also calling into play visuo-motor control. As if this were not enough, bisection is a psychophysical task: There is a region around the subjective centre, whose size depends on the magnitude of the Weber fraction, within which every position is perceived as splitting the line in identical parts (Marshall & Halligan 1989). Thus, also processes influencing the magnitude of the Weber fraction are likely to have an impact over bisection performance.

In spite of this impressive amount of evidence, demonstrating the "impure" nature of the bisection task in functional terms, the use of it in both clinical practice (as a diagnostic tool) and research (as a selection criterion for classifying patients as "neglect" vs. "non-neglect") is still very widespread.

In principle, there are three main reasons that would justify the use of a given task in the above contexts. First, a task can be used if it has good diagnostic properties. Second (the weakest reason), a task can be used if it is easy to apply. Third, a task can be used if it successfully reproduces in the lab the spontaneous phenomena (everyday-life "neglect" in this case) that the researcher is trying to study. The usefulness of such a controlled reproduction is that it allows a standardized, repeatable measurement of the phenomenon. A very basic requirement for this reproduction to be meaningful is that the phenomena recorded in the lab have an obvious *empirical similarity* to spontaneously-occurring phenomena.

We argue that none of these three reasons applies to bisection.

(1) A good diagnostic test has both high sensitivity and high specificity. While perhaps quite sensitive, bisection is extremely non-specific, as in fact it measures a huge variety of cognitive functions (see list above).

(2) Bisection is at most as easy to apply as classical cancellation tasks, with the latter being more specific (although not entirely specific) for the cognitive deficit that researchers are usually trying to measure, i.e. a deficit of visuo-spatial attention.

(3) The set of spontaneous phenomena researchers refer to when using bisection go under the label of "neglect". As the literal meaning of the word suggests ("to leave out", to "omit"), these phenomena are everyday-life situations in which patients fail to react to stimuli located on one side. Failure to react to contralesional targets on a *cancellation* task has an unambiguous similarity to such prototypical situations, and therefore constitutes a valid (and repeatable) reproduction of them in the lab. No such similarity can instead be found between bisection errors and everyday-life omission phenomena. What is *omitted* in line bisection? That a portion of the line is "omitted" from processing is not an empirical fact: It is a hypothesis. Therefore, bisection can in no way be considered as an "experimental reproduction" of the set of spontaneous empirical phenomena labelled as "neglect".[11]

The overuse – and misuse – of the line bisection task might be due to an irreducible semantic association ("neglect" – "bisection"), which survived every empirical falsification (like e.g. the already classic double dissociation between cancellation and bisection, Halligan & Marshall 1992), no matter how fine the analysis became in showing that bisection requires processes that have nothing to do with those inducing the behavioural omissions labelled as "neglect". The neglect-bisection semantic association has also resisted the attacks of intuitive reasoning: the bisection task explicitly contains the request to make a *metric* judgment, so its inadequacy as a tool for assessing omission behaviour in a pure way is clear already at this gross task analysis.

Beyond diagnosis and classification, bisection also fascinated theoreticians, sometimes (paradoxically) becoming the main source of evidence that researchers strove to account for in their models of "neglect" (see e.g. Anderson 1996). Part of this phenomenon might be due to the interest bisection *per se* seems to evoke, independently of the functions underlying it. In other words, bisection becomes the object of investigation. In our view, this task-related approach is misleading as it loses the real target of neuropsychological research, i.e. the human cognitive architecture. A neuropsychological investigation should propose a hypothetical construct of the cognitive architecture, from which predictions are derived that are tested empirically by means of a *variety* of tasks – the more, the better. In this scheme, the nature of the tasks would be determined by the process of prediction-derivation itself, and never chosen a priori.

## Notes

**1.** Also relevant for the omissions/shifts dichotomy is the literature about the dissociation between optic ataxia and neglect; see Milner & Harvey, this volume.

**2.** In the relevant literature, overwhelming confusion emerges from an ambiguous use of the word "neglect"; sometimes this word is used to denote the *behavioural* (empirically observable) finding, e.g., the omission of contralesional targets in visual search; the same word is used elsewhere to denote the *hypothetical* (non-observable) cognitive deficit, e.g., a defective internal representation of space, or defective attentional mechanism, that is supposed to cause the observable phenomena. To avoid confusion in this Chapter, we used the term (visual) "neglect" in its empirical meaning, i.e. referring to the *observable* finding of contralesional omission of details in visual search; instead, the term "attentional disorder" was used referring to the putative cognitive dysfunction ("attention" was chosen as it is sufficiently abstract to avoid eliciting the idea of an observable fact). There are two exceptions in the Chapter which, however, are entirely disambiguated by the context: the expressions "perceptual neglect" and "premotor neglect" refer to *hypothetical* cognitive deficits (and are taken from the literature, see Bisiach et al. 1990); indeed the adjectives "perceptual" and "premotor" clarify the conjectural (non-empirical) nature of the concepts.

**3.** The affected spatial representation was assumed to be allocentric (i.e. presumably implemented in the ventral stream, see Milner & Goodale 1995) because if it had been egocentric (i.e. presumably implemented in the visuo-motor dorsal stream), the illusory "shifts" of visual targets would also have affected reaching movements, with GL reaching out towards the illusory,

and not the real position of stimuli – in other words, GL should have shown some form of optic ataxia, which was not the case.

**4.** As argued by some authors (e.g. Ferber & Karnath 2001; Toraldo & Reverberi 2004), anisometry might be associated with posterior lesions, most likely of relatively early visual areas (see also Irving-Bell et al. 1999); this would explain the frequent association of anisometry with the combination hemianopia-neglect, and the relatively low frequency of dissociations (like in GL).

**5.** Some confusion has arisen because the term "auditory neglect" has sometimes been used referring to auditory *extinction* on dichotic tasks (see Beaton & McCarthy 1995, and related papers for throughout discussion).

**6.** One of the patients, ES, had a performance compatible with a strong response bias; the interpretation of data from the other patient with the same dissociation, A.J., is more straightforward (but see comments by the author themselves, p. 684).

**7.** If the reference frame of the representation (e.g., the subjective "straight ahead" in egocentric space) is assumed to be shifted *contra*lesionally, stimuli should be misperceived as more *ipsi*lesional than they really are. See Karnath (1997, 1999) for discussion of this complex topic.

**8.** An often "neglected" methodological principle is that no measure or measuring technique is appropriate in absolute terms – the appropriateness of a measure entirely depends on a theory of reference. The existence of an underlying theoretical model is a necessary condition for providing any measure with meaning and thus justifying its use. If no model is provided, there is no way of judging the appropriateness of a given measure (see e.g. Toraldo et al. 2004, who recently tried to propose a theoretically-based measure of perceptual and response biases in neglect).

**9.** Optic ataxia, strictly speaking, is a deficit of movement misdirection (under visual control). However, errors in optic ataxia do not depend on a hand-centred coordinate system, but rather, on a retinocentric system (errors are made towards the fixation point). Thus the deficit should be attributed to an earlier stage in visuo-motor transformation along the dorsal stream.

**10.** We agree that this position might seem a step backward after the well-known disputes about the (putative) "representational/attentional" distinction (Bisiach 1993). Yet again, while much time has been spent in discussing the philosophical implications of neglect, relatively too little time has been devoted to deriving experimental predictions from valuable models, as e.g. Posner et al.'s (1984). As Feynman (1998: 77) clarifies, if some models (ideas) are available, "[. . .] whether we *like* them or we do *not* like them is an irrelevant question. The only relevant question is whether the ideas are consistent with what is found experimentally" (see also Lakatos 1978). A more delicate point is how to disentangle attention from implicit "ocular premotor" components in "attentional" tasks. According to Rizzolatti et al.'s (1987) premotor theory of attention, such disentanglement is impossible by definition: "Spatial attention" and "premotor program of an eye movement" are synonyms. According to Treisman's (Treisman & Gelade 1980; Treisman 1982) theory, spatial attention and eye movement programming are functionally separate, with attention subserving perceptual binding. In our view, no a-priori prejudice against one or the other theory should be taken: If the two theories made different predictions on a set of relevant experiments, evidence from these should act as the ultimate judge.

**11.** Furthermore, the hypothesis that patients who misbisect lines are omitting a contralesional portion of the lines at some processing level is far from accepted. Many accounts do not state that something is omitted from processing (e.g., the hypotheses of directional hypo*metria*, of anisometry, of representational shifts of the contralesional endpoint, of a pathologically increased Weber fraction, etc.).

## References


Adair, J. C., Na, D. L., Schwartz, R. L., & Heilman, K. M. (1998). Analysis of primary and secondary influences on spatial neglect. *Brain and Cognition, 37*, 351–367.

Anderson, B. (1996). A mathematical model of line bisection behaviour in neglect. *Brain, 119*, 841–850.

Azzopardi, P., & Cowey, A. (1997). Is blindsight like normal, near-threshold vision? *Proceedings of the National Academy of Science, USA, 94*, 14190–14194.

Azzopardi, P., & Cowey, A. (1998). Blindsight and visual awareness. *Consciousness and Cognition, 7*, 292–311.

Beaton, A., & McCarthy, M. (1995). On the nature of auditory neglect: A reply to Hugdahl and Wester. *Brain and Language, 48*, 351–358.

Bellmann, A., Meuli, R., & Clarke, S. (2001). Two types of auditory neglect. *Brain, 124*, 676–687.

Bisiach, E. (1993). Mental representation in unilateral neglect and related disorders: The twentieth Bartlett Memorial Lecture. *Quarterly Journal of Experimental Psychology, 46*, 435–61.

Bisiach, E., Cornacchia, L., Sterzi, R., & Vallar, G. (1984). Disorders of perceived auditory lateralization after unilateral lesions of the right hemisphere. *Brain, 107*, 37–52.

Bisiach, E., Geminiani, G., Berti, A., & Rusconi, M. L. (1990). Perceptual and premotor factors of unilateral neglect. *Neurology, 40*, 1278–1281.

Bisiach, E., Pizzamiglio, L., Nico, D., & Antonucci, G. (1996). Beyond unilateral neglect. *Brain, 119*, 851–857.

Bisiach, E., Ricci, R., & Modona, M. N. (1998). Visual awareness and anisometry of space representation in unilateral neglect: A panoramic investigation by means of the line extension task. *Consciousness and Cognition, 7*, 327–355.

Bisiach, E., Rusconi, M. L., Peretti, V. A., & Vallar, G. (1994). Challenging current accounts of unilateral neglect. *Neuropsychologia, 32*, 1431–1434.

Doricchi, F., & Angelelli, P. (1999). Misrepresentation of horizontal space in left unilateral neglect. Role of hemianopia. *Neurology, 52*, 1845–1852.

Doricchi, F., Galati, G., DeLuca, L., Nico, D., & D'Olimpio, F. (2002a). Horizontal space misrepresentation in unilateral brain damage I. Visual and proprioceptive-motor influences in left unilateral neglect. *Neuropsychologia, 40*, 1107–1117.

Doricchi, F., Guariglia, P., Figliozzi, F., Solvetti, M., Bruno, G., & Gasparini, M. (2005). Causes of cross-over in unilateral neglect: Between-group comparisons, within-patient dissociations and eye movements. *Brain, 128*, 1386–1406.

Doricchi, F., Onida, A., & Guariglia, P. (2002b). Horizontal space misrepresentation in unilateral brain damage II. Eye-head centered modulation of visual misrepresentation in hemianopia without neglect. *Neuropsychologia, 40*, 1118–1128.

Faglioni, P., Scotti, G., & Spinnler, H. (1971). The performance of brain-damaged patients in spatial localization of visual and tactile stimuli. *Brain, 94*, 443–454.

Ferber, S., & Karnath, H.-O. (2001). Size perception in hemianopia and neglect. *Brain, 124*, 527–536.

Feynman, R. P. (1998). *Six not-so-easy pieces*. London: Penguin.

Halligan, P. W., Burn, J. P., Marshall, J. C., & Wade, D. T. (1992). Visuo-spatial neglect: Qualitative differences and laterality of cerebral lesion. *Journal of Neurology, Neurosurgery and Psychiatry, 55*, 1060–1068.

Halligan, P. W., & Marshall, J. C. (1989). Line bisection in visuo-spatial neglect: Disproof of a conjecture. *Cortex, 25*, 517–21.

Halligan, P. W., & Marshall, J. C. (1992). Left visuo-spatial neglect: A meaningless entity? *Cortex, 28*, 525–35.

Harris, J. A., Thein, T., & Clifford, C. W. G. (2004). Dissociating detection from localization of tactile stimuli. *Journal of Neuroscience, 24*, 3683–3693.

Harvey, M., Krämer-McCaffery, T., Dow, L., Murphy, P. J. S., & Gilchrist, I. D. (2002). Categorisation of "perceptual" and "premotor" neglect patients across different tasks: Is there strong evidence for a dichotomy? *Neuropsychologia, 40*, 1387–1395.

Harvey, M., & Olk, B. (2004). Comparison of the Milner and Bisiach Landmark Tasks: Can neglect patients be classified consistently? *Cortex, 40*, 659–665.

Heilman, K. M., Bowers, D., Coslett, H. B., Whelan, H., & Watson, R. T. (1985). Directional hypokinesia: Prolonged reaction times for leftward movements in patients with right hemisphere lesions and neglect. *Neurology, 35*, 855–859.

Heilman, K. M., & Valenstein, E. (1972). Auditory neglect in man. *Archives of Neurology, 26*, 32–35.

Heilman, K. M., & Valenstein, E. (1979). Mechanisms underlying hemispatial neglect. *Annals of Neurology, 5*, 166–170.

Hunter, J. P., Katz, J., & Davis, K. D. (2003). The effect of tactile and visual sensory inputs on phantom limb awareness. *Brain, 126*, 579–589.

Irving-Bell, L., Small, M., & Cowey, A. (1999). A distortion of perceived space in patients with right-hemisphere lesions and visual hemineglect. *Neuropsychologia, 37*, 919–925.

Ishiai, S., Furukawa, T., & Tsukagoshi, H. (1989). Visuospatial processes of line bisection and the mechanisms underlying unilateral spatial neglect. *Brain, 112*, 1485–1502.

Karnath, H.-O. (1997). Spatial orientation and the representation of space with parietal lobe lesions. *Philosophical Transactions of the Royal Society of London (B), 352*, 1411–1419.

Karnath, H.-O. (1999). Spatial orientation and the representation of space with parietal lobe lesions. In N. Burgess, K. Jeffery, & J. O'Keefe (Eds.), *The hippocampal and parietal foundations of spatial cognition* (pp. 50–66). New York: Oxford University Press.

Khan, A. Z., Pisella, L., Vighetto, A., Cotton, F., Luauté, J., Boisson, D., Salemme, R., Crawford, J. D., & Rossetti, Y. (2005). Optic ataxia errors depend on remapped, not viewed, target location. *Nature and Neuroscience, 8*, 418–420.

Lakatos, I. (1978). *The Methodology of Scientific Research Programmes*. Cambridge, UK: Cambridge University Press.

Lebedev, M. A., Mirabella, G., Erchova, I., & Diamond, M. E. (2000). Experience-dependent plasticity of rat barrel cortex: Redistribution of activity across barrel-columns. *Cerebral Cortex, 10*, 23–31.

Marshall, J. C., & Halligan, P. W. (1989). When right goes left: An investigation of line bisection in a case of visual neglect. *Cortex, 25*, 503–515.

Mattingley, J. B., Corben, L. A., Bradshaw, J. L., Bradshaw, J. A., Phillips, J. G., & Horne, M. K. (1998). The effect of competition and motor reprogramming on visuomotor selection in unilateral neglect. *Experimental Brain Research, 120*, 243–256.

McIntosh, R. D., McClements, K. I., Dijkerman, H. C., & Milner, A. D. (2004). "Mind the gap": The size-distance dissociation in visual neglect is a cueing effect. *Cortex, 40*, 339–346.

Meador, K. J., Watson, R. T., Bowers, D., & Heilman, K. M. (1986). Hypometria with hemispatial and limb motor neglect. *Brain, 109*, 293–305.

Milner, A. D., Dijkerman, H. C., Pisella, L., McIntosh, R. D., Tilikete, C., Vighetto, A., & Rossetti, Y. (2001). Grasping the past: Delay can improve visuomotor performance. *Current Biology, 11*, 1896–1901.

Milner, A. D., Harvey, M., Roberts, R. C., & Forster, S. V. (1993). Line bisection errors in visual neglect: Misguided action or size distortion? *Neuropsychologia, 31*, 39–49.

Milner, A. D., & Goodale, M. A. (1995). *The Visual Brain in Action*. Oxford: Oxford University Press.

Milner, A. D., Paulignan, Y., Dijkerman, H. C., Michel, F., & Jeannerod, M. (1999). A paradoxical improvement of misreaching in optic ataxia: New evidence for two separate neural systems for visual localization. *Proceedings of the Royal Society of London (B), 266*, 2225–2229.

Posner, M. I., Walker, J. A., Friedrich, F. J., & Rafal, R. D. (1984). Effects of parietal injury on covert orienting of attention. *Journal of Neuroscience, 4*, 1863–1874.

Rizzolatti, G., Riggio, L., Dascola, I., Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favour of a premotor theory of attention. *Neuropsychologia, 25*, 31–40.

Shallice, T. (1988). *From neuropsychology to mental structure*. Oxford: Oxford University Press.

Tegner, R., & Levander, M. (1991). Through a looking glass. A new technique to demonstrate directional hypokinesia in unilateral neglect. *Brain, 114* 1943–1951.

Toraldo, A. (1996). *Ipotesi distorsiva per la negligenza spaziale unilaterale ("Distortion" hypothesis for unilateral spatial neglect)*. Unpublished degree dissertation, Padua University.

Toraldo, A. (2003). A ruler for measuring representational space. *Visual Cognition, 10*, 567–603.

Toraldo, A., McIntosh, R. D., Dijkerman, H. C., & Milner, A. D. (2004). A revised method for analyzing neglect using the Landmark Task. *Cortex, 40*, 415–431.

Toraldo, A., & Reverberi, C. (2004). Misprojection of landmarks onto the spatial map. *Brain and Cognition, 55*, 479–489.

Treisman, A. (1982). Perceptual grouping and attention in visual search for features and for objects. *Journal of Experimental Psychology: Human Perception and Performance, 8* 194–214.

Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology, 12*, 97–136.

Weiskrantz, L., Warrington, E. K., Sanders, M. D., & Marshall, J. C. (1974). Visual capacity in the hemianopic field following a restricted occipital ablation. *Brain, 97*, 709–728.

# Name index


**A**

Aarsland, D. 243
Abbott, L. F. 89, 331
Abrahams, S. 86
Acker, J. D. 209
Ackerman, P. L. 116
Acredelo, L. P. 40
Acuca, C. 297
Adair, J. C. 406
Adamovich, S. V. 310
Adams, J. K. 120
Adelstein, T. B. 231
Agazzi, D. 16, 106, 174
Aglioti, S. M. 337, 368, 373
Agnoli, E. 262
Aguirre, G. K. 87, 88, 114, 261, 286, 299
Ahissar, M. 107
Aimard, G. 337
Ajuriaguerra, J. 242, 246
Akhavein, R. 157
Ala, T. A. 243, 248, 249
Albert, M. L. 24, 246
Alderton, D. L. 18
Aleman, A. 114, 115
Alexander, G. A. 305
Alexander, M. P. 343, 350, 353
Allamano, N. 16
Allen, P. A. 221
Allport, A. 301
Alpert, N. M. 111
Alsop, D. C. 261
Altmann, G. T. M. 121
Always, D. 70
Amunts, K. 349
Andersen, R. A. 297, 298, 302, 304, 382, 383, 386, 391
Anderson, B. 41
Anderson, J. R. 103, 109, 139, 261
Anderson, N. D. 187
Anderson, S. W. 247
Andrade, J. 40, 110, 111, 123, 144, 204, 216
André-Deshays, C. 90
Andres, M. 163
Andrew, C. M. 240
Angelelli, P. 349, 350, 351, 352, 353, 354, 355, 356, 399, 410
Angelini, R. 240, 241
Anllo-Vento, L. 76
Antonietti, A. 112
Antonucci, G. 343, 345, 349, 350, 351, 352, 353, 354, 355, 356, 365, 366, 398, 399
Arbuckle, T. 221
Archibald, Y. M. 301, 302, 305
Ardila, A. 241
Arditi, A. 115
Arenberg, D. 188, 190
Arleo, A. 89
Arnell, K. M. 122
Aronen, H. J. 70
Arrigoni, C. 242
Arthur, G. 7
Asada, T. 249
Asselman, P. 71
Aurora, S. K. 349
Averbeck, B. B. 249
Avons, S. E. 141
Awh, E. 114, 174
Ayres, T. J. 174
Azzopardi, P. 396

**B**

Baars, B. J. 123, 124
Babcock, H. 7
Babcock, R. L. 188, 193, 194, 196, 197
Babinski, J. 367
Bachtold, D. 166
Backman, L. 196
Baddeley A. D. 15, 16, 18, 21, 27, 28, 89, 101, 102 103, 104, 105, 107, 110, 111, 116, 118, 119, 123, 124, 139, 140, 142, 143, 145, 146, 147, 173, 178, 187, 192, 203, 204, 216
Baizer, J. S. 297
Bak, T. H. 243
Bakker, N. H. 90
Bálint, R. 298, 299
Ball, T. M. 10, 51, 52, 57, 58, 62, 66, 108
Ballard, C. 243
Ballard, D. 114
Baloh, R. W. 90
Baltes, M. M. 189
Baltes, P. B. 189, 196, 197, 215
Banai, K. 107
Bandinelli, S. 70
Bandura, M. 268
Bar, M. 123
Barbieri, S. 337, 373
Barett, A. 16
Barnard, P. J. 114, 139
Barnes, C. A. 284
Barrash, J. 285
Barratt, P. E. 11
Barrett, A. M. 17, 203, 205
Barrios, M. V. 120
Barrodale, P. 349
Barsalou, L. W. 261
Bartolomeo, P. 381
Barton, M. 241
Bassani, C. 24
Batista, A. P. 298
Battaglini, P. P. 382, 387, 388, 389, 391
Battelli, L. 15
Baumgartener, G. 349
Baumuller, M. 166
Baylis, G. C. 381
Becker, S. 86, 87, 88, 89
Beers, van, R. J. 91
Behrmann, M. 114, 304, 338, 346, 348, 381
Beier, M. E. 116
Belleville, S. 187, 248, 252

Bellmann, A. 405, 406
Bellocci, S. 106
Bellugi, U. 103
Belotti, M. 23, 32
Benali, K. 221
Bender, M. B. 324
Benedict, R. H. 223
Benjamin, A. S. 187
Benjamin, J. 351
Benke, T. 339
Benowitz, L. I. 242
Benson, D. F. 241, 243, 248, 299
Benson, P. J. 309
Bent, N. 276
Benton, A. L. 239, 240, 241
Berbaum, K. 113
Berberovic, N. 311
Berch, D. B. 9, 18, 142, 160, 181
Berembaum, S. A. 106
Bergeron, C. 243
Berkinblit, M. B. 310
Bernard, B. A. 241
Bernardini, B. 288, 372
Berthoz, A. 85, 86, 88, 89, 90, 91, 94, 221, 289, 391
Berti, A. 75, 328, 337, 338, 347, 365, 366, 367, 368, 369
Berto, R. 24
Bertuccelli, B. 115
Beschin, N. 119, 174, 243, 249, 365, 366
Betts, G. H. 4, 9, 10
Bianchetti, A. 242, 247, 248
Bignamini, L. 69, 75
Bilder, R. M. 88
Binder, J. 351
Binetti, G. 242, 247, 248
Binkofski, F. 372
Binks, S. 114
Birkett, D. P. 223
Bisch, S. 284
Bishop, D. 142
Bisiach, E. 69, 74, 75, 76, 78, 79, 165, 287, 288, 301, 337, 338, 339, 342, 343, 348, 345, 351, 353, 354, 365, 366, 368, 369, 370 , 371, 397, 398, 399, 405
Bizzi, E. 181
Bjoertomt, O. 75
Black, F. W. 241, 390
Black, S. E. 77, 231, 243, 381
Blangero, A. 306
Blanton, M. 391
Blaxton, T. 114
Bles, W. 90
Block, E. W. 90, 91, 94
Bloise, S. M. 189, 191
Blonder, L. X. 77
Bly, B. M. 113
Boake, C. 7
Bohbot, V. D. 285
Boisson, D. 165, 288, 299, 305, 306, 308, 309, 337
Bollen, E. L. E. M. 232, 233
Bonnard, M. 94
Bonneau, D. 209
Bonnerot, V. 10
Boone, K. B. 243, 246
Boring, E. G. 108, 340
Borod, J. C. 242
Borst, G. 17, 59, 62
Bossini, S. 158, 159, 160, 166, 168
Bottini, G. 246, 288, 337, 338, 366, 368, 369, 370, 371, 372, 373
Boucart, M. 353
Boulanouar, K. 304
Bouras, C. 248
Bowers, D. 77, 408
Bowie, T. 221
Bowman, M. 285
Boyle, M. O. 116
Braak, E. 232
Braak, H. 232
Bradshaw, J. A. 340, 347, 348, 350, 353, 354, 408
Bradshaw, J. L. 340, 347, 348, 350, 353, 354, 408
Braga, C. 23, 32
Brammer, M. J. 240
Brandimonte, M. A. 113, 142
Brands, A. M. A. 223, 225
Brechmann, M. 301
Bremmer, F. 333, 382
Bressler, K. 364
Breveglieri, R. 387, 391
Brewer, W. F. 261
Breznen, B. 391
Bricogne, S. 10, 65
Bricolo, E. 161
Briggs, S. D. 206, 209
Brighina, F. 74, 75, 76, 78, 79, 349
Bright, J. E. H. 121
Briscogne, S. 86
Brockmole, J. R. 112
Brodie, E. E. 365, 366
Bromiley, A. 204
Brooks, B. S. 373
Brooks, L. R. 102, 113, 142
Brovelli, A. 391
Brown, G. D. A. 21, 104
Brown, H. D. 206, 216
Brown, J. 147
Brown, M. M. 311
Brown, P. 262
Brugger, P. 165, 166
Bruno, G. 403, 404
Bruyer, R. 188, 206, 207, 216
Bryant D. 196
Bryden, M. P. 10, 106, 269
Brysbaert, M. 160, 163, 168
Buchanan, M. 114
Buchel, C. 87, 88
Buckner, R. L. 145
Bucks, R. S. 223, 224, 231
Buffa, D. 74, 78
Buhler, R. 74
Bulgarelli, C. 338, 343
Bullier, J. 297
Bullmore, E. T. 240
Bunting, M. F. 145, 146
Bunton, L. J. 17, 18
Burgess, N. 86, 87, 88, 89, 90, 125
Burns, A. 190, 243
Burpee, A. 276
Burson, L. L. 115
Burton, L. J. 262, 263
Butefisch, C. 71
Butler, A. J. 311
Butters, N. 242, 246, 248, 249
Butterworth, B. 163, 168
Buxbaum, L. J. 305, 363
Byrd, M. 210
Byrne, E. J. 224, 243, 248

C

Caine, D. 248
Calcaterra, J. A. 115
Caldwell, C. B. 77, 381, 390
Caldwell, J. I. 228, 229
Calhoun, J. 343, 355
Calise, C. 241, 246, 251
Caltagirone, C. 16, 70, 71, 72, 73, 76, 78, 114, 241, 242
Calvanio, R. 16, 106, 174, 262, 368
Calzavara, R. 391
Camarda, R. 366
Caminiti, R. 297
Cantor, J. 103
Caplan, J. B. 87, 88

Cappa, S. F. 242, 247, 248, 350, 352, 353, 354, 355, 356, 372, 373
Cappelletti, J. Y. 364
Caramia, M. D. 71
Cardebat, D. 304
Cardullo, F. M. 91
Carella, J. 187
Carey, D. P. 301, 302, 304, 305, 310
Carfantan, M. 16
Carlesimo, G. A. 16, 106, 114, 241, 242
Carlomagno, S. 246
Carlson, R. A. 122
Caroli, M. G. 23, 32
Carpenter, P. A. 21, 23, 105, 114, 262
Carper, M. 242
Carreiras, M. 15
Carson, R. G.
Carson, R. E. 114
Cartright, D. S. 120
Carullo, J. J. 103
Carver, C. S. 120
Case, R. D. 21
Castel, A. D. 162
Castiello, U. 308
Cattaneo, Z. 42, 43, 115
Cattel, R. B. 18
Caufield, K. 340, 348
Cavallini, E. 106, 107, 181, 194, 195, 197
Cavanaugh, J. C. 260
Cave, C. B. 16
Celani, M. G. 338, 372
Cesa-Bianchi, M. 16, 106, 174
Chafee, M. V. 249
Chajzyck, D. 122
Chalfonte, B. L. 189, 191, 222, 226, 227
Chalmers, D. J. 120
Chalmers, P. 143
Chambers, C. D. 74, 78, 113
Changeux, J. P. 122
Chapman, R. 103
Charade, O. 90
Charles, N. 337
Charlot, V. 208
Chatterjee, A. 114, 343, 346, 353, 355
Chen, J. 23, 190, 191
Chen, R. 71
Cherrier, M. M. 231
Cherry, K. E. 191, 222
Chevignard, M. 251
Chiacchio, L. 240, 241, 242, 243, 246
Chieffi, S. M. 301
Chin, J. 247
Chiu, C. Y. 122
Choate, P. A. 17
Chokron, S. 381
Chong, C. D. R. 349, 355
Christie, D. F. M. 140, 141, 142
Chronicle, E. P. 349
Chung, C. S. 113
Chute, D. L. 246, 249
Cicinelli, P. 70, 71, 72, 73, 78, 115
Cipolotti, L. 86, 87
Clark, A. S. 85
Clark, J. M. 106
Clark, V. P. 114
Clarke, K. 328, 330, 405, 406
Clavagnier, S. 311
Clifford, C. W. G 396, 397
Cloud, P. S. 246, 248
Coakley, D. 243, 249
Coates, R. O. 19
Cocchini, G. 119, 139, 174
Cocude, M. 12, 53, 54, 55, 62, 63, 110, 208
Codina, M. 115
Coen, R. F. 243, 249
Cohen, J. D. 106, 122
Cohen, L. G. 70
Cohen, L. 157, 158, 163, 354, 355
Cohen, T. 231
Colby, C. L. 324, 325
Coleman, M. J. 114
Coleman, R. J. 305
Collerton, D. 243
Collett, T. S. 284
Collett, M. 284
Collewijn, H. 90
Collins, M. 7
Colombo, M. R. 75, 353
Committeri, G. 88, 89
Conchiglia, G. 243, 246
Connolly, J. D. 302
Connor, C. E. 353
Conrad, R. 104
Conson, M. 247
Conway, A. R. A. 116, 117
Conway, M. A. 143, 144
Cook, S. 114
Cooney, R. 221
Cooper, L. A. 19, 108, 144
Corben, L. A. 408
Cordes, J. 248
Coren, S. 340, 353, 355
Corkin, S. 248
Cormack, F. 243
Cornell, E. L. 7
Cornet, J. A. 156
Cornoldi, C. 15, 17, 19, 20, 23, 24, 25, 26, 28, 29, 31, 32, 33, 101, 102, 103, 104, 106, 107, 108, 111, 112, 113, 115, 116, 117, 118, 119, 124, 125, 173, 178, 181, 193, 195, 197, 203, 204, 207, 210, 211
Correra, G. 241, 242, 251
Corsi, P. M. 9, 16, 18, 19, 22, 23, 27, 142, 176
Cortesi, A. 115
Corwell, B. 71
Casentino, T. 288, 289
Cosentino, S. 246, 249
Coslett, H. B. 247, 287, 305, 363, 364
Cotton, F. 299
Courtney, S. N. 114, 174
Cowan, N. 116, 117, 118, 125, 145, 146
Cowey, A. 15, 69, 75, 348, 366, 396
Coxe, W. W. 7
Craighero, L. 369
Craik, F. I. M. 187, 192, 195, 206, 209, 210, 234, 270
Crane, J. 221
Craver-Lemley, C. 113
Crémieux, J. 90
Crick, F. 124
Cristinzio, C. 240, 241, 242
Critchley, M. 365
Crivello, F. 65, 85, 86, 88, 114
Cronbach, L. J. 263
Crowe, D. A. 249
Cubelli, R. 240
Cuénod, C. A. 10
Culham, J. C. 298, 302, 303, 304
Cumming, N. 125, 243
Cummmings, J. L. 299
Currie, G. 109

**D**

D'Esposito, M. 87, 88, 114, 187, 191, 222, 227, 242, 261, 286, 299
D'Olimpio, F. 399, 403, 404, 405
Dagher, A. 285

Daini, R. 339, 341, 343, 344, 346, 349, 350, 352, 353 354, 355, 356
Dale, A. M. 123, 349, 355
Dalla Porta, F. 364
Dalla Vecchia, R. 31
Daly, P. F. 17, 203, 205
Danckert, J. 299, 302, 311
Daneman, M. 21, 23, 104
Daniel, M. P. 15
Daniele, O. 75, 79
Darling, W. G. 311
Davare, M. 163
Davidson, N. S. 116, 188
Davies-Jones, G. A. B. 302
Davis, G. 345
Davis, K. D. 401
Davis, R. J. 248
Dawson, J. 247
Day, B. L. 71
Day, D. 40
De Beni, R. 107, 108, 111, 112, 113, 115, 203, 204, 207, 208, 210, 211, 213, 214, 216, 270
DeBlois, S. 120
De Bonis, C. 241, 351
De Haan, E. H. F. 15, 16, 40, 4, 114, 115, 221, 224, 229, 233, 240
De Hevia, M. D. 161, 168
De La Sayette, V. 147
De Lillo, C. 181
De Meo, T. 23, 32
De Recondo, J. 302
De Renzi, E. 18, 174, 239, 242, 242, 247, 287, 324, 363
De Ribaupierre, A. 16 , 17, 19
De Vega, M. 112
De Volder, A. 164
De Vos, R. A. 243
De Vries, L. 240
Dean, G. M. 262, 263, 276
Decety, J. 90, 302, 310, 369
Decker, J. 354
Degos, J. D. 354, 355
Dehaene, S. 76, 122, 157, 158, 159, 160, 163, 164, 165, 166, 168, 354, 355
Dehaene-Lambertz, G. 157, 158
Deiber, M. P. 391
Delaney, P. F. 118
Delapaz, R. L. 349
Delis, D. C. 246, 248
Della Corte, M. 368
Della Sala, G. 119
Della Sala, S. 16, 18, 19, 21, 27, 28, 105 , 139, 142, 143, 174, 178, 243, 249, 305
Deloche, G. 156
Delon-Martin, C. 369
DeLuca, L. 399, 403, 404, 405
Demattè, M. L. 325, 328, 329, 330
Démonet, J. -F. 303, 313
Denes, G. 242, 364
Deneve, S. 382, 383
Denis, M. 15, 49, 50, 52, 53, 54, 55, 56, 57, 59, 62, 63, 65, 66, 85, 86, 88, 108, 109, 111, 112, 114, 203, 208
Dennett, D. C. 353
Denney, N. W. 221
Denny-Brown, D. 331, 337
Dent, K. 41, 42
D'Erme, P. 351
Dermen, D. 18
Desgranges, B. 146, 221
Desimone, R. 297
Desmurget, M. 299, 302, 305, 308
DeSouza, J. F. X. 304
Desrocher, M. 229
Detre, J. A. 87, 88, 261
Dew, J. R. 221
DeYoe, E. A. 297
Di Cesare, G. 240, 241, 242
Di Lollo, V. 122
Di Pellegrino, G. 324, 325, 354, 355
Di Russo, F. 301
Di Vesta, F. J. 204
Diamond, M. E. 401
Dick, H. 300
Dickson, D. W. 243
Dienes, Z. 121
Dijkerman, H. C. 298, 299, 301, 303, 304, 307, 310, 312, 313, 345, 351, 401, 407
Dirkx, E. 206, 209, 270
Dittmann-Kohli, F. 215
Dixon, R. A. 188, 196, 215
Dobraski, M. 223
Dodd, M. D. 162
Dolan, R. J. 391
Donadello, E. 33
Donaldson, H. 222
Donnelly, N. 353
Doricchi, F. 77, 349, 351, 354, 381, 390, 391, 399, 401, 403, 44, 405, 410
Dow, L. 342, 348, 350, 406
Drever, J. 7
Driver, J. 78, 300, 323, 324, 328, 330, 333, 345, 381, 381
Dronkers, N. F. 243
Dror, I. E. 17, 191, 203, 205, 206, 207, 261
Dubois, B. 241
Duensing, F. 241
Duff, S. C. 111
Duhamel, J. R. 74, 324, 325, 333, 382
Dulaney, C. L. 40, 122
Dulaney, D. E. 122
Dunbar, K. 122
Duncan, J. 324
Dunchon, A. P. 90
Dunlosky, J. 260, 264, 265, 267, 268, 269, 270, 271, 273 274, 275, 276
Dunn, B. D. 231
Dupont, P. 164
Dupoux, E. 76, 157
Dupui, P. 90
D'Ydewalle, G. 160, 163, 168

E

Eagle, M. N. 267
Easton, R. D. 112
Ebert, P. L. 77, 381, 390
Edwardson, J. A. 243
Egeth, H. E. 353
Ehrlich, L. E. 381, 390
Einstein, G. O. 203, 207, 210
Ejima, A. 246
Ekstrom, A. D. 87, 88
Ekstron, R. B. 18
Elble, R. J. 243, 248
Elderkin-Thompson, V. 246
Elgin, C. Z. 111
Elias, L. 285
Elliott, E. 268
Ellis, N. C. 174
Ellis, N. R. 226
Ellis, S. 366, 368
Ellison, A. 15, 74, 78, 302
Enbar, S. 227
Endo, K. 246
Engelkamp, J. 112
Engle, R. W. 103, 116, 117
Enns, J. T. 122
Epstein, C. M. 305
Epstein, R. 299

Erchova, I. 401
Ericsson, K. A. 116, 118, 119, 125, 260
Erminio, F. 373
Eslinger, P. J. 240
Essik, G. K. 382, 383, 387, 391
Esterman, M. 343, 350, 353
Etard, O. 65, 86
Ettlinger, G. 298
Eustache, F. 147, 221
Evans, D. 103

F
Fadda, L. 242, 242
Fadiga, L. 324
Faglioni, P. 363, 396
Farah, M. J. 16, 18, 50, 106, 120, 174, 261, 262, 363
Farnè, A. 165, 306, 308, 309, 325, 326, 328, 329, 330, 331
Farrell, M. J. 90, 285, 288
Fastame, M. C. 19, 106, 125, 181
Fattori, P. 382, 387, 388, 393
Faugier-Grimaud, S. 298
Feijen, J. 230, 232
Feinberg, T. 77
Felbinger, J. 74
Feldman, J. 260
Feldstein, S. 276
Ferber, S. 77, 302, 348, 354, 399
Ferbert, A. 71
Fernald, G. M. 6
Ferraina, S. 297
Ferrer-Caja, E. 187
Ferrier, D. 298
Ffytche, D. H. 349
Fias, W. 160, 163, 164, 166, 168
Fields, T. A. 87, 88
Fierro, B. 74, 75, 76, 78, 79, 349
Figliozzi, F. 301, 349, 403, 404
Filippi, M. M. 71, 72, 73, 78
Findlay, G. M. 112
Findlay, J. M. 391
Fink, G. R. 75, 333, 339, 352, 353, 391
Finke, R. A. 18, 57, 58, 109, 111, 113, 144, 261
Finney, G. R. 77
Fischer, M. H. 161, 162, 163
Fischl, B. 123, 349
Fleishman, D. A. 232
Fleming, J. 348
Fleming, K. 114
Fleminger, S. 86
Fletcher, W. A. 90, 91, 94
Floyd, M. 210
Flude, B. 125
Fodor, J. A. 109
Fogarty, G. J. 17, 18, 262, 263
Fogassi, L. 324
Fogel, M. L. 241
Foley, E. J. 142, 160
Fontaine, R. 15, 209
Fookson, O. I. 310
Formisano, E. 113
Forster, S. V. 301, 348, 353, 398
Fox, P. T. 373
Foxe, J. J. 349, 350, 355
Foxe, D. M. 349, 355
Frackowiak, R. S. J. 86, 372, 373
Fraenckel, R. 355
Fragassi, N. A. 240, 241, 242, 243, 246
Franchi, G. 324
Franklin, S. 123, 124
Frassinetti, F. 328, 354, 355, 366
Freedman, M. 231, 243, 248
Freeman, R. Q. 246
Freeman, T. 353
French, J. W. 18
Frenois, C. 298
Frentzel, W. J. 276
Freund, H. J. 75, 372
Freund, J. S. 209
Fried, I. 87, 88
Friedland, R. P. 246
Friedman, D. 232
Friedman, N. P. 22
Friedrich, F. J. 405
Frith, C. D. 78, 86, 87, 232, 234, 333, 373, 391
Fritsch, A. 71
Fry, A. F. 191
Frost, D. 121
Fujii, T. 246, 391
Fujimori, M. 243
Fukatsu, R. 249, 391
Fukuyama, H. 249
Furey, M. L. 110, 112
Furukawa, T. 403
Fyer, A. 88

G
Gabriele, G. 349
Gabrieli, J. D. E. 147, 232
Gaffan, D. 381, 390
Gainotti, G. 241, 246, 340, 348, 351, 354, 381
Galasko, D. 243
Galati, G. 88, 89, 289, 381, 391, 399, 403, 404, 405
Galiana, H. L. 90
Galik, E. 190
Gallace, A. 168
Gallana, A. 364
Gallese, V. 324, 366
Galletti, C. 382, 387, 391
Gallistel, C. R. 157, 158
Gallo, P. 241
Galton, C. J. 3, 4, 6, 231
Galton, F. 143, 155, 203
Gamberini, M. 388, 391
Gandola, M. 337, 369, 373
Ganis, G. 49, 112, 113, 261
Garcin, R. 302
Garden, S. 15
Gardini, S. 204, 207, 208, 210, 216
Gardner, T. 251
Garvin E. A. 32
Gasparini, M. 403 404
Gathercole, S. E. 16, 21, 27, 31
Gaw, F. 7
Gaylord, S. A. 190
Gebhard, P. 40
Gelade, G. 19
Gelman, R. 157, 158
Geminiani, A. 368, 370
Geminiani, G. 69, 75
Gentilucci, M. 90, 297, 301, 323
Georges-François, P. 90
Georgopoulos, A. P. 249, 297
Gerbino, W. 142
Gerrard, J. L. 284
Gerstmann, J. 364, 365, 370
Gerstner, W. 89
Geva, A. 187
Gevers, W. 166, 168
Geypens, F. 160, 163, 168
Ghaëm, O. 65, 85, 86, 88
Gialanella, B. 367
Giannarelli, C. 367, 368, 369
Gick, M. L. 192, 195
Giglia, G. 349
Gilchrist, I. D. 112, 406
Gilhooly, K. J. 142, 144
Gillihan, S. J. 120
Gindri, P. 301, 343, 348, 349, 350, 353, 354
Giovannetti, T. 246

Giraux, P. 158, 159, 160, 166, 168
Gircus, J. S. 340
Girelli, L. 74, 106, 107, 161, 163, 168
Girgus, J. S. 353, 355
Giusberti, F. 108, 113, 115
Glickstein, M. 297
Gnanalingham, K. K. 243, 248
Gobbini, M. I. 110, 112
Göbel, S. 164
Goddard, S. 158
Gold, S. R. 114, 120
Goldberg, J. 21
Goldberg, M. E. 324, 325
Goldberg, T. E. 114
Goldknopf, E. J. 17, 203, 205
Goldman-Rakic, P. S. 89
Goldston, D. B. 16
Golledge, R. G. 115
Gollin, E. S. 189, 203
Golomer, E. 90
Gomez-Tortosa, E. 70
Gon, van, der, J. J. D. 91
Gonçalves, M.-R. 14
Goodale, M. A. 114, 297, 298, 301, 302, 304, 305, 306, 309, 310, 402, 404, 406, 407, 408
Goode, A. 121
Goodglass, H. 242, 363
Gooding, P. A. 146, 147
Goodman, N. 111
Goodrich, S. 324
Goodrich, S. J. 381
Goossens, L. 210
Gordon, C. R. 91, 94
Gordon, R. 1
Gore, J. C. 89
Gorno-Tempini, M. L. 243
Gothard, K. 284
Gouteaux, S. 285
Govoni, P. 391
Grady, C. L. 86, 87, 114, 234
Graf, W. 333, 382
Grafman, J. 70, 364
Grafton, S. T. 305, 308
Graham, N. L. 243, 248
Grasso, R. 90, 91
Graziano, M. S. A. 323, 324, 326, 331
Gray, C. 16, 19, 21, 105, 178
Gray, F. 354, 355
Giano, M. S. A.
Gréa, H. 299, 302, 305, 308
Green, C. 143, 144
Green, S. 115
Greene, A. J. 112
Greenwood, R. 311
Greer, D. 77
Greve, D. N. 123
Grey, C. 16, 18, 27, 28, 103
Gribbin, K. 106
Grimoldi, M. 28
Grober, E. 223
Gron, G. 285
Groninger, L. 223
Grosof, D. H. 349
Gross C. G. 323, 324, 326, 331
Grosse-Ruyken, M. 75
Grossi, D. 240, 241, 242, 243, 246, 247, 251
Grossman, M. 242
Growden, J. H. 248
Grun, J. 88
Gruppo, M. T. 26
Guariglia, C. 286, 287, 288, 289, 291, 337, 338, 364, 365, 402
Guariglia, P. 349, 399, 403, 404, 405
Guazzelli, M. 110, 112
Guerin, F. 248, 252
Guillery, B. 147
Gulyas, B. 114, 349
Gustafson, L. 243
Gutbrod, K. 87, 88
Gwyn, M. K. 7

H

Haaland, K. Y. 229
Habib, M. 86, 286, 299
Hackmann A. 144
Hakstian, A. R. 18
Hale S. 23, 187, 188, 189, 190, 191
Halgren, E. 349, 355
Hall, M. 16
Hallett, M. 70, 391
Halliday, M. S. 104
Halligan, P. W. 75, 78, 339, 340, 348, 352, 353, 366, 370, 381, 391, 397, 403, 410, 411
Halmagyi, G. M. 90
Hamberger, M. 232
Hambrick, D. Z. 116
Hamel, R. 113
Hamilton, C. H. 19
Hamilton, S. 204
Hammond, K. M. 16, 106, 174, 262
Hampson, E. 106
Hanihara, T. 243
Hanley, J. R. 15, 103
Hannay, H. J. 239
Hansen, L. A. 243
Harman, H. H. 18
Harris, J. A. 396, 397
Harshman, R. A. 106, 262, 265, 266, 269
Hartley, T. 87, 90
Hartman, M. L. 9, 112, 210
Harvey, M. 74, 298, 299, 300, 301, 340, 342, 343, 347, 348, 350, 353, 354, 398, 406, 407
Hasher, L. 39, 42, 45, 122, 187, 210, 213, 216, 226
Hashimoto, M. 243
Hatta, T. 166
Hawken, M. J. 349
Haxby, J. V. 110, 114, 144
Hazeltine, E. 74
He, S. 147
Head, H. 328
Heald, A. 231
Held, R. 121
Healy, W. 6
Hecker, R. 114, 174
Hedden, T. 116, 188
Heeley, D. W. 309
Hegarty, M. 22
Heider, B. 303
Heilman, K. M. 77, 337, 338, 343, 347, 353, 365, 405, 406, 408
Heinemann, D. 74
Heller, M. A. 115
Helstrup, T. 142
Hénaff, M.-A. 304
Henderson, B. B. 120
Hendriks, M. P. H. 232
Henik, A. 163
Hennelley, R. A. 174
Henson, R. N. A.
Herbert, A. M. 85
Hermer, L. 285, 289
Hermer-Vasquez, L. 285
Herrnstein, R. J. 108
Herscovitch, P. 114
Hertzog, C. 188, 191, 260, 263, 264, 265, 267, 268, 269, 270, 271, 273, 274, 275, 276
Hess, C. W. 74, 87, 88
Hewes, A. K. 103
Higgins J. A. 189, 191, 349, 350, 355

Hilgetag, C. C. 74
Hill, R. 163
Hill, R. J. 160
Hillyard, S. A. 76
Himmelbach, M. 77, 300, 301, 302, 311
Hindle, J. V. 300
Hinrichs, J. V. 16
Hirayama, K. 286
Hirono, N. 243
Hirsch, J. 349
Hirstein, W. 114
Hiscock, M. 11
Hitch, G. J. 101, 103, 104, 105, 107, 124, 125, 139, 142, 173, 203
Hobbel, D. 226, 227
Hock, H. S. 61
Hodapp, R. M. 103
Hodges, J. R. 231, 243, 247, 369
Hof, P. R. 248
Hoffernan, T. 19
Hoffmann, K. 333
Holding, D. H. 340
Holmes, N. P. 328, 329
Holmes, E. 144
Holt, R. R. 12
Holtzman, J. D. 115
Holzman, P. S. 114
Honda, M. 391
Honoré, J. 337
Hood, B. M. 301, 309
Hoogenraad, T. U. 331
Horenstein, S. 331, 337
Horn, J. 188
Hornak, J. 381, 390
Horne, M. K. 408
Horowitz, G. 204
Horwitz, B. 114
House, A. 369
Hu, X. T. 147, 324, 331
Huha, E. M. 18, 142, 181
Hulme, C. 21, 104
Hultsch, D. F. 188
Humphrey, G. K. 303
Humphreys, G. W. 353
Hunt, R. R. 259
Hunter, J. P. 401
Husain, M. 300, 328, 330, 381, 390
Huttenlocher, J. 285
Hwang, S. 246
Hyde, J. S. 106

I
Hyvärinen, J. 297, 323
Iaria, G. 285, 286, 289, 291
Ickes, W. 120
Iddon, J. L. 231
Idzikowski, C. 16
Ilmoniemi, R. J. 70
Imamura, T. 243
Ince, P. G. 243
Incisa della Rocchetta, A. 286
Incoccia, C. 286
Ingersoll, G. 204
Inman, V. 190
Ino, T. 249
Intons-Peterson, M. J. 110, 142
Iriki, A. 326, 327, 329, 330
Irving-Bell, L. 348
Irwin, D. E. 112
Isaac, C. L. 146, 147
Isaacs, E. B. 18, 142
Isableu, B. 90
Ishai, A. 114, 144
Isham, E. A. 87, 88
Ishiai, S. 403
Ishihara, M. 306
Isingrini, M. 209
Israël, I. 90, 91, 94
Ito, Y. 166
Ivanenko, Y. P. 91, 94
Iwamura, Y. 327, 330
Izzo, G. 240, 241, 242
Izzo, O. 240, 241, 242

J
Jackendoff, R. 114
Jacklin, C. N. 106
Jackson, P. L. 369
Jackson, S. R. 300
Jacobs, R. A. 89
Jacoby, L. L. 227
Jacquin-Courtois, S. 165
Jager, H. R. 311
Jagust, W. J. 246
Jakobson, L. S. 301, 302, 303, 305, 309
James, M. 239
James, T. W. 303
Jansen, E. N. 243
Jarrold, C. 103
Javitt, D. C. 349, 349, 355
Jeannerod, M. 90, 297, 299, 302, 305, 308, 310, 369
Jefferies, E. 147
Jefferson, A. 246, 249
Jellinger, K. A. 243
Jenkins L. 188, 189, 191
Jeong, Y. 77
Jewell, G. 75, 161
Jezzard, P. 10
Joerding, J. A. 188, 189
Johnsen. J. A. 113
Johnson S. H. 269
Johnson, B. 7
Johnson, J. K. 243
Johnson, M. K. 189, 191, 222, 226, 227
Johnson, S. H. 206
Johnson-Laird, P. 110
Johnsrude, I. 221
Johnston, R. S. 309
Jolicoeur, P. 11
Joliot, M. 114
Jolles, J. 232
Jonides, J. 15, 114, 124, 174
Jordan, T. R. 309
Jouvent, R. 94
Judd, C. H. 251, 340
Judica, A. 365, 366
Juhel, J.
Jung, M. W. 284
Just, M. A. 114, 262

K
Kahana, M. J. 87, 88
Kahn, R. S. 114
Kahneman, D. 122
Kalsbeck, J. E. 298
Kaminaga, T. 251
Kan, I. P. 261
Kang, S. J. 247
Kanisza, G. 340, 345
Kanwisher, N. G. 123, 298, 299, 302
Kaplan, E. 246, 248, 249
Kappelle, L. J. 16, 233
Karhu, J. 70
Karnath, H. O. 77, 300, 301, 302, 311, 348, 354, 367, 373, 399
Kartsounis, L. D. 345
Karttunen, M. 40
Kasahata, N. 286
Kaszniak, A. 190
Katila, T. 70
Katz, E. 226
Kaufmann, G. 113
Kavanagh, D. J. 144

Kawamura, M. 286
Kay, B. A. 90
Kazui, H. 243
Keil, K. 114, 174
Keillor, J. M. 309
Kemps, E. 18, 106, 142, 175, 178, 180, 181
Kennard, C. 77, 300, 302, 381, 390
Kennedy, C. 246, 248
Kennett, S. 330
Kerkhoff, G. 240, 301, 348
Kerr, N. H. 115, 181
Kerszberg, M. 122
Kertesz, A. 241, 242, 243
Kesner, R. P. 89, 231
Kessels, R. P. C. 16, 221, 223, 224, 225, 226, 227, 228, 229, 230, 232, 233
Keus, I. M. 167
Khan, A. Z. 299
Kihlstrom, J. F. 221
Kim, I. J. 111, 247
Kim, K. 349
Kimura, D. 106, 249
King, J. A. 86, 87, 88, 89
Kingsley, D. 44
Kinsbourne, M. 70, 348
Kintsch, W. 116, 118, 119, 125
Kirk, A. 241, 242
Kishikawa, Y. 249
Kita, H. 249
Kitabayashi, Y. 249
Kitamura, S. 120
Klatzky, R. L. 115
Klein, D. A. 190
Kleist, K. 240, 241
Kliegl, R. 23, 188, 193, 196, 197
Knauff, M. 112
Knierim, J. J. 284
Knopman, D. 230
Knox, H. A. 7, 9
Koch, C. 124
Koch, G. 71, 76
Koda, V. 88
Koenig, O. 16, 203
Koeppe, R. A. 114, 174
Konczak, J. 300
Kooistra, C. A. 337, 338
Kopelman, M. D. 44
Kosaka, K. 243
Koss, E. 246
Kosslyn, S. M. 15, 16, 49, 50, 51, 52, 57, 58, 59, 62, 66, 108, 110, 111, 112, 113, 115, 143, 148, 191, 203, 204, 205, 206, 216, 261
Krampe, R. T. 188, 193
Kramer-McCaffery, T. 406
Kreiman, G. 124
Krikorian, R. 18, 142, 181
Krolak-Salmon, P. 306
Kubischik, M. 333
Kudrimoti, H. 284
Kufta, C. 70
Kujirai, T. 71
Kumada, T. 89
Kumar, A. 246
Kunesch, E. 372
Kunst-Wilson, W. R. 121
Kurland, M. 21
Kuse, A. R. 17, 18
Kutz, D. F. 388, 391, 401
Kwak, Y. T. 246, 247
Kwan, L. 121
Kyrouac, G. A. 243, 248
Hughes, L. H. 243, 248

L
La Bua, V. 74, 75, 78, 79
LaBerge, D. 204
Lachman, M. E. 268
Lacquaniti, F. 310
Lackner, J. R. 90
Làdavas, E. 309, 325, 326, 328, 329, 330, 331, 367, 368, 369
Laiacona, M. 143
Lamar, M. 246
Lamassa, M. 338, 372
Lambrey, S. 88, 90, 91, 94
Lamme, V. A. F. 122, 204
Lammertyn, J. 164, 168
Landau, B. 114
Landauer, T. K. 156, 157
Landis, T. 298, 345, 346, 347, 351, 353
Lanfranchi, S. 23, 103
Larsen, J. P. 243
Larsson, J. 349
Larue, A. 229
Laughlin, J. E. 117
Lautenschlager, G. 116, 188
Lauwereyns, J. 164, 168
Lawlor, B. A. 243, 249
Lawrence, B. 188
Lazar, R. 351
Le Bihan, D. 10, 164, 165, 168, 391
Le Bras, C. 251
Lê, S. 304
Leach, L. 248
Learmonth, A. E. 285
Lease, J. 114
Lebedev, M. A. 401
Lebiere, C. 103, 139
LeBihan, D. 88, 89, 164
Lecerf, T. 16, 17, 19
Lee, B. H. 247
Lee, G. P. 373
Lee, T. S. 204, 349
Leibovitch, F. S. 77, 302, 381, 389
Lemay, M. 226
Lennox, G. 243
Lepore, M. 247
Leung, H. C. 89
Levander, M. 408
Levine, D. N. 16, 106, 174, 242, 262, 302, 368
Levy, B. A. 174
Levy, D. L. 114
Levy, R. 231
Lewandowsky, S. 142
Lewis, J. L. 121
Lewis, V. J. 139, 140
Lezak, M. D. 187
Li, K. Z. H. 187
Li, L. 165
Li, S. C. 142
Li, T. 349
Li, Z. 147
Libon, D. J. 246, 248, 249
Lieberman, K. 16
Liepert, J. 71
Light, L. L. 40, 191, 222
Likert, R. 15
Lima, F. 115
Lincoln, N. B. 391
Linderberger, U. 196, 197
Lineweaver, T. T. 267
Linn, M. C. 10
Lipshits, M. 90
Litvan, I. 243
Liu, A. K. 349
Lloyd, S. A. 16
Lo, Y. 114
Lobel, E. 391
Lockhead, G. R. 61
Loeb, J. 324
Loffredo, S. 337, 373
Logie, R. H. 15, 16, 19, 31, 102, 103, 104, 107, 111, 112, 113, 116, 119, 139, 142, 143, 144, 146, 173, 174, 178, 181

Lohman, D. F. 18
Lomber, S. G. 72, 79
Loomis, J. M. 115
Lorenz, C. 11
Loring, D. W. 373
Lovestone, S. 243
Lowe, J. 243
Lualdi, M. 75, 353
Luauté, J. 299, 306
Lucangeli, D. 163, 168
Luck, S. J. 145
Luppino, G. 323, 324, 331, 369, 391
Luzzatti, C. 16, 106, 114, 165, 174, 287
Lyketsos, C. G. 190
Lynch, J. C. 297
Ghobrial, M. W. 243, 248

**M**
Macaluso, E. 78, 333
Maccoby, E. E. 106
MacFadden, A. 285
MacWalter, R. S. 301
Madden, D. J. 221
Maeshuets, C. 187
Magni, E. 242, 247, 248
Magnotti, L. 349
Maguire, C. P. 243, 249
Maguire, E. A. 86, 87, 88, 232, 234
Maisog, J. M. 114
Makino, Y. 89
Makuuchi, M. 249
Malamut, B. 248
Malenfant, D. 187
Malhotra, P. 77, 311, 381, 390
Malijkovic, A. 349
Malijkovic, V. 204
Mammarella, I. C. 19, 24, 28, 29, 31, 32, 33
Mandler, J. M. 40
Mann, D. M. 246
Mannan, S. K. 77, 300, 381, 390
Mantione, M. H. M. 115
Mapelli, D. 158
Mapperson, B. 114, 174
Maravita, A. 246, 328, 330
Marcel, A. J. 368, 369
March, G. R. 191
Marchetti, C. 16, 103, 173
Marcoen, A. 210
Marconato F. 31
Marder, K. 232
Marenzi, R. 165
Margolis, J. A. 17, 203, 205
Marks, D. F. 4, 5, 17, 261
Marks, W. 206, 209
Marmor, G. S. 115
Marotta, J. J. 304
Marquardt, C. 240
Marschark, M. 259
Marsden, C. D. 71
Marshall, J. C. 75, 78, 339, 340, 348, 352, 353, 366, 370, 381, 391, 397, 403, 410, 411
Marshall, R. 351
Martin, A. 114
Martin, M. 263
Marucci, F. S. 108, 115
Marzi, C. A. 74
Marzocchi, G. M. 23, 32
Mason, A. 141
Mason, S. E. 209
Massarelli, R. 369
Massironi, M. 108, 113, 115
Masson, M. E. J. 228, 229
Masterson, J. 251
Masunaga, H. 188
Matelli, M. 323, 324, 331, 366, 369, 391
Mather, M. 187, 191, 222, 227
Mattingley, J. B. 74, 78, 300, 311, 340, 345, 347, 348, 350, 353, 354, 408
Matsuda, M. 249
Matthysse, S. 114
Mattingley, J. B.
Mattioli, F. 367
Maughan, S. 21, 104
Maurer, J. J. 196
May, C. P. 210, 213
May, J. G. 144, 297
Mayer, A. B. 297
Mayer-Gross, W. 246
Mayes, A. R. 146, 147, 221, 227, 234
Maylor, E. 276
Mayr, U. 23, 188, 193
Mazoyer, B. 10, 65, 85, 86, 88, 114
Mazzoni, G. 108, 115
McClelland, J. L. 122
McClements, K. I. 345, 351, 401
McConnell, J. 16, 104, 173
McCourt, M. E. 75, 161
McDaniell, M. A. 204, 207, 210
McDermott, K. B. 353
McDonald, R. P. 29
McDougall, S. 261
McGlinchey-Berroth, R. 338, 343, 350, 353
McGuire, K. 246, 248, 267
McInnes, L. 276
McIntosh, A. R. 234, 401, 407
McIntosh, R. D. 299, 301, 303, 304, 307, 310, 311, 312, 313, 345, 351, 365, 366
McIntyre, J. 310
McKeith, I. G. 243
McKelvie, S. J. 1, 6, 11, 262
McMahon, R. P. 114
McNamara, D. S. 267
McNaughton, B. L. 284
McPherson, M. W. 6
Meador, K. J. 373, 408
Meares, K. 144
Meehl, P. E. 263
Mehler, J. 76, 157, 158
Mellet, E. 10, 65, 85, 86, 88, 114
Melling, L. 141
Meltzer, J. 108, 191
Melvill Jones, G. 91
Melvill Jones, G. M. 90, 91, 94
Memmi, D. 14
Menard, W. E. 196
Mendez, M. 231
Mendola, J. D. 123, 349, 355
Meneghello, F. 165, 331
Mesulam, M. M. 391
Metcalfe, J. 277
Metras, F. 209
Metzler, J. 106, 115, 203, 262
Meuli, R. 405, 406
Meyer, J. S. 331, 337
Meyrignac, C. 354, 355
Michael, A. 231
Michel, C. M. 165
Michel, F. 299, 302, 304, 310
Mickanin, J. 242
Middelkoop, H. A. M. 232, 233
Milberg, W. 343, 350, 353
Miller, A. I. 144
Miller, B. L. 243, 243
Miller, E. K. 114
Milner, A. D. 114, 297, 298, 299, 300, 301, 302, 303, 305, 306, 307, 309, 310, 311, 312, 313, 340, 235, 348, 351, 353, 354, 398, 401, 402, 404, 406, 407, 408
Milner, B. 18, 85, 142, 174, 176, 221, 233

Milner, D. 74, 78
Miniussi, C. 74
Minor, J. K. 261
Minoshima, S. 114, 174
Mintun, M. 174
Mirabella, G. 401
Mirra, S. S. 243
Mishkin, M. 15, 114, 240, 297
Mitchell, D. B. 16
Mitchell, D. R. D. 188, 192, 194, 19, 196, 197
Mitchell, K. J. 187, 189, 191, 222, 227
Miyake, A. 22
Mòdona, M. N. 301, 398
Moffat, S. D. 190
Moffet, A. 285
Mohr, J. P. 351
Molhotra, P. 300, 302
Molin, A. 31
Monteleone, D. 246
Montenero, P. 366
Monticelli, M. L. 115, 173, 178, 181
Montinari, C. 31
Mon-Williams, M. 303, 304, 313
Moon-Ho Ring Ho 29
Moore, B. 276
Morel, A. 297
Moro, V. 338
Morrell, R. W. 263
Morris, J. C. 190, 192, 195
Morris, P. E. 262, 263, 276
Morris, R. G. 86, 231, 240
Morrison, J. H. 248
Morrow, D. G. 196
Mort, D. J. 77, 300, 302, 381, 390
Moscovitch, M. 86, 87, 114, 338, 381
Mottaghy, F. M. 113
Mosimann, U. P. 74
Mountcastle, V. B. 297
Moya, K. L. 242
Moyer, R. S. 156, 157, 164
Mulleners, W. M. 349
Muller, R. U. 284
Muller, H. M. 353
Muller, M. 242, 246
Müller-Lyer, F. C. 340
Mummery, C. J. 87, 88
Munkholm, P. 285
Muri, R. M. 74, 87, 88
Murphy, K. J. 303, 310
Murphy, P. J. S. 342, 348, 350, 406
Murray, D. J. 104, 140, 174, 349, 350, 355
Mussa-Ivaldi, F. A. 181
Muzur, A. 391
Myerson, J. 23, 188, 189, 190, 191
Myram, D. 231

**N**

Na, D. L. 247, 406
Naatanen, R. 70
Nabatame, H. 249
Naccache, L. 122
Nadel, L. 40, 86, 233, 284, 285
Nagahama, Y. 249
Nakamura, K. 249
Narayanan, K. 147
Narens, L. 259
Narumoto, J. 249
Naveh-Benjamin, M. 40, 174, 259
Nawrot, M. 247
Neary, D. 243, 246
Neggers, S. F. W.
Neilsen, J. M. 370
Neisser, U. 1, 11, 338
Nelson, T. O. 121, 259
Neppi-Mòdona, M. 301, 348, 349, 354, 368, 369
Newcombe, N. S. 285
Newman, E. L. 87, 88
Newman, M. 190
Newport, R. 300
Ng, V. W. 240
Nguyen, M. 349
Nichelli, P. 18, 70, 114, 174, 176, 354, 355
Nico, D. 286, 287, 289, 291, 309, 337, 345, 351, 398, 399, 403, 404, 405
Nieder, A. 158
Nilsson, L. G. 221
Nimmo-Smith, I. 368, 369
Noe, A. 123
Noël, M. P. 155
Norris, D. 125
North, A. 301
Nuerk, H. C. 160
Nyffeler, T. 87, 88
Nys, G. M. S. 223, 225

**O**

O'Keefe, J. 86, 87, 88, 89, 90, 233, 283
Obayashi, S. 327, 330
Ober, B. A. 246
Oberauer, K. 23, 116
Obersteiner, H. 372
Ochsner, K. N. 122
Ogar, J. M. 243
Ogden, J. A. 248, 364
Ohlmann, T. 90
Okina, T. 249
Olivier, E. 74, 163
Olivieri M. 70, 71, 72, 73, 74, 75, 76, 78, 79
Olk, B. 342, 343, 347, 348, 350, 406
Olson, C. R. 381, 391
Olson, I. R. 189, 190
Olson, M. G. 40
Olson, R. K.
Oltman, P. K. 106
Onida, A. 349, 399, 401, 404, 405
Onishi, K. 242
Opfer, J. E. 158
Oppenheim, H. 324
Orban, G. A. 164
Orgass, B. 364
Ortigue S. 165
Ossola, A. 367, 368, 369
Osterreith, P. 241
Ota, H. 165, 391
Otsuka, Y. 246

**P**

Paciaroni, L. 13
Padovani, A. 242, 247, 248, 287
Page, M. 125
Pagliarini, L. 301
Pailhous, J. 94
Paivio, A. 106, 108, 109, 110, 111, 209, 259, 260, 262, 265, 266, 267, 269
Palladino, P. 106, 107, 181, 210, 213, 214, 216, 270
Pallis, C. A. 286
Palmer, E. P. 299
Palmer, S. E. 347, 353
Palmieri, M. G. 70
Palmon, R. 188, 196, 197
Pambakian, A. 77, 300, 302, 381, 390
Panagiotaki, P. 90
Pani, J. R. 261
Panisset, M. 231
Papagno, C. 102, 337

Paradis, A.-L. 88, 89
Pardo, J. V. 373
Park, D. C. 116, 188, 191, 222, 263
Parlato, V. 246
Parslow, D. M. 86
Parton, A. 311
Pascual-Leone, A. 70, 74, 113
Pasqualetti, P. 70, 71, 72, 73, 78
Passant, U. 243
Passenier, P. O. 90
Passerini, D. 337, 373
Paterson, A. 285
Paterson, D. G. 7
Patterson, K. 248
Pattini, P. 288
Pattison, L. L. 78, 302
Paulesu, E. 288, 337, 366, 372, 373
Paulignan, L. 299
Paulignan, Y. 306, 308
Paus, T. 74
Pause, M. 372
Pavesi, G. 366
Payne, B. R. 72, 74, 79
Payne, J. M.
Payne, T. W. 116
Pazzaglia, F. 15, 17, 19, 25, 28, 29, 31, 106, 203, 204, 207, 208, 210, 211, 216
Peaker, M. 27
Pearson, D. 107, 111, 112, 141, 142, 143, 144, 146, 149, 173, 178, 181
Pearson, N. A. 15, 19, 103
Pece, A. 115
Pélisson, D. 305
Pellegrino, J. W. 18, 115
Pendleton, L. R. 104, 173
Perani, D. 69, 75, 77, 300, 302, 337, 365, 366
Perenin, M. T. 165, 288, 299, 300, 301, 302, 311, 337
Peretti, V. A. 345, 351, 397, 399, 405
Perini, N. 243, 249
Perrett, D. I. 309
Perri, R. 16, 114
Perrotta, C. 243, 246
Perry, E. K. 243
Perry, R. H. 243
Perryman, K. 231
Perts, I. 187
Peru, A. 365, 366
Pesenti, M. 155, 163, 164
Peterhans, E. 349
Petersen, A. C. 10
Peterson, L. R. 147
Peterson, M. J.
Petit, L. 65, 86
Petrides, M. 285
Pettenati, C. 255
Pflugshaupt, T. 87, 88
Phengrasamy, L. 243
Phillips, J. G. 408
Phillips, W. A. 140, 141, 142
Philpot, M. 231
Pia, L. 301, 343, 348, 349, 350, 353, 354, 368, 369
Piazza, A. 74, 75, 76, 78, 79, 349
Piazza, M. 157, 158, 164, 165, 168
Piccardi, L. 286, 289, 364
Pietrini, P. 110, 112, 115
Pick, A. 364
Pick, H. L. 40
Pickering, S. J. 16, 19, 21, 27, 31
Pike, B. 285
Pillon, B. 251
Pine, D. S. 88
Pinel, P. 157, 158, 164, 165, 168
Pinker, S. 18, 57, 58
Pinna, G. 365, 366
Pintner, R. 7, 9
Piolino, P. 221
Pisella, L. 165, 299, 302, 305, 306, 307, 308, 309, 310, 311, 312, 407
Pitzalis, S. 301
Pizzamiglio L. 88, 89, 287, 288, 289, 291, 337, 345, 351, 366, 391, 398, 399
Playford, E. D. 311
Pleydell-Pearce, C. W. 143, 144
Poe, G. R.
Poeck, K. 364
Poizner, H. 310
Polk, M. 248
Poltrock, S. E. 262
Popov, K. 90
Poppel, E. 121
Popplestone, J. A. 6
Porac, C. 340
Poranen, A. 297, 323
Posner, M. I. 338, 405
Post, R. B. 340, 348
Postle, B. R. 16, 114
Postma, A. 15, 16, 40, 41, 42, 43, 44, 221, 224, 226, 227, 228, 229, 230, 232, 233, 240
Potter, G. 112
Pouget, A. 382, 383, 384, 385, 386, 390
Powell-Moman, A. 274
Pra Baldi, A. 203, 204, 207, 210, 211
Prabhakaran, V. 147
Prablanc, C. 305, 308
Pradat-Diehl, P. 251
Pratt, J. 162
Predebon, J. 355
Pressley, M. 260
Preti, D. 115
Price, J. 276
Price, L. 229
Priftis, K. 76, 165
Prigatano, G. P. 367
Prins, M. 248
Pritchard, C. L. 301
Probst, T. 90
Proteau, L. 226
Proverbio, A. M. 349
Puglisi Allegra, M. C. 364
Pylyshyn, Z. W. 49, 56, 109, 112, 145

**Q**

Qin, Y. 16, 284
Quasha, W. H. 15
Quig, M. B. 210, 213
Quinette, P. 147
Quinn, J. G. 104, 142, 173, 181
Quinn, N. P. 243
Quinton, A. M. 3

**R**

Rabbitt, P. 276
Rachofsky, L. M. 9
Radloff, L. S. 273
Rafal, R. D. 70, 342, 343, 350, 354, 381, 405
Rahman, Q. 86
Raichle, M. E. 373
Rainer, G. 114
Ralph, M. A. L. 147
Ralston, G. E. 173, 181
Ramachandran, V. S. 114
Ramos, L. M. 331
Ranck, J. B. 284
Randolph, C. 114
Rankin, K. P. 243
Rao, C. 114
Raos, V. 324
Rapaport, S. I. 114
Rapone, P. 243, 246
Ratcliff, G. 302

Rausei, V. 76
Raven, J. C. 18
Raybaudi, M. 369
Raye, C. L. 187, 191, 222, 227
Raymond, J. E. 122
Raz, N. 206, 209
Razzano, C. 366
Reber, A. S. 121
Recce, M. 86
Reder, L. M. 103, 260, 277
Redish, D. A. 284
Redish, A. D. 88
Reed, C. L. 363
Reed, S. K. 61, 113
Rees, G. 124
Reeves, A. 112
Regian, J. W. 18
Reichle, E. D. 114
Reige, W. H. 190
Reingold, E. M. 121
Reisberg, D. 113
Reiser, B. J. 10, 51, 52, 57, 58, 62, 66, 108
Reiss, L. 222
Relkin, N. R. 349
Rensink, R. A. 122
Resnick, S. M. 190
Restle, F. 156, 157, 166, 354
Rettinger, D. A. 22
Reuter-Lorenz, P. A. 187, 188
Reverberi, C. 399 400, 401, 403, 404, 406
Revol, P. 299, 311
Rey, P. 209
Reymert, M. L. 9
Reynvoet, B. 160, 166, 168
Rhee, S. H.
Ricciardi, E. 110, 112
Ricci, R. 75, 288, 291, 343, 346, 348, 349, 350, 353, 354, 355, 368, 369, 398
Ricci, S. 338
Rice, N. J. 313
Richardson, A. 1, 6, 11, 26, 261
Richardson, J. T. E. 7, 9, 11, 18, 19, 106, 107, 181, 193, 195, 197, 209, 214, 215, 216, 260, 261, 262, 267, 270, 276
Richman, C. L. 16
Rickard, T. C. 40
Ridding, M. C. 71
Riddoch, M. J. 353
Riepe, M. W. 285
Rieser, B. J. 108
Riggio, L. 415
Righetti, E. 338, 372
Rigoni, F. 31, 33, 104, 113
Rinck, M. 109
Rinn, W. E. 368
Rivière, D. 164
Rizzo, M. 247, 311
Rizzolatti, G. 297, 300, 323, 324, 331, 366, 369
Ro, T. 70, 342, 343, 350, 354
Robbins, T. W. 231
Robert, P. H. 243
Roberts, R. C. 300, 301, 348, 353, 398
Robertson, I. H. 90, 288, 301, 309, 365, 366
Robinson, A. E. 264, 265, 268, 271, 273, 275
Robinson, K. M. 242
Rocchi P. 113, 115
Rode, G. 165, 288, 299, 302, 305, 306, 309, 311, 337, 338
Roediger, H. L. 353
Rogers, J. 89
Roland, P. E. 114, 349, 372
Roncato, S. 251
Rondot, P. 302
Rorden, C. 77, 300, 302, 367, 381, 390
Rosen, B. R. 123
Rosen, H. J. 243
Rosenbaum, R. S. 86, 87
Rosenblatt, A. 190
Rosenthal, R. 1
Ross, S. J. M. 248
Rossan, S. 209, 214, 215, 216
Rosselli, M. 241
Rossetti, Y. 165, 287, 297, 299, 305, 306, 307, 308, 309, 310, 311, 312, 338, 407
Rossi, S. 106, 181
Rossini, P. M. 70, 71, 72, 73, 78
Roth, M. 369
Rothwell, J. C. 71
Rouleau, I. 242, 246, 248, 249
Rourke, B. P. 31, 107
Rousseau, S. 251
Rowe, E. J. 267
Roy, A. C. 306, 308
Rozzi, S. 391
Royall, D. 248
Rouw, R. 113
Rubin, D. C. 215
Rubin, D. B. 114
Rumiati, R. 251
Ruohonen, J. 70
Rusconi, M. L. 69, 75, 246, 288, 337, 338, 342, 345, 351, 370, 372, 373, 397, 399, 405
Rusconi, E. 158
Rushworth, M. F. S. 74, 164
Ryan, P. M. 160
Rybash, J. M. 206, 269
Rympa, B. 191

S
Sabatini, U. 286
Sabes, P. N. 391
Saffran, E. M. 247, 286, 363, 364
Sagiv, N. 74
Sahakian, B. J. 231
Sahuc, S. 90
Saito, H. 246
Sakata, H. 297
Salemme, R. 414
Salinas, E. 331
Salmon, D. P. 242, 243, 246, 248, 249
Salthouse, T. A. 107, 187, 192, 193, 194, 195, 196, 197, 270
Sanchez, M. 223
Sanders, M. D.
Sandroni, P. 337, 373
Sands, L. P. 248
Sandson, J. 246
Sartori, G. 251
Sasso, E. 300
Sato, M. 286
Sato, S. 70
Saucier, D. 285
Saveriano, V. 193
Sbrana B. 115
Scailquin, J. C. 206, 207, 215
Scalia, S. 349
Scalquin, J.-C. 188
Scandolara, C. 323
Scarpa, P. 337, 373
Schaafstal, A. M. 104
Schacter, D. L. 122, 123, 366
Schaie, K. W. 106, 107
Scheier, M. S. 120
Schenk, T. 89
Schindler, I. 78, 302, 313
Schlack, A. 333
Schlaepfer, T. E. 74
Schlag, J. 387
Schlag-Rey, M. 387

Schneider, W. 260
Scholey, K. A. 175, 178
Schouten, J. 233
Schouten, J. L. 114
Schraagen, J. M. C. 104
Schretlen, D. 223
Schriefer, L. 7
Schroeder, C. E. 349, 350, 355
Schulkind, M. D. 215
Schulze, R. 116
Schuhmacher, E. H. 114
Schunn, C. D. 260, 277
Schwartz, R. L. 406
Schwarz, W. 166
Schwoebel, J. 363, 364
Scogin, F. 210
Scotti, G. 363, 396
Seegmiller, D. 40
Segal, B. 91, 94, 113
Segebarth, C.
Seidler, B. 15, 23, 47, 148
Sejnowki, T. J. 382, 383, 384, 385, 386, 390
Selnes, O. 230
Semenza, C. 242, 363, 364
Semple, J. 231
Sergent, C. 122
Seron, X. 155, 163, 164
Seyal, M. 70
Shacter 40
Shah, N. J. 22, 75, 333
Shallice, T. 398
Shanks, D. R. 121, 122
Shapiro, M. B. 114, 122
Shapley, R. M. 349
Sharps, M. J. 189, 203
Shaw, R. L. 193, 194
Sheenan, P. W. 4, 5
Shepard, R. N. 19, 106, 108, 115, 144, 191, 203, 262
Sheppard, J. M. 190
Shimomura, T. 243
Shin, R. K.
Shiota, J. 286
Shipp, S. 391
Shpritz, B. 223
Shulman, K. I. 248, 249
Shulze, R. 23
Shuren, J. E. 77
Siegel, R. M. 382, 383, 387, 391
Siegler, I. 91, 94
Siegler, R. S. 158
Simard, M. 231
Simon, H. A. 260
Simon, J. R. 158
Singer, J. L. 120
Singh, A. 222
Sirigu, A. 86, 286, 299, 364
Sittig, A. C. 91
Ska, B. 248, 252
Skaggs, W. E. 284
Skovronek, E. 188, 196, 197
Skrap, M. 391
Slayton, K. 144
Sliwinski, M. 188, 221
Small, B. J. 188
Small, M. 348, 366, 368
Smania, N. 337, 338, 369, 373
Smetanin, B. 310
Smirni, P. 142
Smith, A. D. 116, 188, 209
Smith, E. E. 15, 114, 124, 174, 187
Smith, M. L. 229, 233
Smith, P. K. 116
Smith, S. M. 111, 144
Smyth. M. M. 41, 42, 104, 142, 173, 175, 178
Snodgrass, J. G. 26, 193
Snowden, J. S. 243, 246
Snyder, B. D. 247
Snyder, L. H. 298
Solomon, K. O. 261
Solvetti, M. 403, 404
Southwood, M. H. 114
Sparing, R. 113
Speiser, H. R. 15, 23, 47, 148
Spelke, E. S. 158, 284, 285, 287, 289
Spence, C. 168, 323, 329, 330
Spiers, H. J. 90
Spinelli, D. 301
Spinnler, H. 396
Spitzer, M. 285
Spreen, O. 10
Srinivas, K. 112
Stackman, R. W. 85
Stallcup, M. 261
Standart, S. 144
Stanhope, N. 44
Stark, M. 247, 287
Steele, C. 190
Stein, D. G. 298
Steinberg, M. 190
Sterken, Y. 240
Stern, R. A. 246
Stern, Y. 232
Sterzi, R. 337, 338, 343, 370, 371, 372, 373
Stine-Morrow, E. A. L. 196
St. Jones, M. 122
Stokes, M. G. 74, 78
Stone, M. H. 9
Storch, P. 71
Storm, R. W. 145
Stracciari, A. 367, 368, 369
Strafella, A. P. 74
Strassberg, D. S. 231
Stratta, F. 310
Straube, A. 90
Strauss, E. 10
Stuart-Green, L. 248
Stuss, D. 243
Suckling, J. 240
Sugishita, M. 251
Sukel, K. E. 113
Suler, J. 120
Sun, X. 147
Sunderland, T. 364
Sunshine, P. 204
Suster. M. 284
Suvajac, B. 231
Suzuki, K. 246, 249, 391
Süβ, H. M. 23, 116
Swainson, R. 231
Swanwick, G. R. J. 243, 249
Swenson, R. 248
Szalai, J. P. 77, 381, 390
Szeszko, P. R. 88
Szmalec, A. 19, 106, 181

**T**

Tadary, B. 90
Taguchi, Y. 286
Taillefer, C. 251
Takahashi, N. 286
Takeda, Y. 89
Tam, A. 71
Tanaka, M. 327, 330
Tanimukai, S. 243
Tanji, J. 369
Taube, J. S. 85, 284
Te Boekhorst, S. 229
Tegner, R. 368, 369, 408
Tek, C. 114
Telban R. 91
Teller, T. 196
Thein, T. 396, 397
Theoret, H. 74
Thinsi-Blanc, C. 293
Thioux, M. 164
Thompson, E. E. 373

Thompson, P. D. 71
Thompson, W. 204
Thompson, W. L. 49, 111, 112, 113, 261
Thompson, W. O. 373
Thompson-Schill, S. L. 261
Thomson, N. 174
Thornton, A. 243, 248
Thurstone, L. L. 18
Thurstone, T. G. 18
Tiacci, C. 340, 348, 354, 381
Tilikete, C. 299, 302, 305, 308, 407
Tinti, C. 115
Tipper, S. P. 381
Tippet, L. J. 261
Tisserand, D. J. 232
Tissot, R. 242, 246
Tomaiuolo, F. 16, 70, 72, 73, 77, 78, 114, 381, 390, 391
Tomczak, R. 285
Toniolo, S. 309
Tootell, R. B. 123, 349
Töpper, R. 113
Toraldo, A. 397, 398, 399, 400, 401, 403, 404, 406
Torri, T. 240
Torriero, S. 71, 76
Toso, C. 28
Toth, J. P. 227
Touretzky, D. S. 88, 284
Tovee, M. J. 243
Traballesi, M. 364
Trabucchi, M. 242, 247, 248
Traversa, R. 70, 71, 72, 73, 78
Treccani, B. 240
Treisman, A. M. 19
Tresilian, J. R. 304, 313
Tressoldi, P. E. 31, 113
Trillet, M. 337
Trinkler, I. 87
Trojano, L. 240, 241, 242, 243, 246, 247, 251
Tsukagoshi, H. 403
Tsukamoto, T. 286
Tsuzuku, T. 90
Tuccillo, R. 243, 246
Tuholski, S. W. 116, 117
Tulving, E. 122
Tunney, R. J. 121
Turnbull, O. 243, 249
Turner, R. S. 10, 120, 305
Turriziani, P. 16, 76, 114
Tye, M. 109
Tyler, L. A. 115
Tzelgov, J. 163
Tzourio, N. 85, 86, 88, 114
Tzourio-Mazoyer, N. 10, 65, 86

U
Udwin, O. 106
Ueda, H. 249
Umiltà, C. 76, 158, 165, 338, 405
Underwood, G. 120, 121
Ungerleider, L. G. 15, 114, 144, 174, 240, 297

V
Vaishnavi, S. 346, 353
Vakil, E. 227
Valenstein, E. 343, 347, 353, 405, 406, 408
Valenza, N. 351, 353
Vallar, G. 69, 75, 77, 102, 140, 146, 161, 165, 168, 246, 288, 300, 302, 337, 338, 339, 341, 342, 343, 344, 345, 346, 347, 348, 349, 350, 351, 352, 353, 354, 355, 356, 365, 366, 370, 371, 372, 373, 391, 397, 399, 405
Valoroso, L. 243, 246
Van Asselen, M. 40, 44, 225, 233
Van Buchem, M. A. 232, 233
Van den Heuvel, D. M. J. 232, 233
Van der Flier, W. M. 232, 232
Van der Lubbe, R. H. J. 44
Van Essen, D. C. 297
Van Gijn, J. 331
Van Lee, L. 115
Van Reekum, R. 231
Van Sommers, P. 251
Van Zandvoort, M. J. E. 223, 225
Vanderberg, S. G. 17, 18
Vanderplas, J. M. 32
Vanderwart, M. 26, 193
Vandierendonck, A. 18, 19, 106, 181
Vargha-Khadem, F. 90, 142
Varney, N. R. 239
Varraine, E. 94
Vecchi, T. 9, 15, 16, 17, 18, 19, 20, 25, 26, 33, 42, 43, 101, 102, 103, 104, 105, 106, 107, 108, 111, 115, 116, 117, 118, 119, 124, 125, 173, 174, 178, 181, 193, 194, 195, 197
Vecera, S. P. 346
Velmans, M. 260
Venneri, A. 31, 33, 104, 204
Verfaellie, M. 222
Vergani, C. 16, 106, 174
Vergha-Khadem, F. 18
Verhaeghen, P. 210
Verkoijen, I. G. 115
Viader, F. 147
Vianello, R. 23, 103
Viaud-Delmon, I. 91, 94
Vicari, S. 106
Victor, J. 349
Vighetto, A. 299, 300, 301, 302, 305, 337, 407
Villa, G. 241
Villardita, C. 142
Vinacke, W. E. 12
Vio, C. 28, 31, 113
Virtanen, J. 70
Vitello, G. 349
Vogel, E. K. 145
Vogt, B. A. 248
Von der Heydt, R. 349
Von Wright, J. M. 40
Voyer, D. 10, 106, 269
Voyer, S. 10, 106, 269
Vuilleumier, P. 74, 165, 345, 346, 347, 351, 353
Wade, D. T. 370
Walker, J. A. 405
Walker, R. 381, 391
Wallace, B. 113
Wallach, R. W.
Walsh, V. 15, 69, 74, 75, 163, 164
Wang, R. F. 112, 284, 287
Wang, P. P. 103
Wang, Z. 147
Wapner, W. 251
Warburton, E. 372, 373
Ward, R. 324
Ward, G. 141
Ward, T. B. 111, 144
Wardak, C. 74
Warlop, N. 163
Warren, A. 190
Warren, Jr. W. H. 90
Warrington, E. K. 7, 239, 345
Wartburg, V. R. 87, 88
Watson, R. T. 353, 408
Watt, R. 345
Waverling-Rijnsburger, A. W. E. 232
Weaver, K. L. 284
Weaver, S. L. 268

Weber, K. D. 90, 91
Wechsler, D. 7, 8, 21, 241
Weeks, R. A. 391
Weger, U. 160
Wehner, R. 284
Weiller, C. 71
Weiner, M. W. 243
Weise, M. 227
Weiskrantz, L. 121, 396
Weiss, P. H. 75
Welch, R. B. 340, 348
Welford, A. T. 191
Wentzel-Larsen, T. 243
Werkhoven, P. J. 90
Westendorp, R. G. J. 232, 233
Weverling-Rijnsburger, A. W. E. 232, 233
Wheeler, M. E. 145
Wijnalda, E. M. 221, 233
Wilcock, G. K. 243
Wilhelm, O. 23, 116
Wilk, C. 114
Williams, J. E. 40, 226
Williams, S. C. 240
Willison, J. R. 223, 224, 232
Willmes, K. 160
Wilson, M. A. 284
Wilson, B. A. 146
Wilson, L. 16, 21, 27, 28, 105, 178
Winocur, G. 86, 87, 114, 248
Wise, R. J. 372, 373
Wise, S. P. 391
Witte, K. L. 209
Wittman, W. W. 23, 116
Wroe, S. 71
Wu, W. H. 110, 112
Wunderlich, A. P. 285
Wylie, G. R. 349, 350, 355
Wynn, V. 142, 143

X
Xu, F. 158
Xuereb, J. 248

Y
Yamadori, A. 246, 391
Yantis, S. 353
Yates, F. A. 267
Yeo, G. F. 298
Yerkes, R. M. 7
Yoakum, C. S. 7
Yokosawa, K. 89
Yonelinas, A. P. 227
Young, A. W. 103, 391
Young, M. P. 297
Yuille, J. C. 259, 260, 267
Yule, W. 106

Z
Zaback, L. A. 115
Zacks, R. T. 39, 42, 45, 122, 187, 210, 213, 216, 226
Zafiris, O. 333
Zago, L. 65, 86
Zajonc, R. B. 121
Zampini, M. 338
Zangwill, O. L. 285
Zani, A. 349
Zappala, G. 142
Zarahn, E. 88, 114, 299
Zebian, S. 160
Zeffiro, T. A. 10
Zeki, S. 349, 391
Zelinski, E. M. 40, 191
Zeloni, G. 326
Zenderland, L. 6
Zhang, D. 147
Zhang, J. X. 147, 189, 190
Zhao, Z. 147
Zhen, Y. 189
Ziegler, P. E. 284
Ziegler, M. 86, 87
Ziemann, U. 71
Ziemons, K. 75
Zilles, K. 75, 333, 349
Zilli, T. 364
Zimmer, H. D. 15, 23, 47, 62, 110, 148
Zingerle, H. 364
Zoccolotti, P. 365, 366
Zonderman, A. B. 190
Zorzi, M. 76, 165
Zosh, W. D. 90
Zucco, G. M. 102

# Subject index


**A**
Active processes 192
Active task 26, 27, 28, 193
Allocentric cognitive map 86
Allocentric spatial memory 229
Allocentric strategy 86
Allocentric task 86
Alzheimer's disease (AD) 187, 230, 231, 232, 242, 243, 244, 245, 246, 247, 248, 249
Anisometry 398, 399
Anosognosia for hemiplegia 369
Anosognosia 365, 368, 369, 370
Anterograde disorientation 286
Asymmetrical hemispheric extinction 78
Auditory extinction 405
Auditory neglect 405
Autobiographical memory 144, 148
Automatic operation 39
Autotopoganosia 364

**B**
Battery of Visuospatial Abilities (BVA) 240
Bearing map 90
Behavioral specificità principle 262, 263
BENViS Battery 24, 25, 28, 31, 32
Bisection task 161, 300
Body centered neglect 381
Body image 363
Body representation 363
Body schema 364
Body structural description 364
Brief Visuospatial Memory Test – Reised (BVNT-R) 223

**C**
Caloric Vestibular Stimolation (CVS) 372, 373, 374
Central Executive (CE) 102
Cerebrovascular disease 230
Clock drawing test (CDT) 247, 249, 250
Closing-in 244, 246
Cognitive aging 188
Complex linear configuration 61
Concurrent reports 267
Constructional apraxia (CA) 240, 241, 242, 247
Corsi block test 27
Corsi blocks task 9, 21
Cortico-basal degeneration 243
Counsciousness 120, 122, 123, 338
Creative imagery 52
Crystallised intelligence 146
Cube Imitation Test 7, 8, 9

**D**
Digit span 9, 28
Dinamic Mazes 27
Directional Hypokinesia 406
Directional Hypometria 406
Distance Judgment Task (DJT) 398, 400, 401, 403
Distant effect 157
Dorsal premotor area (BA6) 251
Dorsal Visual stream 75, 247, 297, 298, 304, 314, 407, 408
Dots reproduction test 27
Dual task paradgm 195

**E**
Effortul processes 39
Egocentic space 303
Egocentric centered neglect 381
Egocentric disorientation 286
Egocentric representation 86, 288
Egocentric strategy 86
Egocentric task 86
Episodic buffer 143, 144, 145, 148
Episodic memory 144, 229
Event related potentials (ERP) 232
Event-specific Knowledge (ESK) 144, 145, 146
Excitatory-Inhibitory interactions 72
Explicit memory 228, 229, 232
Extinction 324, 328, 330
Extrapersonal neglect 366
Extrinsic encoding 16

**F**
Far space 328
FP task 58
Fronto-temporal dementia (FTD) 243, 246, 247

**H**
Heading disorientation 286
Hemianesthesia 331, 337, 374, 375
Hemianopia 387, 350, 404
Hemiplegia 331, 387
Hemispatial neglect 300, 302
Hippocampus 85
House Recognition test 26
Huntington's disease 230
Hypokinesia 367

**I**
Illusion in neglect 340, 346
Illusion of neglect 340, 347, 350
Image scanning 49, 50
Imagery strategies 141, 142
Imagination images 52
Implicit memory 228, 229, 232
Individual Differences Questionnaire (IDQ) 262, 264, 265, 266, 268, 270, 271, 272, 273, 274, 275, 276
Inner scribe 15

Interaural time differences (ITD) 405
Interhemispheric interaction 72
Intrinsic encoding 16

J
Jigsaw Puzzle Test (JPT) 26, 193, 194, 195
Judgement of line orientation test (JOLT) 239, 240, 248

K
KBR task 58, 60, 61

L
Landmark agnosia 286
Landmark test 353, 398
Lenght Judgment Task (LJT) 399, 400, 403
Lewy – body – dementia 231, 243
Line bisection task 74, 409
Location Learning Test (LLT) 223, 224, 231
Long Term Memory (LMT) 21, 51, 110, 116, 118, 119, 125, 204, 205, 206, 291

M
Memory images 52
Memory of routes 85
Mental imagery 91, 108, 143, 188, 203, 205, 206, 209, 210
Mental images 204, 206
Mental number line representation 164
Mental Number Line 76, 156, 157, 165
Mental rotation task 206, 208, 209
Mental rotation task 59, 209
Mental rotation test 17
Mental Scanning 108
Mental Status Questionnaire (MSQ) 223
Metric information 52
Mini Mental State Examinaiton (MMSE) 249
Misoplegia 367
Motor imagery 369
Multimodal spatial representation 324
Multisensory visuo-tactile system 325

N
Near peripersonal space 324, 324, 325, 327, 330
Near space 328
Number representation 156

O
Object centered neglect 382, 383
Object location binding 16
Object location memory 39, 42, 46, 222, 225, 230, 234
Object Relocation 224
Optic ataxia 299, 300, 302, 306, 308, 309, 314

P
PA: paired associate:
PA items 260
PA learning 260, 264, 272, 275, 276
PA recall 260, 267, 268, 270
Paired TMS 71, 72, 73
Paired-associate (PA) task 259
Paradigm of paired-TMS 73
Paradigm of selective interference 50
Parallel Map Theory (PMT) 89, 90
Parkinson disease 246, 248
Passive task 26,27, 28, 193, 195
Path encoding 16
Path integration 284
Pathway Span Task 27
Pattern encoding 16
Perceptual map 409
Performance test 8, 9, 12
Peripersonal neglect 366
Personal body space 364
Personal Encoding Preferences (PEP) questionnaire 265, 272
Personal neglect 365, 366
Phonological Loop (LP) 21, 102, 103
Pointing task 300
Posterior parietal cortex (PPC) 74, 288, 297
Premotor map 407
Prosopoagnosia 286
Pseudo-hemiplegia 367

Q
Questionnaire upon Mental Imagery – QMI 4, 5, 6

R
Relative controlesional overextenction (rCO) 397, 398
Reorientation 284
Repetitive TMS (rTMS) 70, 74, 75, 76, 79
Representational neglect 287, 291
Representational scotoma 338
Reproductive Imagery 51
Retrospective reports 267
Reversed SNARC effect 166
Rey-Osterreith Complex Figure (ROCF) 241, 242, 243, 246, 248
Right angular gyrus 77
Right parahippocampal gyrus 77
Right posterior parietal cortex 77, 78
Route learning 190

S
Scanning processes 56
Self-representational processes 120
Signs reproduction test 26
Simon Effect 158
Single-pulse TMS 71, 72
Size effect 157
Sketch map 90
SNARC effect (Spatial Numerical Association of Response Codes) 157, 158, 159, 160, 164, 165, 166, 168
Somatoparaphrenia 3697, 370, 374
Somatosensory neglect 372
Spatial distribution 396
Spatial encoding 89
Spatial extinction 69
Spatial memory 40
Spatial Memory 85
Spatial navigation 283
Spatial retrieval 89
Spatial span 9
Static Mazes 27

Subcortical vascular dementia 246
Superior Temporal gyrus (STG) 77, 78
Syllables Span Test 28

T
Tactile Perception 70, 73
Target location (TL) 289, 290
Test of Visual Imagery Control – TVIC 5, 6
Tests of spatial ability 8, 10, 11
Topographic memory 86
Topographical agnosia 286
Topographical disorientation 285
Topographical memory 190
Topokinetic memory 89
Topological Representation of Egocentric Space (TRES) 370
Transient global amnesia (TGA) 147

U
Unilateral Spatial Neglect (USN) 165

V
Ventral premotor area (BA44) 251
Ventral visual stream 75, 247, 297, 298, 300, 311, 314, 407, 408
Verbal interfrence effect 41
Verbal re-coding strategies 142
Verbal short-term memory 141
Vestibular-ocular reflex (VOR) 90, 95
View dependent place recognition 284
Virtual Reality (VR) 87, 92
Visual cache 15, 19
Visual Comparison Test 7
Visual form agnosia 302
Visual mental imagery 203
Visual Object and Space Perception Battery (VOSP) 239, 247
Visual Pattern Test (VPT) 18, 19, 21, 23, 27, 28, 32, 33
Visual Pattern Test Active Version (VPTA) 28
Visual peripersonal space 324, 325, 326, 327, 330
Visual search 59
Visual short-term memory 140
Visual spatial neglect 77
Visuo Spatial Sketch Pad (VSSP) 102, 103, 124, 140
Visuo spatial span 176, 181
Visuoconstructional disorders 239
Visuospatial abilities 239
Visuospatial disorders 239
Visuospatial Learning Disabilities (VSLD) 31
Visuo-spatial mental imagery 110
Visuospatial perception 76
Visuo-Spatial Working Memory (VSWM) 15, 16, 17, 18, 19, 22, 23, 24, 25, 29, 32, 33, 101, 107, 108, 109, 111, 112, 113, 114, 115, 116, 117, 118, 123, 124, 174, 181, 187, 188, 189, 190, 191, 192, 194, 195, 196, 198
Vividness of Visual Imagery Questionnaire – VVIQ 4, 5, 6, 18, 261, 262, 263, 264, 265, 270, 271, 276

W
What system 15
Where system 15
Word lengh effect 175
Working memory (WM) 101, 102, 103, 104, 105, 106, 107, 108, 116, 117, 119, 123, 124, 174, 188, 191, 192, 193, 194, 196, 198, 204, 205, 206, 210, 232, 311

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