Review

Effects of peripheral and central visual impairment on mental imagery capacity

David Dulin [a], Yvette Hatwell [b], Zenon Pylyshyn [c], Sylvie Chokron [a,b,*]

[a] ERT Treat Vision, CNRS UMR 5105 and Service de Neurologie, Fondation Ophtalmologique Rothschild, 75019 Paris, France
[b] Laboratoire de Psychologie et NeuroCognition, CNRS UMR 5105, Grenoble, France
[c] Center for Cognitive Science, Rutgers University, Piscataway, NJ 08854-8020, USA

A B S T R A C T

This paper reviews a number of behavioral, neuropsychological and neuroimaging studies that bear on the question of whether and how visual disorders of peripheral or central origin lead to disorders of mental imagery capacity. The review of the literature suggests that in cases of blindness of peripheral origin lack of vision can progressively lead to representational disorders. However, in patients suffering from peripheral visual deficits, representational disorders can partially or completely be compensated by other sensory modalities as well as by cortical reorganization. Interestingly, in brain-damaged patients, neurovisual disorders following occipital or parietal lesions are not systematically associated with representational deficits, thus demonstrating that visual perception and visual imagery may not rely on the same cortical structures as previously hypothesized. Impairments seen on mental imagery tasks among brain-damaged patients with visual and/or spatial deficits might be due to an often co-existing attentional deficit. We discuss this possible dissociation between visual perception and visual mental imagery and its implications for theoretical models of mental representation.

© 2008 Elsevier Ltd. All rights reserved.

Contents

* Corresponding author at: Equipe Treat Vision, Service de Neurologie, Fondation Ophtalmologique A de Rothschild, 25 rue Manin, F-75019 Paris, France.
Tel.: +33 1 48 03 66 45; fax: +33 1 48 03 68 59.
    E-mail address: chokron@ext.jussieu.fr (S. Chokron).
    URL: http://www.upmf-grenoble.fr/upmf/RECHERCHE/lpe/index.html

1. Introduction: the notion of mental imagery

Binet (1886) and Titchener (Evans, 1984) defended the idea that mental images should be considered as the central elements of thought. In Europe, the Wurzburg school put forth the idea that certain mental process elements were non-pictorial and that imaging activity should be considered as the result of these non-image processes. Arguments between these two schools went on until the 1920s when a provisional solution was adopted: if images can play a role in thought, then they might contain information inaccessible to introspection. Soon after, with the emergence and growth of the behaviorist revolution, the associationist tradition and the "thought without images" school resulted in the decline in investigation of imagery and other subjective sources of evidence, such as introspection. As a result, for over 30 years, from the beginning of the 1920s until the 1950s, imagery was nearly totally excluded from experimental psychology.

Perhaps due in part to Piaget's research, cognitive psychology put mental images back into the center of psychological research in the 1960s. Indeed, the main aspects of Piaget's works were followed up by numerous authors who studied mental imagery in the context of learning and memory (Neisser, 1967; Paivio, 1971). From then on, mental image was not considered as the continuation of perceptual activity or as a residual form of sensation, but as the result of symbolic activity. It was no longer viewed as a passive copy of former perceptive experience, but as an active construction operated by the cognitive system.

In 1971, Paivio proposed a dual code model, in which mental activities involve two distinct systems each having structural and functional properties. The first system consists of verbal representations and derives from language experience, whereas the second, the image, derives from perceptual experience. According to Paivio, these two systems are complementary in the construction of mental representation. Some theorists (e.g., Pylyshyn, 1981) claimed that what were called "verbal representations" and "imaginal representations" differ primarily in their content (i.e., image representations encode appearances while propositional representations encode more abstract properties) and that current evidence does not support the view that they comstitute a different format.

Those who maintain that mental images are encoded in a distinct (perhaps analogical) form attempt to characterize the functional properties of images and to determine which cerebral structures are responsible for these properties. As we will see later in this review, functional neuroimaging have been extensively used to examine whether the same areas are involved in visual perception and in mental imagery. Kosslyn (1994) argued that visual mental images are quasi-pictorial representations: "*Depictive representations convey meaning via their resemblance to an object with parts of the representation corresponding to parts of an object*" (Kosslyn, 1994). Kosslyn and Shwartz (1977) formalized the hypothesis of the imagery/perception equivalence in a computational model, in which a unique visual buffer is used both in an ascending (bottom-up) pathway to accumulate and hold visual percepts and a descending (top-down) pathway to hold the images generated internally Consequently any perceptual deficit should be associated with a corresponding deficit in mental imagery.

Conversely, Pylyshyn (2003a) suggested that experimental findings supporting the picture theory could be explained by the fact that when asked to imagine something, people ask themselves what it would be like to see it and then simulate various properties of the world as they might perceive it. He refers to this explanation as the "null hypothesis", since it makes no assumptions about the format of the mental image. According to Pylyshyn (2003b), the distinction between effects attributable to the intrinsic nature of

mental mechanisms and those attributable to more transitory states (e.g., people's beliefs, utilities or interpretation of a task) is central not only for understanding the nature of mental imagery but also for understanding mental processes in general. The former explanation, which appeals to cognitive architecture (Fodor and Pylyshyn, 1988; Newell, 1990; Pylyshyn, 1980, 1984, 1991, 1996), is not directly altered by changes in knowledge, goals, or any other representations (e.g., hope and fear), whereas the latter, referring to non-architectural thought, may be recognized by the ease with which mental images are revised by changes in beliefs or "tacit knowledge" (it is "cognitively penetrable"). "*In interpreting the results of imagery experiments, it is clearly important to distinguish between cognitive architecture and tacit knowledge as possible causes*" (Pylyshyn, 2003b).

The aim of the present paper is to understand to what extent the integrity of visual perception is necessary for visual mental imagery. As mentioned above, according to Kosslyn (1994) and Kosslyn and Shwartz (1977), a unique visual buffer is used in an ascending (bottom-up) pathway for visual percepts and a descending (top-down) pathway for images generated internally. Therefore, any visual deficit of central or peripheral origin should induce a corresponding deficit in generating or manipulating mental images. Whereas, according to Pylyshyn (1980, 1984, 1991, 1996), visual perception and mental image generation should be seen as relying on dissociable processes. The interest of studying mental imagery performance in patients with peripheral and central visual disorders is both theoretical and clinical. From a theoretical point of view, we need to understand if visual perception and mental imagery rely on the same functional processing and/or anatomical structures. Studying patients with ophthalmologic diseases can illustrate how the absence of visual information affects mental imagery; whereas in patients with neurovisual deficits the effects of cortical lesions on mental imagery performance can be investigated. From a clinical point of view, if the deficit observed is in visual perception and mental imagery is spared, this ability can perhaps be trained to compensate for the lack of useful perception in problem solving, spatial localization, conceptualization and other cognitive tasks.

Before specifically discussing mental imagery capacities in patients with visual and neurovisual disorders, we will present neuroimaging studies of mental imagery which have focused on the general versus specific cortical areas involved in visual perception and visual mental imagery.

2. Neuroimaging studies of mental imagery

Kosslyn et al. (1993) reported experiments using positron emission tomography (PET) to compare cortical activity during mental imagery with activity during visual perception. Participants were first presented with a grid of 5×4 cells in which one of the cells contained an X-mark. In the imagery condition, participants had to visualize an uppercase letter and decide whether this letter would have covered the X-mark if it were present in the grid. In the perceptual visual condition, the uppercase letter was superimposed on the grid and the same kind of decision was required. The primary visual cortex was activated in both conditions suggesting that imagery and perception call upon common cerebral mechanisms. Activation was also greater in imagery than in perception indicating that the generation of a visual image is a more demanding cognitive task than perception. Tootell et al. (1998) conducted a variant of Experiment 3 of Kosslyn et al. (1993), asking a participant to visualize letters at the smallest visible size or visualize a field of letters (sparing a small central region). A cortical unfolding algorithm was used to demonstrate that areas 17 and 18 were

activated during both conditions, although as reported by Kosslyn et al. (1993, 1995), there was greater activation in the foveal region when images were formed at a small size than when they covered the field. Interestingly, using a similar protocol as Kosslyn et al. (1993), a hemispheric specialization was found. Forty participants performed both a perceptual and an imagery task. In the imagery task, simple dot patterns were presented for 5 s in free vision, followed by a 3 s fixation field. Subsequently, a circle was briefly presented in either the right or the left visual field and participants were required to indicate whether or not the circle surrounded a point previously occupied by a dot. The perceptual task was similar except that the dot patterns remained on the screen while the circle was presented. Reaction times and error data indicated a left visual field advantage on the imagery task only, suggesting a right hemisphere superiority for extraction of spatial information from images.

Transcranial magnetic stimulation (TMS) was also used to study the anatomical correlates of mental imagery. In order to determine if visual mental imagery can modulate visual cortex excitability, Sparing et al. (2002) stimulated the primary visual cortex of 20 healthy blindfolded participants with TMS. Participants performed a visual imagery task and an auditory control task. The visual imagery task was based on that previously used by Kosslyn et al. (1993). The authors hypothesized that analogous to the finding that motor imagery increases the excitability of motor cortex visual imagery should increase visual cortex excitability as indexed by a decrease in the phosphene threshold (PT). In order to test visual cortex excitability, the primary visual cortex was stimulated with TMS, so as to elicit phosphenes in the right lower visual quadrant. TMS was applied with increasing intensity to determine the PT for each participant. Independent of the quadrant in which participants placed their visual images, imagery decreased PT compared to baseline PT; in contrast, the auditory task did not change PT. According to the authors, these results constitute evidence that early visual areas participate in mental imagery processing. In the same vein, Sack et al. (2005) combined triple-pulse transcranial magnetic stimulation (tpTMS) and repetitive TMS (rTMS) to determine which distinct aspect of mental imagery is carried out by the left and right parietal lobe and to reveal interhemispheric compensatory interactions. The left parietal lobe was predominant in generating mental images, whereas the right parietal lobe was specialized in the spatial comparison of the imagined content. Furthermore, in the case of an rTMS-induced left parietal lesion, the right parietal cortex could immediately compensate such a left parietal disruption by taking over the specific function of the left hemisphere.

Regarding the implication of the parietal and primary visual cortex found in these TMS studies, it should be noted that the tasks were not pure imagery tasks since they involved allocating visual attention to places in the visual scene. Thomas (1999), Bartolomeo and Chokron (2002a,b), and Rode et al. (2007) had postulated that visual mental imagery involves some of the attentional exploratory mechanisms that are employed in visual behavior and may thus be affected by a deficit in orienting attention in extracorporeal space, such as what is seen in unilateral spatial neglect. In the same vein, Pylyshyn (2003c, 2007) has argued that imagined space intrinsically rests on concurrently perceived spatial layouts so these types of "spatial imagery" tasks require spatial (in these cases, visual) attention. In this way, the occipital activation seen during visuospatial mental imagery tasks could be the consequence of visuo-attentional processing during the representational task rather than an argument in favor of mental images being quasi-pictorial representations (Kosslyn et al., 2006).

The same might be said of the many other studies that have compared cortical areas activated by mental imagery and by visual

perception through the use of flashing lights (Le Bihan et al., 1993; Sabbah et al., 1995), mental navigation tasks (Chen et al., 1998), shape and color perception and representation (Goldenberg et al., 1992), sets of stripes (Ishai et al., 2002; Thompson et al., 2001), faces (O'Craven and Kanwisher, 2000), and shape and object rotation (Klein et al., 2004; Slotnick et al., 2005; Wraga et al., 2005), which have all found an activation of area 17 during execution of the tasks.

Quite different results have been reported by several other investigators who did not find primary visual area involvement in a variety of mental imagery tasks (Roland and Gulyas, 1994). Roland et al. (1987) asked 10 participants to close their eyes and imagine walking through their hometown. They were instructed to imagine going out the door and taking the first left turn, then alternating right and left turns while paying attention to their surroundings. The participants were to imagine their surroundings vividly and in full color, and they were not to pay attention to their own movements. Imagery was monitored continuously for 180–200 s. The baseline was rest during which participants were instructed to avoid thinking about anything in particular and especially to avoid mental images. All participants reported that during rest, it had been "dark in their mind's eye" (Roland et al., 1987). After the participants finished the task, they indicated the location where they had arrived and this location was looked up on a map. Authors did not report whether the participants made the appropriate alternating left and right turns, but did claim that the participants were never lost and were always able to recall images of their surroundings. In this case there was no activation of area 17, but there was an activation of the bilateral posterior superior parietal cortex, as well as other areas.

Mellet et al. (2000) used positron emission tomography to investigate the neural activity during a mental spatial task. One group of participants performed a mental exploration task in an environment after being trained in real navigation (i.e., mental navigation task). Another group of participants explored the same environment learned from a map (i.e., mental map task). The results showed an activation of a parieto-frontal network composed of the intraparietal sulcus, the superior frontal sulcus, the middle frontal gyrus and the pre-SMA, as well as other areas regardless of learning conditions. Similarly, many other studies found no primary visual area involvement during a variety of mental imagery tasks, including mental navigation (Ghaëm et al., 1997; Mellet et al., 1995), imagining three-dimensional objects (Mellet et al., 1996), imagining the appearance of verbally named objects (Formisano et al., 2002; Goldenberg et al., 1987; Mellet et al., 1998), and constructing vivid images of faces (Ishai et al., 2000).

In contrast with the primary visual area debate (see Cocude et al., 1999; Kosslyn and Thompson, 2003 for reviews), there is general consensus on the role of associative visual areas in mental imagery. Most studies suggested that the two visual systems observed in visual perceptual information processing (occipito-temporal and occipito-parietal pathways) are reflected in the mental imagery domain.

The occipito-temporal pathway is specialized in the processing and recognizing of object forms and faces. In general terms, it is specialized in the storage and the retrieval of figurative aspects of visual representations. Mellet et al. (1998) demonstrated that a network that includes a part of the bilateral ventral stream is recruited when mental imagery of concrete words is performed on the basis of continuous spoken language. In their study, the functional anatomy of the interactions between spoken language and visual mental imagery was investigated with PET in eight normal volunteers during a series of three conditions: listening to concrete word definitions and generating their mental images,

listening to abstract word definitions, and during a period of silence. The concrete task specifically elicited activations of the bilateral inferior temporal gyri of the left premotor and prefrontal regions. Activations in the bilateral superior temporal gyri were smaller during the concrete task compared to the abstract task. During the abstract task, an additional activation of the anterior part of the right middle temporal gyrus was observed.

In a functional magnetic resonance imaging (fMRI) study, Ishai et al. (2000) measured activations in nine participants by comparing MR images obtained during performance of the following tasks: perception (passive viewing of faces), perception-control (passive viewing of scrambled pictures), imagery (generation of vivid images of familiar faces from long-term memory while viewing a gray square), and imagery-control (passive viewing of a gray square). The results revealed an activation of regions in the ventral temporal cortex during the imagery task. Other studies have found activation in ventral visual areas during the generation of mental images of either visually recalled or named common objects (Ghaëm et al., 1997; D'Esposito et al., 1997; Mellet et al., 1998), letters (Kosslyn et al., 1993), and unusual objects (Mellet et al., 1996). Nevertheless, while it is well established that ventral visual areas are involved in object mental imagery, the existence of functional hemispheric asymmetry remains in debate. In an fMRI study in which participants had to generate a mental image of an object or animal upon listening to its name, D'Esposito et al. (1997) reported left lateralized activations of the inferior temporal and fusiform gyri. These results are in disagreement with previous reports of bilateral (Kosslyn et al., 1993) or right lateralized (Mellet et al., 1996) activations of the same areas during mental image generation of letters or complex forms, respectively.

Several recent PET studies have demonstrated that the dorsal pathway can be recruited by spatial tasks performed on mental images in absence of any visual input. For example, it has been shown that mentally displacing one's gaze along the border of the mental image of an imaginary island (Mellet et al., 1995, 1996), mental navigation along routes previously memorized through a walk in the real environment (Ghaëm et al., 1997) and mental rotation of patterns (Cohen et al., 1996; Jordan et al., 2001; Kosslyn et al., 1998; Ng et al., 2001; Richter et al., 2000) activated the occipito-parietal route. Sack et al. (2002) investigated the functional relevance of brain activity during visuospatial tasks by combining fMRI with unilateral rTMS. The cognitive tasks involved visuospatial operations on visually presented and mentally imagined material (e.g., "mental clock task"). The results showed that visuospatial operations were associated with bilateral activation of the intraparietal sulcus region and demonstrated the capacity of the right parietal lobe to compensate for a temporary suppression of the left parietal lobe.

Studies have also found that visual cortical areas are active during tactile perception. According to most of these studies, the dichotomy between occipito-temporal ("what") and occipito-parietal ("where") pathways could also be found in tactile mental imagery. A dorsal extrastriate region in the parieto-occipital cortex was shown to be activated by visual discrimination of grating orientation (Sergent et al., 1992). Sathian et al. (1997) have demonstrated that this region was also activated by tactile discrimination of grating orientation. Further, Zangaladze et al. (1999) and Sathian and Zangaladze (2002) showed that TMS over this area interfered with performance of the tactile version of this task, thus establishing the functional relevance of the parieto-occipital cortex activity for tactile perception. Other groups found that haptic object identification engages striate and extrastriate visual cortex (Deibert et al., 1999; Stoeckel et al., 2003), especially the lateral occipital complex (Amedi et al., 2001, 2002). To

investigate possible interactions between the visual and haptic systems, James et al. (2002) used fMRI to measure the effects of cross-modal haptic-to-visual priming on brain activation. The results showed that haptic exploration produced activation in primary somatosensory cortex, an area of the central ventrolateral temporal lobe, middle occipital area, the lingual gyrus and the peripheral representation of area V1. Therefore, haptic exploration of three-dimensional objects produced activation, not only in the somatosensory cortex, but also in areas of the occipital cortex associated with visual processing (i.e., middle and lateral occipital areas). Furthermore, previous haptic experience with these objects enhanced activation in visual areas when these same objects were subsequently viewed. According to the authors, these results suggest that the object-representation systems of the ventral visual pathway are also used for haptic object perception. Along the same lines, it has been found that haptic form recognition is dependent on visual experience. Bailes and Lambert (1986) thus demonstrated that normally sighted participants are both faster and more accurate than the adventitiously and congenitally blind groups; with sighted participants reporting using strategies with a strong verbal component while the blind tended to rely on imagery coding. The authors interpret these results in terms of information-processing theory consistent with dual encoding systems in working memory.

According to the studies mentioned above, the anatomo-functional duality between dorsal and ventral pathways related to the spatial or object nature of imagery tasks appears to closely match the one evidenced in the visual perception domain, regardless of whether the stimuli is visual, verbal or tactile. However, all regions recruited by visual sensory processing are not systematically involved in mental imagery. The hypothesis of an anatomo-functional similarity between vision and mental imagery was confirmed in the spatial domain by French and Painter (1991). These authors submitted normal participants to an imagery task in which simple dot patterns were presented for 5 s in free vision, followed by a 3 s fixation field. Subsequently, a circle was briefly presented in either the right or the left visual field and participants were required to indicate whether or not the circle surrounded a point previously occupied by a dot. The perceptual task was similar except that the dot patterns remained on the screen while the circle was presented. The authors found a right hemisphere superiority for the extraction of spatial information for mental imagery mimicking the well-known right hemisphere superiority for spatial cognition (in right-handed participants).

Amedi et al. (2005a) argued that visual perception cannot be dissociated from multisensory experience of the object (Amedi et al., 2005b; Beauchamp, 2005; Pascual-Leone et al., 2005), and that imagery can be either multisensory or purely visual (simply involving seeing a given object or pattern "with the mind's eye"). To test this hypothesis, the authors examined the difference in brain activity as indexed by fMRI between visual perception and visual imagery of objects, while nine participants performed either a visual object recognition task (VO), viewed scrambled images of the same objects (SCR), or created vivid mental images of familiar objects retrieved from memory (VI). As contrasted with rest, both VO and SCR tasks showed positive activation in specific visual brain regions and showed negative activation in medial posterior and lateral posterior areas. They found that VI showed a positive activation involving visual object areas (lateral occipital complex), retinotopic areas, as well as prefrontal and parietal areas, in concordance with previous reports (Ishai and Sagi, 1995; Ishai et al., 2000; Kosslyn et al., 1999; Kreiman et al., 2000; Mechelli et al., 2004; O'Craven and Kanwisher, 2000). The main finding of this research was that visual imagery seems to be associated with deactivation of non-visual sensory processing (auditory cortex and

somatosensory cortex) as well as with bottom-up input into early visual areas (LGN and SC). According to the authors, this might functionally isolate the visual cortical system from multisensory and bottom-up influences and thus increase one's ability to create a vivid mental visual image. In this way, an activation of the visual cortex is expected during mental imagery tasks; however, several studies have failed to report an activation of primary visual areas during such tasks (Ishai et al., 2000; Knauff et al., 2000; Mellet et al., 1995, 2000; Wheeler et al., 2000). Interestingly, some authors have also shown that EEG measures may reveal object-related differences rather than a common cortical activation during perception as well as during imagery (Schupp et al., 1994). As described above, studies recording brain activity during mental imagery have repeatedly focused on an activation of visual cortical areas during mental imagery and thus argue in favor of a strong anatomical and functional link between visual perception and mental imagery. However, as we will discuss below, studies in patients with peripheral or central visual deficits do not confirm this hypothesized dependence between visual perception and mental representation.

3. Visual and neurovisual disorders and mental imagery capacity

Visual perception begins at the level of the eye, which is a peripheral receptive organ. The eye's retinal cells transmit visual information to cortical areas, converting the electromagnetic energy into electrical pulses, which are then transmitted to the cortex, passing through the optic chiasm, optic tracts, and the lateral geniculate body. Consequently, damage to the visual system can result from disorders affecting the input from the eyes, disturbance of visual processing by the brain, as well as impaired control of eye movement and disordered focusing. The study of visual imagery capacity in patients with either peripheral (eye or optic nerve damage) or central (optic tract or visual cortical areas) visual disorders represents a direct way of studying the link between vision (processes and neuroanatomical basis) and mental imagery. Despite the obvious relevance of cases of visual impairment, mental imagery in blind people has not been extensively investigated. Only a few studies have focused on the effect of a cortical lesion of visual areas on mental imagery. However, comparing the effects of vision loss and cortical damage gives us the opportunity to study both the roles of visual processing and of visual cortical areas on mental imagery processing. Below we review some of the experimental studies on mental imagery in patients with a peripheral or a central visual disorder and subsequently discuss their theoretical implications for mental imagery models.

3.1. Visual impairments of peripheral origin and mental imagery capacity

As previously mentioned, observing patients with peripheral visual lesions during mental imagery activities should provide evidence of links between perceptual and representational processes. Additionally, mental imagery processes can also be studied in modalities other than vision. Observing blind participants in this type of activity is therefore an excellent means of increasing our knowledge of mental imagery in sensory modalities other than vision. We can ask: In the absence of any visual experience, how do congenitally blind people create images of their surroundings? Do mental images depend essentially on perceptual experience?

Most recent work in this area shows that vision is not a prerequisite for the acquisition of spatial concepts (Aleman et al., 2001; Bértolo et al., 2003; Dulin, in press; Kaski, 2002; Thinus-Blanc and Gaunet, 1997; Tinti et al., 2006; Vanlierde and Wanet-Defalque, 2004; Vecchi et al., 2001). Early blind people clearly have spatial images. However, some studies have shown that blind people may experience some limitations in their mental imagery capacities. These are reviewed below.

3.1.1. Sighted versus blind people: structural and functional similarities of mental imagery

Kerr (1983) used a mental exploration task and showed that it takes more time to mentally explore greater distances for the sighted as well as for the blind. However, the congenitally blind took longer overall than the late blind participants (i.e., blinded after complete development of the visual system). It seems, therefore, that the blind may create and manipulate spatial representations just as the sighted do, although visual experience allows a faster generation and treatment of mental spatial images. This conclusion was questioned by Röder and Rösler (1998). These authors presented a task of mental distance exploration to congenitally blind adults and sighted adults who were blindfolded, with a phase of spatial representation learning through tactile exploration. In this condition, there was no difference between the two groups in chronometric data. Zimler and Keenan (1983) compared congenitally blind and sighted adults and children on three tasks presumed to involve visual imagery. The first experiment used a paired associate task with words whose referents were high in either visual or auditory imagery. Experiment 2 used a free recall task for words grouped according to modality-specific attributes, such as color and sound. In the third experiment, participants formed images of scenes in which target objects were described as either visible in the picture plane or concealed by another object and thus not visible. In all three tasks, blind participants' performances were remarkably similar to the sighted. In their experiment, Haber et al. (1993) asked seven sighted and seven blind participants who were all familiar with a room, and six sighted participants who were unfamiliar with it, to estimate the absolute distances between ten salient objects in the room. The 14 familiar participants made their estimates twice: while they were in the room and while they were far from it. The results revealed no qualitative differences as a function of blindness. The effect of location of testing was the same for both the sighted and the blind: all participants displayed better spatial knowledge when tested in the room and substantially underestimated true distance when tested out of the room.

3.1.2. Mental imagery capacity limitation in the blind?

A number of studies have shown that early blind adults have a more limited capacity to generate spatial mental images than do sighted adults. Arditi et al. (1988) found that in the congenitally blind, imagery capacities were worsened by the presence of certain typically visual aspects and, therefore, unknown to the blind (i.e., perspective). De Beni and Cornoldi (1988) explored the limitations of representations that maintained some properties of visible objects and are constructed on the basis of information from various sources. In a series of experiments requiring memorization of single nouns, pairs of nouns, or triplets of nouns associated with a cue noun, they found that the recall of blind participants was impaired for multiple interactive images (with noun pairs and triplets). Similarly, according to Cornoldi et al. (1991) and Cornoldi and Vecchi (2000, 2003), early visual experience has a facilitating effect on spatial mental imagery generation and use. These authors presented blind and blindfolded sighted participants either two-dimensional (3×3 or 4×4) or three-dimensional ($2 \times 2 \times 2$ or $3 \times 3 \times 3$) matrices made of wooden cubes. Participants were asked to memorize the starting position and the movements of a

dot given verbally by the experimenter ("one step ahead, one step to the right, etc."), and then to indicate the final position of the dot. The congenitally blind manifested more difficulties when they had to work quickly and when working with three-dimensional matrices. Gaunet and Thinus-Blanc (1996) studied the ability of blind and blindfolded sighted adults to localize objects in small and large scale spaces. They observed a mental imagery capacity limitation in the blind. The place of one object was changed between presentation and test phases, which the participants had to detect. Results showed that the exchange of places between two objects (topological change) was equally well-discriminated by the blindfolded sighted, as well as by early and late blind participants; whereas, the congenitally blind demonstrated some difficulty in detecting an object's shift in centimeters (metric change).

Vecchi et al. (2004) suggested that the difficulties experienced by the blind in spatial processes are due to the simultaneous treatment of independent spatial properties by the visual modality. These authors demonstrated that although the lack of vision does not impede on the capacity to generate and transform mental images, the congenitally blind are significantly poorer in the recall of multiple patterns than in the recall of the corresponding materials integrated into a single pattern. Therefore, the authors suggested that the simultaneous maintenance of different spatial information is affected by congenital blindness, while cognitive processes which imply a sequential manipulation are not. Another possibility is that blindness could result in slower mental imagery manipulations rather than a disturbance per se. On a mental rotation task, Marmor and Zaback (1976) demonstrated that the blindfolded sighted performed mental rotations at 233° per second, whereas the late and congenitally blind were rotating at 114° and 59° per second, respectively. According to these authors, the congenitally blind also had a significantly higher matching error rate. This experimental paradigm was used in other studies and, even if the response times were similar, no difference was found between the early blind, the late blind and the blindfolded sighted's error rates (Carpenter and Eisenberg, 1978).

A number of authors agree on the fact that the mental images of blind people partly share the same structural and functional characteristics as those of sighted individuals, but with specific differences. Any early blind person can access visual spatial imagery by organizing information sources differently given that his/her mental image is mostly based on haptic, vestibulary, and verbal spatial information (Cornoldi et al., 1988; Hatwell, 2003; Vecchi et al., 2001). Hollins (1985), using a pictorial imagery task (i.e., a checkered matrix) and a non-pictorial imagery task (i.e., assembly of three-dimensional cubes) suggested that blindness progressively erases any trace of information filed in a visual form. Participants were asked to mentally represent patterns and then name common objects that resemble the patterns they had imagined. The results indicated that recently blinded participants performed better in the pictorial imagery task, whereas the blind, whose blindness had a longer history, had better performance on the non-pictorial task. According to Hollins (1985), the nature of mental imagery progressively changes with the loss of sight, the visual element being progressively replaced by a representation based on haptic experiences. Along the same line, Dulin and Hatwell (2006) suggested that the prior expertise in the use of raised-line materials could influence the performance of blind participants (whose blindness was of peripheral origin) in different activities of mental imagery. The authors presented a mental rotation task and a mental spatial displacement task to groups of late and congenitally blind adults. Blind participants were divided into 'experts' and 'non-experts' according to their interest and mastery of raised-line drawings and their performances on a pretest which included thermoformed shape identification, draw-

ing tasks, and puzzle construction. The authors observed that (i) the congenitally blind 'experts' performed significantly better in the two imagery tasks than the 'non-expert' late blind, and (ii) the 'expert' late blind, who lost sight between the ages of 4 and 8 years, performed better than the 'non-expert' late blind, who lost sight after the age of 8.

3.1.3. Neuroimaging studies of mental imagery capacities in the blind

Using cerebral metabolic rate for glucose as a marker of neuronal function, Wanet-Delfaque et al. (1988) showed that long-standing visual deprivation (early blind participants) led to higher regional use of glucose in striate and prestriate cortical areas compared to blindfolded, sighted controls, whether at rest or during an auditory or tactile task. In a related study, De Volder et al. (1997) showed that the regional analysis of cerebral blood flow, metabolic rates for oxygen and glucose utilization revealed that these parameters were not significantly different between blind participants and blindfolded, sighted controls. Veraart et al. (1990) compared glucose metabolism in early and late blind individuals. They found similar patterns in the visual cortex of early blind participants and healthy, sighted controls with eyes open. In contrast, late blind participants demonstrated a lower pattern of glucose metabolism in the visual areas than that observed in healthy, sighted controls with eyes closed. In a PET study, Buchel et al. (1998) demonstrated that congenitally blind participants showed task-specific activation of extrastriate visual areas and parietal association areas during Braille reading, compared with auditory word processing. In contrast, blind participants who lost their sight after puberty showed additional activation in the primary visual cortex with the same tasks. The authors hypothesized that activation of area V1 in late blind participants was the result of visual imagery associated with early visual experience. Kosslyn et al. (1999) argued that visual perception and visual mental imagery share a similar neuro-anatomical substrate. The authors examined the contribution of early visual cortex, specifically V1, toward visual mental imagery by the use of two convergent techniques. In one experiment, participants closed their eyes during PET while they visualized and compared properties of sets of stripes. In the other, rTMS was applied to the medial occipital cortex before presentation of the same task. The results suggested that the primary visual cortex is activated in normal sighted individuals during visual imagery and that disruption of medial occipital cortex with rTMS impairs the ability to carry out imagery tasks.

It could be argued that the activation of occipital networks in the blind reflects the visual representations of stimuli generated by tactile stimulation as discussed above. However, this argument does not seem to hold true for congenitally blind individuals who have not had prior visual experience (Burton et al., 2002; Gizewski et al., 2003).

3.1.4. Cortical plasticity and mental imagery capacities in blind people

Uhl et al. (1994) recorded patterns of cortical activity by scalp-recorded, event-related, slow negative dc potential shifts in nine early blind and 23 sighted participants while they imagined the feel of textures with the fingertips of one hand. The results showed that activity significantly differed between groups, indicating that the occipital potentials of the blind were relatively more negative as related to the other scalp areas than were the occipital potentials of the sighted as related to the other scalp areas. The authors suggested that this occipital finding might indicate a participation of the blind's visually deprived occipital cortex in tactile imagery. To investigate if cross-modal plasticity contributes to sensory compensation when visual loss occurs at an older age, Cohen et al. (1997) used H2(15)O PET to identify cerebral regions activated in

association with Braille reading and rTMS to induce focal transient disruption of function during Braille reading in eight participants who became blind after age 14 (late-onset blind). The results showed that visual cortex activations during Braille reading were not significant in participants who lost their vision after age 14, while primary and extrastriate visual areas were activated in both congenitally and early blind individuals. The authors suggested that the sensitive period for this form of functionally relevant cross-modal plasticity does not extend beyond age 14. In a related study, Sadato et al. (2002) measured the change of regional cerebral blood flow (using 3.0 T fMRI) during passive tactile tasks performed by 15 blind and 8 sighted participants to investigate the reorganized network of the primary visual cortex (V1). The results showed that V1 was activated during a tactile discrimination task in blind participants who lost their sight before sixteen years of age, whereas it was suppressed in blind participants who lost their sight after age 16. The authors suggested that the first sixteen years of life represents a critical period for a functional shift of V1 from processing visual stimuli to processing tactile stimuli. Pascual-Leone and Hamilton (2001) have confirmed these observations by demonstrating that a 5-day period of complete blindfolding was enough to induce functionally relevant occipital recruitment in response to tactile processing in healthy, adult participants. These results argue against the establishment of new connections to explain cross-modal interactions in the blind. Rather, latent pathways that participate in multisensory percepts in sighted participants might be unmasked and may be potentiated in the event of complete loss of visual input (Theoret et al., 2004).

To determine if the activation of the occipital cortex is involved in Braille reading, Cohen et al. (1997) delivered rTMS to different scalp positions during Braille reading. Stimulation of occipital areas induced more accuracy errors than stimulation of control positions. The authors suggested that occipital cortex is not only active in Braille reading, but is one of the important functional components of the network mediating Braille reading in the blind. Consistent with this idea is the case of a patient suffering from 'braille alexia' after a bilateral occipital lesion (Hamilton et al., 2000; see Pascual-Leone et al., 2005 for discussion).

Many studies using neuroimaging techniques have also established that posterior visual areas in blind individuals may be active during the performance of non-visual tasks, such as auditory localization (Leclerc et al., 2000; Weeks et al., 2000) as well as other auditory functions (Arno et al., 2001; Burton et al., 2002; De Volder et al., 2001; Röder et al., 2002). A group of authors demonstrated that some early blind people localize sounds more accurately than sighted controls using monaural cues (Kujala et al., 1995, 1997; Lessard et al., 1998; Liotti et al., 1998). In order to investigate the neural basis of these behavioral differences in humans, Gougoux et al. (2005) carried out functional imaging studies using PET and a speaker array that permitted pseudo-free-field presentations within the scanner. The results showed that blind persons who perform better than sighted persons recruit occipital areas to carry out auditory localization under monaural conditions. According to the authors the implication of occipital areas in auditory processing suggests intermodal compensatory mechanisms.

Röder et al. (2002) employed fMRI to map language-related brain activity in congenitally blind adults. Participants listened to semantically meaningful or meaningless sentences having either an easy or difficult syntactic structure. The results showed that blind adults not only activate classic left-hemispheric perisylvian language areas during speech comprehension, as did a group of sighted adults, but that they also display an activation in the homologous right-hemispheric structures and in the extrastriate and striate cortices. Both the perisylvian and occipital activities

varied as a function of syntactic difficulty and semantic content. The authors concluded that the cerebral organization of complex cognitive systems, such as the language system is significantly shaped by the sensory input provided to the system. In the same vein, Raz et al. (2007) found superior serial verbal memory in the blind than in sighted participants when instructed to recall 20 orally presented words in their original list order. The blind participants recalled more words than the sighted participants, indicating better item memory. Their greatest advantage was in recalling longer word sequences (according to their original order). The authors hypothesized that this advantage in sequential recall may be especially important for the blind to generate a mental picture of the world and should be seen as a refinement of a specific cognitive ability to compensate for blindness in humans. It thus appears that good mental imagery abilities in the blind can be observed despite the loss of vision which rules out hypotheses of mental images being quasi-pictorial, as formally proposed by Kosslyn (1994). Mental imagery in the blind may depend on several specific factors, such as other sensory modalities at work, in addition to both cortical and functional reorganization consecutive to the loss of vision.

3.2. Neurovisual disorders and mental imagery capacities

Kosslyn's model of mental visual imagery appears to be supported by neuropsychological data showing an association of imagery deficits with perceptual problems in the same visual field (Behrmann et al., 1998; Crary and Heilman, 1988; Farah et al., 1998; Friedman and Alexander, 1989; Gomori and Hawryluk, 1984; Levine et al., 1985; Rizzo et al., 1993; Young et al., 1994). Although Farah (1988, 1989), Farah et al. (1992, 1988) had defended this idea, several studies comparing sighted participants to patients with a visual deficit following cortical damage have found a double dissociation between perceptual and mental imagery abilities.

3.2.1. Visual field defects after cortical damage and mental imagery

Regarding the hypothesis that an association exists between perception and imagery deficits following cortical damage of the visual system, it is relevant to ask what happens in patients suffering from a massive visual field defect following a cortical lesion. For example, Kosslyn's model predicts that patients with cortical blindness following bilateral occipital damage are no longer capable of forming a visual mental image, since they are missing the visual buffer's neuronal substrate. The simultaneous presence of deficits in vision and in imagery has often been observed, collected and discussed by Farah (1988). However, recent observations reported cases of perception preservation along with imagery impairments, and conversely, perception impairments with preservation of imagery, thus showing the double dissociation for these deficits (Bartolomeo, 2002). Cases of cortically blind patients with visual imagery preservation are not rare in the literature (Anton, 1899; Chatterjee and Southwood, 1995; Goldenberg et al., 1995).

On the other hand, Butter et al. (1997) tested eight patients with unilateral visual field defects (homonymous hemianopia; HH) and 24 control participants in an image-scanning task and demonstrated that hemianopics had more difficulties to imagine the spots in their blind visual field compared to their healthy visual field. The task consisted of a brief sequential presentation of random dot patterns, which were then removed and replaced by an arrow that pointed to an unexpected location. Participants judged whether or not the arrow was pointing at the location occupied by one of the dots in the previous dot pattern. Butter and co-workers interpreted their data as consistent with the claim central to the Kosslyn model

that occipital visual areas are essential to visual mental imagery. However, as Bartolomeo (2002) pointed out, three out of eight patients with HH tested in the previous study did not undergo any neuroimaging studies. Consequently, a lesion extending beyond the occipital cortex could not be excluded. In addition, one hemianopic patient performed the imagery task normally, contrary to the predictions of the Kosslyn model. Finally, patients are typically unaware of their hemianopias so it would be surprising if they could imagine them. One cannot imagine things when one does not know what they look like (e.g., imagine a four-dimensional cube).

Aiming to confirm that mental images occur in a spatially mapped (i.e., analog or array-format) representational medium as initially proposed by Kosslyn (1978), Farah et al. (1992) tried to measure the visual angle of "the mind's eye" to estimate the extent of the imagery medium before and after unilateral occipital lobectomy. It was found that the overall size of the largest possible image was reduced following the surgery. In addition, only the horizontal extent, but not the vertical extent, of the imagery medium was reduced. According to the authors, these findings confirmed the hypothesis that mental imagery occurs in a spatially mapped representational medium dependent on the integrity of the occipital cortex. However, the methodology used to measure the visual angle of "the mind's eye" was too weak (i.e., walk in front of the imagined object until the object in your mind fell out of your visual field) to truly investigate the nature of mental imagery in patients suffering from visual field defects of central origin. In addition, as Pylyshyn (2002) argued, nearly a year passed between the patient's surgery and her imagery testing, during which she became familiar with how the world now looked to her. Consequently, when asked to imagine objects and indicate when they filled her field of view, she might very well have reported what things now looked to her. The penetrability of such imagery tests to patients' knowledge of how things look is always a potential confound.

3.2.2. Visual recognition deficits after cortical damage and mental imagery

Numerous case studies have reported an association between perceptual and representational (imaginal) disorders in object, shape, and color processing (Farah et al., 1988, 1998; Gomori and Hawryluk, 1984; Levine et al., 1985; Rizzo et al., 1993; Young et al., 1994) and verbal material processing (Behrmann et al., 1998; Crary and Heilman, 1988; Friedman and Alexander, 1989). However, this association between perceptual and representational disorders is not systematic. Behrmann et al. (1992) showed that a brain-damaged patient (CK) with severely impaired object recognition (visual object agnosia) may have fully preserved visual imagery. CK drew objects in considerable detail from memory and used information derived from mental images in a variety of tasks. In contrast, he could not identify visually presented objects, even those he had drawn himself. He had normal visual acuity and intact perception of equally complex material in other domains. The authors concluded that rich internal representations could be activated to support visual imagery even when they could not support visually mediated perception of objects. The case of Madame D, described by Bartolomeo et al. (1998) is another case illustrating the possible dissociation between perception and imagery. Madame D developed severe alexia, agnosia, achromatopsia and prosopagnosia following bilateral brain lesions restricted to the extrastriate visual areas. She suffered a hematoma located across left Brodmann areas 18, 19 and 37. Seven months later, she sustained a second hematoma but on the right and almost symmetrical to the first (Brodmann areas 18, 19 and the underlying white matter). She was profoundly impaired in the

recognition of objects presented visually, except if they had a very simple visual shape, such as polygons. In spite of this, she produced plausible drawings when requested to draw items from memory but was incapable of identifying her own drawings afterwards. She performed well on an object imagery test. She would always answer quickly with a high level of confidence. Such a dissociation was present for the verbal material, as well as for object recognition, colors and faces. According to Kosslyn's model, mental images are produced via a top-down activation of the primary visual areas from more anterior areas. It might be argued that such a mechanism might explain the profile of Madame D's performance, since the primary visual areas were spared by the lesions. However, explanations based on a retro-activation should predict at least a relative disorder of mental imagery because the anterograde flux of information was massively interrupted (anterograde and reciprocal connections are linked in the cerebral white matter). Contrary to this prediction, Madame D succeeded in the imagery tasks, performing not only at ceiling, but also with a speed and ease suggesting that her imagery resources were entirely spared. This type of dissociation between perception and imagery is reported in numerous case studies, for the processing of shapes (Behrmann et al., 1994; Jankowiak et al., 1992; Riddoch and Humphreys, 1987; Servos and Goodale, 1995), colors (Shuren et al., 1996), faces (Riddoch and Humphreys, 1987), and also verbal material (Behrmann et al., 1994; Goldenberg, 1992; Perri et al., 1996).

Opposite dissociations, preserved perception, and altered imagery have also been observed in the processing of spatial (Morton and Morris, 1995) and color imagery (De Vreese, 1991; Goldenberg, 1992; Luzzatti and Davidoff, 1994). Sirigu and Duhamel (2001) also found this type of dissociation between perception and representation in the processing of verbal material. In the same vein, Basso et al. (1980) described a patient, MG, whose main deficit was in verbally describing familiar places from memory. The authors hypothesized that loss of visual imagery was the result of a functional disconnection. This hypothesis is supported by the frequent association of 'pure alexia' with disorders of color gnosis, which also have been argued to be dependent on a visuoverbal disconnection. Both these disorders were present in MG, whose lesion, involving the striate area and extending to the juxtacallosal region of the left occipital lobe, could lay the conditions for a partial visuoverbal cleavage.

Regarding the association between pure alexia and mental imagery disorders, Bartolomeo (2002) reported the related case of a patient with left hemisphere temporal and parietal lesions and spared occipital lobe, like in the other cases of visual imagery deficits. VSB, a pure alexic patient with preservation of the writing skill, had lost his capacity to revisualize letters, both introspectively and in letter or word imagery tasks. Therefore, this patient mainly had to use a strategy, though defective, of "mental reading" to imagine the verbal material. When a strategy based on spelling was encouraged, he could succeed in these tasks, which were previously impossible to him, since his writing ability had been preserved. These findings confirm Goldenberg's (1993) hypothesis, which suggests that two different codes, one based on vision, the other on the motor control system, can be used to solve tasks which demand a visual mental imagery of letters.

3.2.3. Unilateral spatial neglect and mental imagery

Unilateral spatial neglect is the tendency to ignore objects in the contralesional hemispace after a unilateral parietal lesion (Bisiach and Vallar, 2000). More convincing evidence that unilateral spatial neglect is not strictly speaking "visual" was provided by Bisiach and Luzzatti (1978) who first described representational neglect when a patient was asked to describe a well-known place from

memory. In their article, Bisiach and Luzzatti (1978) reported two left neglect patients who, when asked to imagine and describe the Piazza del Duomo in Milan from memory, omitted to mention the left-sided details regardless of the imaginary vantage point that they assumed, thus showing representational or imaginal neglect. This finding was replicated by Bisiach et al. (1981) in 28 neglect patients. The authors proposed that neglect patients suffer from "a representational map reduced to one half". The observation of unilateral neglect that appears not only in activities demanding a processing of the sensory entrance, but also in tasks not involving visual perception, such as the description of scenes from memory (Bisiach and Luzzatti, 1978) or the estimation of the angle between both arrows of an imaginary clock (Grossi et al., 1993). These have been proposed as another line of support for the perception/imagery equivalence of Kosslyn's model. Nevertheless, even in this domain, these case studies have proven the existence of two possible types of dissociation between visual neglect and representational neglect: visual neglect in the absence of representational neglect and representational neglect without visual neglect. Bartolomeo et al. (1994) suggested the existence of a double dissociation between visual and representational neglect, indicating that visual neglect in the absence of representational neglect seems to be more frequent than the opposite dissociation. The authors asked 30 patients with right cerebral lesions, 30 with left cerebral lesions and 30 normal participants to describe from memory three Roman plazas, a map of Europe centered on Italy, and the Italian coast seen from Sardinia. Seven right brain-damaged (RBD) patients and two left brain-damaged (LBD) patients had a contralesional, extrapersonal visual neglect. Representational neglect was present only in five RBD patients, all of them also showing signs of extrapersonal neglect. The most frequent observations (19 out of 60 patients) corresponded to an isolated extrapersonal neglect, while representational neglect was observed more rarely (5 out of 60 patients). In this latter case, however, representational neglect was always associated with extrapersonal neglect as many authors have described (Bisiach and Luzzatti, 1978; Rode and Perenin, 1994; Rode et al., 1995, 2001, 2007). Nevertheless, dissociations between representational and visuospatial neglect have been reported: visuospatial neglect in the absence of representational neglect (Anderson, 1993; Bartolomeo et al., 1994; Chokron et al., 2004; Coslett, 1997), representational neglect without visuospatial neglect (Beschin et al., 1997; Cocchini et al., 2006; Coslett, 1997; Guariglia et al., 1993; Ortigue et al., 2001), and right-sided peripersonal and personal visuospatial neglect with left-sided representational neglect (Beschin et al., 2000). These dissociations are consistent with the hypothesis that different mechanisms underlie perceptual and representational neglect.

Chokron et al. (2004) investigated the influence of vision and more precisely of visual feedback on spatial representations in patients suffering from left unilateral spatial neglect. The authors submitted six RBD patients suffering from left unilateral spatial neglect on two tasks involving spatial representations: a clock-drawing task and a drawing from memory task with and without visual feedback. The results confirmed that even in mental imagery, the absence of visual feedback may decrease and even suppress left neglect signs during representational tasks (see also Bartolomeo and Chokron, 2001, 2002a,b). Since vision is largely involved in the orientation of attention in space, suppressing visual control could reduce the magnetic attraction towards the right ipsilesional hemispace and in this way could allow a re-orientation of attention towards the left neglected hemispace even during pure representational tasks. In this way, representational deficits in neglect patients could perfectly be explained in terms of an attentional deficit (for a review on attentional deficits in neglect patients, see Bartolomeo and Chokron, 2002a). This latter hypothesis contrasts with Bisiach and Luzzatti (1978) who suggested that imaginal neglect could either result from patients' inability to explore the left part of an intact map or from an amputation of patients' mental representation of space. Chokron et al. (2004) and Bartolomeo et al. (2005) suggested instead that attentional biases resulting in visual neglect may also operate in visual mental imagery. Consistent with this hypothesis, imaginal neglect can be offset by the same sensory–motor maneuvers which favorably effect visual neglect, such as leftward eye and head turning (Meador et al., 1987), vestibular stimulation (Rode and Perenin, 1994), and visuomotor adaptation to right-deviating prisms (Rode et al., 2001). These procedures may therefore act by facilitating leftward orienting of attention (Chokron et al., 2007; Gainotti, 1993). This interpretation is also consistent with Pylyshyn's (2007) proposal that the spatial properties found in mental imagery studies derive from mapping the representation onto concurrently perceived spatial information. If that were the case, then one would expect focal attention to play an important role in spatial mental images.

4. Conclusions and perspectives

In the past half-century, mental imagery has captured a growing interest among cognitive psychology researchers. Nevertheless, the nature of these images is still unknown. The observation of patients who have visual or neurovisual impairments is a valuable pathological model for studying the relation between imagery, perception and other cognitive capacities. The study of pathological models raises two important questions: (i) what is the effect of a specific brain lesion and/or of visual deprivation on mental imagery; and (ii) to what extent are vision and imagery processes depending upon the same neuroanatomical structures.

Most of the neuropsychological studies we have reviewed show a dissociation between perceptual and imagery deficits and thus tend to suggest that perception and imagery do not rely on the same cortical structures even in cases of cortical blindness (Chatterjee and Southwood, 1995). This double dissociation provides strong evidence against the claim that visual mental images are "displayed" on a visual buffer consisting of topographically organized areas in the occipital lobe (Kosslyn et al., 2006). However, further studies controlling the size and precise location of the brain lesion are still needed to exclude the possibility that lesions extend beyond the occipital lobes, which might explain the deficit in mental imagery.

Regarding mental imagery performance in blind people (after a peripheral lesion), studies are quite divergent. Indeed, even if the majority of the work suggests that vision is not a prerequisite to the acquisition of spatial representations (Aleman et al., 2001; Bértolo et al., 2003; Kaski, 2002; Thinus-Blanc and Gaunet, 1997; Tinti et al., 2006; Vanlierde and Wanet-Defalque, 2004; Vecchi et al., 2001), they do not agree on the functional and structural properties of mental representations in the blind (Carpenter and Eisenberg, 1978; Cornoldi et al., 1988; Kerr, 1983; Marmor and Zaback, 1976; Zimler and Keenan, 1983). Thus, given the contradictory results emerging from different studies, the conclusions in visual imagery properties are as yet difficult to draw. The distinction between a 'visual trace' which shares characteristics with perception and a 'generated image' which has different properties than perception (i.e., an original representation not based on real perceptual representation) proposed by Cornoldi and De Beni (2005), seems able to take into account the different results. But the fact that visual mental images can possess many of the properties of visual stimuli (e.g., metric spatial properties, such as size and inter-object

distances) does not mean these images have a quasi-pictorial format. As Pylyshyn (2003a) explains "*Discussions of mental imagery often confound questions of form with questions of content. There is a clear difference between thinking about how something looks and thinking about what it means. Because thinking about how something looks feels very different from thinking about its non-visual properties, it is plausible that it might involve a different format*".

Many authors agree that visuospatial mental imagery relies on a large variety of information sources, such as visual, tactile and auditory (Cornoldi et al., 1988; Hollins, 1985), as well as cognitive processes, such as attention and memory (Chokron et al., 2004) and tacit knowledge (Pylyshyn, 1981). Even if vision is the modality most adapted to explore spatial patterns, it seems that in its absence, the collection of information by haptic modality allows the blind access to spatial representation. The haptic modality also seems able to modulate certain disorders observed in patients suffering from either a visual or neurovisual impairment (Bartolomeo et al., 2002; Dulin and Hatwell, 2006; Hollins, 1985; Sirigu and Duhamel, 2001). The fact that the compensation of the visual deficit in the collection of information can partly be performed by the haptic modality and allow the blind to 'see' an object with his/her 'mind's eye' suggests that spatial images may be the result of the combination of long term memory information coming from different sources (Hatwell, 2003), and may, as Bartlett (1932) showed some time ago, be penetrated by beliefs, emotions, and conceptual knowledge.

In conclusion, we suggest that in the case of blindness of peripheral origin, the absence of vision could progressively bring disorders of spatial representation. However, these representational disorders may partly or completely be compensated by new strategies of information encoding. In the case of neurovisual impairments, there is likely to be a strong influence of attention, compensatory strategies and cortical plasticity on performance in tasks assumed to rely on mental imagery. As opposed to lesions studies, neuroimaging studies suggest, but do not demonstrate, that the relevant brain areas are necessary to the mental imagery tasks. In this way, dissociations between perception and imagery found in patients with neurovisual disorders strongly demonstrate that patients may retain mental imagery capacities despite lesions of visual and/or parietal areas. For this reason, we think that more clinical and experimental studies conducted in sighted and blind participants, as well as brain-damaged patients with neurovisual disorders, are needed to assess the role of vision on mental imagery both in terms of basic science, adaptation and cortical plasticity.

Acknowledgements

References

Aleman, A., van Lee, L., Mantione, M.H., Verkoijen, I.G., De Haan, E.H., 2001. Visual imagery without visual experience: evidence from congenitally totally blind people. Neuroreport 12, 2601–2604.
Amedi, A., Malach, R., Hendler, T., Peled, S., Zohary, E., 2001. Visuo-haptic object-related activation in the ventral visual pathway. Nat. Neurosci. 4, 324–330.
Amedi, A., Jacobson, G., Hendler, T., Malach, R., Zohary, E., 2002. Convergence of visual and tactile shape processing in the human lateral occipital complex. Cereb. Cortex 12, 1202–1212.
Amedi, A., Malach, R., Pascual-Leone, A., 2005a. Negative BOLD differentiates visual imagery and perception. Neuron 48, 859–872.
Amedi, A., Von Kriegstein, K., Van Atteveldt, N., Beauchamp, M.S., Naumer, M.J., 2005b. Functional imaging of human crossmodal identification and object recognition. Exp. Brain Res. 166, 559–571.
Anderson, B., 1993. Spared awareness for the left side of internal visual images in patients with leftsided extrapersonal neglect. Neurology 43, 213–216.

Anton, G., 1899. Über die Selbstwahrnehmungen der Herderkranungen des Gehirns durch den Kranken bei Rindenblindheit. Archiv für Psychiatrie und Nervenkrankheiten 32, 86–127.
Arditi, A., Holtzman, J.D., Kosslyn, S.M., 1988. Mental imagery and sensory experience in congenital blindness. Neuropsychologia 26, 1–12.
Arno, P., De Volder, A.G., Vanlierde, A., Wanet-Defalque, M.C., Streel, E., 2001. Occipital activation by pattern recognition in the early blind using auditory substitution for vision. Neuroimage 13, 632–645.
Bailes, S.M., Lambert, R.M., 1986. Cognitive aspects of haptic form recognition by blind and sighted subjects. Br. J. Psychol. 77, 451–458.
Bartlett, F.C., 1932. Remembering: A Study in Experimental and Social Psychology. The University Press, Cambridge.
Bartolomeo, P., 2002. The relationship between visual perception and visual mental imagery reappraisal of the neuropsychological evidence. Cortex 38, 357–378.
Bartolomeo, P., Chokron, S., 2001. Unilateral neglect: the effect of competing stimuli on estimated line length. Brain Cogn. 46, 34–38.
Bartolomeo, P., Chokron, S., 2002a. Orienting of attention in left unilateral neglect. Neurosci. Biobehav. Rev. 26, 217–234.
Bartolomeo, P., Chokron, S., 2002b. Can we change our vantage point to explore imaginal neglect? (Commentary on Pylyshyn: mental imagery: in search of a theory). Behav. Brain Sci. 25, 184–185.
Bartolomeo, P., D'Erme, P., Gainotti, G., 1994. The relationship between visuospatial and representational neglect. Neurology 44, 1710–1714.
Bartolomeo, P., Bachoud-Lévi, A.C., De Gelder, B., Denes, G., Dalla Barba, G., Brugieres, P., Degos, J.D., 1998. Multiple-domain dissociation between impaired visual perception and preserved mental imagery in a patient with bilateral extrastriate lesions. Neuropsychologia 36, 239–249.
Bartolomeo, P., Bachoud-Lévi, A.C., Chokron, S., Degos, J.D., 2002. Visually and motor-based knowledge of letters: evidence from a pure alexic patient. Neuropsychologia 40, 1363–1371.
Bartolomeo, P., Bachoud-Levi, A.C., Azouvi, P., Chokron, S., 2005. Time to imagine space: a chronometric exploration of representational neglect. Neuropsychologia 43, 1249–1257.
Basso, A., Bisiach, E., Luzzatti, C., 1980. Loss of mental imagery: a case study. Neuropsychologia 18, 435–442.
Beauchamp, M.S., 2005. See me, hear me, touch me: multisensory integration in lateral occipital–temporal cortex. Curr. Opin. Neurobiol. 15, 145–153.
Behrmann, M., Winocur, G., Moscovitch, M., 1992. Dissociation between mental imagery and object recognition in a brain-damaged patient. Nature 359, 636–637.
Behrmann, M., Moscovitch, M., Winocur, G., 1994. Intact visual imagery and impaired visual perception in a patient with visual agnosia. J. Exp. Psychol. Hum. Percept. Perform. 20, 1068–1087.
Behrmann, M., Nelson, J., Sekuler, E.B., 1998. Visual complexity in letter-by-letter reading: "pure" alexia is not pure. Neuropsychologia 36, 1115–1132.
Bértolo, H., Paiva, T., Pessoa, L., Mestre, T., Marques, R., Santos, R., 2003. Visual dream content, graphical representation and EEG alpha activity in congenitally blind subjects. Cogn. Brain Res. 15, 277–284.
Beschin, N., Cocchini, G., Della Sala, S., Logie, R., 1997. What the eyes perceive, the brain ignores: a case of pure unilateral representational neglect. Cortex 33, 3–26.
Beschin, N., Basso, A., Della Sala, S., 2000. Perceiving left and imagining right: dissociation in neglect. Cortex 36, 401–414.
Binet, A., 1886. La Psychologie du Raisonnement. Alcan, Paris.
Bisiach, E., Luzzatti, C., 1978. Unilateral neglect of representational space. Cortex 14, 129–133.
Bisiach, E., Vallar, G., 2000. Unilateral neglect in humans. In: Boller, F., Grafman, J. (Eds.), Handbook of Neuropsychology. Elsevier, Amsterdam, pp. 459–502.
Bisiach, E., Capitani, E., Luzzatti, C., Perani, D., 1981. Brain and conscious representation of outside reality. Neuropsychologia 19, 543–551.
Buchel, C., Price, C., Frachwick, R.S.J., Freston, K., 1998. Different activation patterns in the visual cortex of late and congenitally blind subjects. Brain 121, 409–419.
Burton, H., Snyder, A.Z., Conturo, T.E., Akbudak, E., Ollinger, J.M., Raichle, M.E., 2002. Adaptive changes in early and late blind: a fMRI study of Braille reading. J. Neurophysiol. 87, 589–607.
Butter, C.M., Kosslyn, S.M., Mijovic-Prelec, D., Riffle, A., 1997. Field-specific deficits in visual imagery following hemianopia due to unilateral occipital infarcts. Brain 120, 217–228.
Carpenter, P.A., Eisenberg, P., 1978. Mental rotation and the frame of reference in blind and sighted individuals. Percept. Psychophys. 23, 117–124.
Chatterjee, A., Southwood, M.H., 1995. Cortical blindness and visual imagery. Neurology 45, 2189–2195.
Chen, W., Kato, T., Zhu, X.H., Ogawa, S., Tank, D.W., Ugurbil, K., 1998. Human primary visual cortex and lateral geniculate nucleus activation during visual imagery. Neuroreport 9, 3669–3674.
Chokron, S., Colliot, P., Bartolomeo, P., 2004. The role of vision in spatial representation. Cortex 40, 281–290.
Chokron, S., Dupierrix, E., Tabbert, M., Bartolomeo, P., 2007. Experimental remission of neglect. Neuropsychologia 45 (14), 3127–3148.
Cocchini, G., Bartolo, A., Nichelli, P., 2006. Left ipsilesional neglect for visual imagery: a mental image generation impairment? Neurocase 12, 197–206.
Cocude, M., Mellet, E., Denis, M., 1999. Visual and mental exploration of visuo-spatial configurations: behavioural and neuroimaging approaches. Psychol. Res. 62, 93–106.
Cohen, M.S., Kosslyn, S.M., Breiter, H.C., DiGirolamo, G.J., Thompson, W.L., Anderson, A.K., Brookheimer, S.Y., Rosen, B.R., Belliveau, J.W., 1996. Changes in cortical

activity during mental rotation. A mapping study using functional MRI. Brain 119, 89–100.

Cohen, L.G., Celnik, P., Pascual-Leone, A., Corwell, B., Faiz, L., Dambrosia, J., Honda, M., Sadato, N., Gerloff, C., Catala, D., Hallett, M., 1997. Functional relevance of cross-modal plasticity in blind humans. Nature 389, 180–183.

Cornoldi, C., De Beni, R., 2005. Asymmetries between perception and mental imagery (imagery and blindness). In: Østreng, W. (Ed.), Synergies. Interdisciplinary Communications 2003/2004. Centre for Advanced Study, Oslo, pp. 40–45.

Cornoldi, C., Vecchi, T., 2000. Mental imagery in blind people: the role of passive and active visuo-spatial processus. In: Heller, M. (Ed.), Touch, Representation and Blindness. Oxford University Press, New York, pp. 143–181.

Cornoldi, C., Vecchi, T., 2003. Congenitally blindness and spatial mental imagery. In: Hatwell, Y., Streri, A., Gentaz, E. (Eds.), Touching for Knowing. Cognitive Psychology of Haptic Manual Perception. John Benjamin Publishers, Amsterdam and Philadelphia, pp. 173–187.

Cornoldi, C., De Beni, R., Giusberti, F., Massironi, M., 1988. Memory and imagery: a visual trace is not a mental image. In: Conway, M., Gathercole, S., Cornoldi, C. (Eds.), Theories of Memory. Psychology Press, Hove, pp. 87–110.

Cornoldi, C., Cortesi, A., Preti, D., 1991. Individual differences in the capicity limitations of visuo-spatial short-term memory; research on sighted and totally congenitally blind people. Mem. Cogn. 19, 459–468.

Coslett, H.B., 1997. Neglect in vision and visual imagery: a double dissociation. Brain 120, 1163–1171.

Crary, M., Heilman, K., 1988. Letter imagery deficits in a case of pure apraxic agraphia. Brain Lang. 34, 147–156.

D'Esposito, M., Detre, J.A., Aguirre, G.K., Stallcup, M., Alsop, D.C., Tipett, L.J., Farah, M.J., 1997. A functional MRI study of mental image generation. Neuropsychologia 35, 725–730.

De Beni, R., Cornoldi, C., 1988. Imagery limitations in totally congenitally blind subjects. J. Exp. Psychol. Learn. Mem. Cogn. 14, 650–655.

De Volder, A.G., Bol, A., Blin, J., Robert, A., Arno, P., 1997. Cécile Grandin, Christian Michel and Claude Veraart brain energy metabolism in early blind subjects: neural activity in the visual cortex. Brain Res. 750, 235–244.

De Volder, A.G., Toyama, H., Kimura, Y., Kiyosawa, M., Nakano, H., Vanlierde, A., Wanet-Defalque, M.C., Mishina, M., Oda, K., Ishiwata, K., Senda, M., 2001. Auditory triggered mental imagery of shape involves visual association areas in early blind humans. Neuroimage 14, 129–139.

De Vreese, L.P., 1991. Two systems for colour-naming defects: verbal disconnection versus colour imagery disorder. Neuropsychologia 29, 1–18.

Deibert, E., Kraut, M., Kremen, S., Hart, J.R., 1999. Neural pathways in tactile object recognition. Neurology 52, 1413–1417.

Dulin, D. Effects of prior experience in raised line materials and prior visual experience on length estimations by blind people. Br. J. Vis. Impair, in press.

Dulin, D., Hatwell, Y., 2006. The effects of visual experience and of training in raised line materials on the mental spatial imagery of the blind. J. Vis. Impair Blind 100, 414–424.

Evans, R.B., 1984. Titchener and American experimental psychology. Rev. Hist. Psicol. 5, 117–125.

Farah, M.J., 1988. Is visual imagery really visual? Overlooked evidence from neuropsychology. Psychol. Rev. 95, 307–317.

Farah, M.J., 1989. The neural basis of mental imagery. TINS 12, 395–399.

Farah, M.J., Peronnet, F., Gonon, M.A., Girard, M.H., 1988. Electrophysiological evidence for a shared representational medium for visual images and visual percepts. J. Exp. Psychol. Gen. 117, 248–257.

Farah, M.J., Soso, M.J., Dasheiff, R.M., 1992. Visual angle of the mind's eye before and after unilateral occipital lobectomy. J. Exp. Psychol. Hum. Percept. Perf. 18, 241–246.

Farah, M.J., Wilson, K.D., Drain, M., Tanaka, J.N., 1998. What is "special" about face perception? Psychol. Rev. 105, 482–498.

Fodor, J.A., Pylyshyn, Z.W., 1988. Connectionism and cognitive architecture: a critical analysis. Cognition 28, 3–71.

Formisano, E., Linden, D.E., 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 visuospatial mental imagery. Neuron. 35, 185–194.

French, C., Painter, J., 1991. Spatial processing of images and hemisphere function. Cortex 27, 511–520.

Friedman, R.B., Alexander, M.P., 1989. Written spelling apraxia. Brain Lang. 36, 503–517.

Gainotti, G., 1993. The role of spontaneous eye movements in orienting attention and in unilateral neglect. In: Robertson, I.H., Marshall, J.C. (Eds.), Unilateral Neglect: Clinical and Experimental Studies. Lawrence Erlbaum Associates, Hove, pp. 107–122.

Gaunet, F., Thinus-Blanc, C., 1996. Early blind subject's spetial abilities and the locomotor space: a study of exploratory strategies and reaction to change performance. Perception 25, 967–981.

Ghaëm, 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.

Gizewski, E.R., Gasser, T., De Greiff, A., Boehm, A., Forsting, M., 2003. Cross-modal plasticity for sensory and motor activation patterns in blind subjects. Neuroimage 19, 968–975.

Goldenberg, G., 1992. Loss of visual imagery and loss of visual knowledge—a case study. Neuropsychologia 30, 1081–1099.

Goldenberg, G., 1993. The neural basis of mental imagery. Baillière's Clin. Neurol. 2, 265–286.

Goldenberg, G., Podreka, I., Steiner, M., Willmes, K., 1987. Patterns of regional cerebral blood flow related to memorizing of high and low imagery words—an emission computer tomography study. Neuropsychologia 25, 473–485.

Goldenberg, G., Steiner, M., Podreka, I., Deecke, L., 1992. Regional cerebral blood flow patterns related to verification of low-and high-imagery sentences. Neuropsychologia 30, 581–586.

Goldenberg, G., Mullbacher, W., Nowak, A., 1995. Imagery without perception—a case study of anosognosia for cortical blindness. Neuropsychologia 33, 1373–1382.

Gomori, A.J., Hawryluk, G.A., 1984. Visual agnosia without alexia. Neurology 34, 947–950.

Gougoux, F., Zatorre, R.J., Lassonde, M., Voss, P., Lepore, F., 2005. A functional neuroimaging study of sound localization: visual cortex activity predicts performance in early-blind individuals. PLoS Biol. 3, 324–333.

Grossi, D., Angelini, R., Pecchinenda, A., Pizzamiglio, L., 1993. Left imaginal neglect in heminattention: experimental study with the O'clock test. Behav. Neurol. 6, 155–158.

Guariglia, C., Padovani, A., Pantano, P., Pizzamiglio, L., 1993. Unilateral neglect restricted to visual imagery. Nature 364, 235–237.

Haber, R.N., Haber, L.R., Levin, C.A., Hollyfield, R., 1993. Properties of spatial representations: data from sighted and blind subjects. Percept. Psychophys. 54, 1–13.

Hamilton, R., Keenan, J.P., Catala, M., Pascual-Leone, A., 2000. Alexia for Braille following bilateral occipital stroke in an early blind woman. Neuroreport 11, 237–240.

Hatwell, Y., 2003. Psychologie Cognitive de la Cécité Précoce. Dunod, pp. 113–115.

Hollins, M., 1985. Styles of mental imagery in blind adults. Neuropsychologia 23, 561–566.

Ishai, A., Sagi, D., 1995. Common mechanisms of visual imagery and perception. Science 268, 1772–1774.

Ishai, A., Ungerleider, L.G., Haxby, J.V., 2000. Distributed neural systems for the generation of visual images. Neuron 28, 979–990.

Ishai, A., Haxby, J.V., Ungerleider, L.G., 2002. Visual imagery of famous faces: effects of memory and attention revealed by fMRI. Neuroimage 17, 1729–1741.

James, T.W., Humphrey, G.K., Gati, J.S., Servos, P., Menon, R.S., Goodale, M.A., 2002. Haptic study of three-dimensional objects activates extrastriate visual areas. Neuropsychologia 40, 1706–1714.

Jankowiak, J., Kinsbourne, M., Shalev, R.S., Bachman, D.L., 1992. Preserved visual imagery and categorization in a case of associative visual agnosia. J. Cogn. Neurosci. 4, 119–131.

Jordan, K., Heinze, H.J., Lutz, K., Kanowski, M., Jancke, L., 2001. Cortical activations during the mental rotation of different visual objects. Neuroimage 13, 143–152.

Kaski, D., 2002. Revision: is visual perception a requisite for visual imagery? Perception 31, 717–731.

Kerr, N.H., 1983. The role of vision in "visual imagery" experiments. Evidence from the congenitally blind. J. Exp. Psychol. Gen. 112, 265–277.

Klein, I., Dubois, J., Mangin, J.F., Kherif, F., Flandin, G., Poline, J.B., Denis, M., Kosslyn, S.M., Le Bihan, D., 2004. Retinotopic organization of visual mental images as revealed by functional magnetic resonance imaging. Cogn. Brain Res. 22, 26–31.

Knauff, M., Kassubek, J., Mulack, T., Greenlee, M.W., 2000. Cortical activation evoked by visual mental imagery as measured by fMRI. Neuroreport 11, 3957–3962.

Kosslyn, S.M., 1978. Imagery and internal representation. In: Rosch, E., Lloyd, B.B. (Eds.), Cognition and Categorization. Erlbaum, Hillsdale, NJ.

Kosslyn, S.M., 1994. Image and Brain: The Resolution of the Imagery Debate. The MIT Press, Cambridge.

Kosslyn, S.M., Shwartz, S.P., 1977. A simulation of visual imagery. Cogn. Sci. 1, 265–295.

Kosslyn, S.M., Thompson, W.L., 2003. When is early visual cortex activated during visual mental imagery? Psychol. Bull. 129, 723–746.

Kosslyn, S.M., Alpert, N.M., Thompson, W.L., Maljkovic, V., Weise, S.B., Charbris, C.F., Hamiston, S.E., Rauch, S.L., Buonanno, F.S., 1993. Visual mental imagery activates topographically organized visual cortex: PET investigations. J. Cogn. Neurosci. 5, 263–287.

Kosslyn, S.M., Thompson, W.L., Kim, I.J., Alpert, N.M., 1995. Topographical representations of mental images in primary visual cortex. Nature 378, 496–498.

Kosslyn, S.M., DiGirolamo, G.J., Thompson, W.L., Alpert, N.M., 1998. Mental rotation of objects versus hands: neural mechanisms revealed by positron emission tomography. Psychophysiology 35, 151–161.

Kosslyn, S.M., Pascual-Leone, A., Felician, O., Camposano, S.E., 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., Thompson, W.L., Ganis, G., 2006. The Case for Mental Imagery. Oxford University Press, New York.

Kreiman, G., Koch, C., Fried, I., 2000. Imagery neurons in the human brain. Nature 408, 357–361.

Kujala, T., Huotilainen, M., Sinkkonen, J., Ahonen, A.I., Alho, K., Hamalainen, M.S., Ilmoniemi, R.J., Kajola, M., Knuutila, J.E., Lavikainen, J., 1995. Visual cortex activation in blind humans during sound discrimination. Neurosci. Lett. 183, 143–146.

Kujala, T., Alho, K., Huotilainen, M., Ihmoniemi, R.J., Leinonen, A., Rinne, T., Salonen, O., Sinkkonen, J., Standertskjöld-Nordenstam, C.G., Näätänen, R., 1997. Electrophysiological evidence for cross-modal plasticity in humans with early and late-onset blindness. Psychophysiology 34, 213–216.

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. Proc. Natl. Acad. Sci. U.S.A. 90, 11802–11805.

Leclerc, C., Saint-Amour, D., Lavoie, M.E., Lassonde, M., Lepore, F., 2000. Brain functional reorganization in early blind humans revealed by auditory event-related potentials. Neuroreport 11, 545–550.

Lessard, N., Paré, M., Lassonde, M., Lepore, F., 1998. Early-blind human subjects localize sound sources better than sighted subjects. Nature 395, 278–280.

Levine, D.N., Warach, J., Farah, M., 1985. Two visual systems in mental imagery: dissociation of "what" and "where" in imagery disorders due to bilateral posterior cerebral lesions. Neurology 35, 1010–1018.

Liotti, M., Ryder, K., Woldroff, M.G., 1998. Auditory attention in the congenitally blind: where, when and what gets reorganized? Neuroreport 9, 1007–1012.

Luzzatti, C., Davidoff, J., 1994. Impaired retrieval of object-colour knowledge with preserved colour naming. Neuropsychologia 32, 933–950.

Marmor, G.S., Zaback, L.A., 1976. Mental rotation by the blind: does mental rotation depend on visual imagery. J. Exp. Psychol. Hum. Percept. Perf. 2, 515–521.

Meador, K.J., Loring, D.W., Bowers, D., Heilman, K.M., 1987. Remote memory and neglect syndrome. Neurology 37, 522–526.

Mechelli, A., Price, C.J., Friston, K.J., Ishai, A., 2004. Where bottom-up meets top-down: neuronal interactions during perception and imagery. Cereb. Cortex 14, 1256–1265.

Mellet, E., Tzourio, N., Denis, M., Mazoyer, B., 1995. A positron emission tomography study of visual and mental spatial exploration. J. Cogn. Neurosci. 7, 433–435.

Mellet, E., Tzourio, N., Crivello, F., Joliot, M., Denis, M., Mazoyer, B., 1996. Functional anatomy of spatial mental imagery generated from verbal instruction. J. Neurosci. 16, 6504–6512.

Mellet, E., Tzourio, N., Denis, M., Mazoyer, B., 1998. Cortical anatomy of mental imagery of concrete nouns based on their dictionary definition. Neuroreport 9, 803–808.

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.

Morton, N., Morris, R.G., 1995. Image transformation dissociated from visuospatial working memory. Cogn. Neuropsychol. 12, 769–791.

Neisser, U., 1967. Cognitive Psychology. Appleton-Century-Crofts, New York.

Newell, A., 1990. Unified Theories of Cognition. Harvard University Press, Cambridge.

Ng, V.W., Bullmore, E.T., de Zubicaray, G.I., Cooper, A., Suckling, J., Williams, S.C., 2001. Identifying rate-limiting nodes in large-scale cortical networks for visuospatial processing: an illustration using fMRI. J. Cogn. Neurosci. 13, 537–545.

O'Craven, K.M., Kanwisher, N., 2000. Mental imagery of faces and places activates corresponding stimulus-specific brain regions. J. Cogn. Neurosci. 12, 1013–1023.

Ortigue, S., Viaud-Delmon, I., Annoni, J.M., Landis, T., Michel, C., Blanke, O., Vuilleumier, P., Mayer, E., 2001. Pure representational neglect after right thalamic lesion. Ann. Neurol. 50, 401–404.

Paivio, A., 1971. Imagery and Verbal Processus. Holt, Rinehart & Winston, New York.

Pascual-Leone, A., Hamilton, R., 2001. The metamodal organization of the brain. Brain Res. 134, 427–445.

Pascual-Leone, A., Amedi, A., Fregni, F., Merabet, L.B., 2005. The plastic human brain cortex. Ann. Rev. Neurosci. 28, 377–401.

Perri, R., Bartolomeo, P., Silveri, M.C., 1996. Letter dyslexia in a letter-by-letter reader. Brain Lang. 53, 390–407.

Pylyshyn, Z.W., 1980. Cognitive representation and the process-architecture distinction. Behav. Brain Sci. 3 (1), 154–169.

Pylyshyn, Z.W., 1981. The imagery debate: analogue media versus tacit knowledge. Psychol. Rev. 88, 16–45.

Pylyshyn, Z.W., 1984. Computation and Cognition: Toward a Foundation for Cognitive Science. MIT Press, Cambridge, MA.

Pylyshyn, Z.W., 1991. The role of cognitive architectures in theories of cognition. In: VanLehn, K. (Ed.), Architectures for Intelligence. Lawrence Erlbaum Associates, Hillsdale.

Pylyshyn, Z.W., 1996. The study of cognitive architecture. In: Steier, D., Mitchell, T. (Eds.), Mind Matters: Contributions to Cognitive Science in Honor of Allen Newell Lawrence. Erlbaum Associates, Hillsdale.

Pylyshyn, Z.W., 2002. Mental imagery: in search of a theory. Behav. Brain Sci. 25, 157–182.

Pylyshyn, Z.W., 2003a. Return of the mental image: are there really pictures in the brain? TICS 7, 113–118.

Pylyshyn, Z.W., 2003b. Mental images: in search of a theory. Behav. Brain Sci. 25 (2), 157–182.

Pylyshyn, Z.W., 2003c. Seeing and Visualizing: It's Not What You Think. MIT Press, Cambridge, MA.

Pylyshyn, Z.W., 2007. Things and Places: How the Mind Connects with the World (Jean Nicod Lectures Series). MIT Press, Cambridge.

Raz, N., Striem, E., Pundak, G., Orlov, T., Zohary, E., 2007. Superior serial memory in the blind: a case of cognitive compensatory adjustment. Curr. Biol. 17, 1129–1133.

Richter, W., Somorjai, R., Summers, R., Jarmasz, M., Menon, R.S., Gati, J.S., Georgopoulos, A.P., Tegeler, C., Ugurbil, K., Kim, S.G., 2000. Motor area activity during mental rotation studied by time-resolved single-trial fMRI. J. Cogn. Neurosci. 12, 310–320.

Riddoch, M.J., Humphreys, G.W., 1987. A case of integrative visual agnosia. Brain 110, 1431–1462.

Rizzo, M., Smith, V., Pokorny, J., Damasio, A., 1993. Color perception profiles in central achromatopsia. Neurology 43, 995–1001.

Rode, G., Perenin, M.T., 1994. Temporary remission of representational hemineglect through vestibular stimulation. Neuroreport 5, 869–872.

Rode, G., Perenin, M.T., Boisson, D., 1995. Négligence de l'espace représenté: mise en évidence par l'évocation mentale de la carte de France. Rev. Neurol. (Paris) 151, 161–164.

Rode, G., Rossetti, Y., Boisson, D., 2001. Prism adaptation improves representational neglect. Neuropsychologia 39, 1250–1254.

Rode, G., Revol, P., Rossetti, Y., Boisson, D., Bartolomeo, P., 2007. Looking while imagining: the influence of visual input on representational neglect. Neurology 68, 432–437.

Röder, B., Rösler, F., 1998. Visual input does not facilitate the scanning of spatial images. J. Mental Imagery 22, 165–181.

Röder, B., Stock, O., Bien, S., Neville, H., Rösler, F., 2002. Speech processing activates visual cortex in congenitally blind humans. Eur. J. Neurosci. 16, 930–936.

Roland, P.E., Gulyas, B., 1994. Visual imagery and visual representation. TINS 17, 281–287.

Roland, P.E., Eriksson, L., Stone-Elander, S., Widen, L., 1987. Does mental activity change the oxidative metabolism of the brain? J. Neurosci. 7, 2373–2389.

Sabbah, P., Simond, G., Levrier, O., Habib, M., Trabaud, V., Muayaama, N., Mazoyer, B., Briand, J.F., Raybaud, C., Salamon, G., 1995. Functional magnetic resonance imaging at 1.5 T during sensorimotor and cognitive task. Eur. Neurol. 35, 131–136.

Sack, A.T., Sperling, J.M., Prvulovic, D., Formisano, E., Goebel, R., Di Salle, F., Dierks, T., Linden, D.E.J., 2002. Tracking the mind's image in the brain. II. Transcranial magnetic stimulation reveals parietal asymmetry in visuospatial imagery. Neuron 35, 195–204.

Sack, A.T., Camprodon, J.A., Pascual-Leone, A., Goebel, R., 2005. The dynamics of interhemispheric compensatory processes in mental imagery. Science 308, 702–704.

Sadato, N., Okada, T., Honda, M., Yonekura, Y., 2002. Critical period for cross-modal plasticity in blind humans: a functional MRI study. Neuroimage 16, 389–400.

Sathian, K., Zangaladze, A., 2002. Feeling with the mind's eye: contribution of visual cortex to tactile perception. Behav. Brain Res. 135, 127–132.

Sathian, K., Zangaladze, A., Hoffman, J.M., Grafton, S.T., 1997. Feeling with the mind's eye. Neuroreport 8, 3877–3881.

Schupp, H.T., Lutzenberger, W., Birbaumer, N., Miltner, W., Braun, C., 1994. Neurophysiological differences between perception and imagery. Brain Res. Cogn. Brain Res. 2 (2), 77–86.

Sergent, J., Ohta, S., MacDonald, B., 1992. Functional neuroanatomy of face and object processing. Brain 115, 15–36.

Servos, P., Goodale, M.A., 1995. Preserved visual imagery in visual form agnosia. Neuropsychologia 33, 1383–1394.

Shuren, J.E., Brott, T.G., Schefft, B.K., Houston, W., 1996. Preserved color imagery in an achromatopsic. Neuropsychologia 34, 485–489.

Sirigu, A., Duhamel, J.R., 2001. Motor and visual imagery as two complementary but neurally dissociable mental processes. J. Cogn. Neurosci. 13, 910–919.

Slotnick, S.D., Thompson, W.L., Kosslyn, S.M., 2005. Visual mental imagery induces retinotopically organized activation of early visual areas. Cereb. Cortex 15, 1570–1583.

Sparing, R., Mottaghy, F., Ganis, G., Thompson, W.L., Toepper, R., Kosslyn, S.M., Pascual-Leone, A., 2002. Visual cortex excitability increases during visual mental imagery—a TMS study in healthy human subjects. Brain Res. 938, 92–97.

Stoeckel, M.C., Weder, B., Binkofski, F., Buccino, G., Shah, N.J., Seitz, R.J., 2003. A fronto-parietal circuit for tactile object discrimination: an event-related fMRI study. Neuroimage 19, 1103–1114.

Theoret, H., Merabet, L., Pascual-Leone, A., 2004. Behavioral and neuroplastic changes in the blind: evidence for functionally relevant cross-modal interactions. J. Physiol. 98, 221–233.

Thinus-Blanc, C., Gaunet, F., 1997. Space representations in the blind: vision as a spatial sens? Psychol. Bull. 121, 20–42.

Thomas, N.J.T., 1999. Are theories of imagery theories of imagination? An active perception approach to conscious mental content. Cogn. Sci. 23, 207–245.

Thompson, W.L., Kosslyn, S.M., Sukel, K.E., Alpert, N.M., 2001. Mental imagery of high- and low-resolution gratings activates area 17. Neuroimage 14, 454–464.

Tinti, C., Adenzato, M., Tamietto, M., Cornoldi, C., 2006. Visual experience is not necessary for efficient survey spatial cognition: evidence from blindness. Q. J. Exp. Psychol. 59, 1306–1328.

Tootell, R.B.H., Hadjikani, N.K., Mendola, J.D., Marrett, S., Dale, A.M., 1998. From retinotopy to recognition: fMRI in human visual cortex. TICS 2, 174–183.

Uhl, F., Kretschmer, T., Lindinger, G., Goldenberg, G., Lang, W., Oder, W., Deecke, L., 1994. Tactile mental imagery in sighted persons and in patients suffering from peripheral blindness early in life. Electroencephal. Clin. Neurophysiol. 91, 249–255.

Vanlierde, A., Wanet-Defalque, M.C., 2004. Abilities and strategies of blind and sighted participants in visuo-spatial imagery. Acta Psychol. 116, 205–222.

Vecchi, T., Philips, L.H., Cornoldi, C., 2001. Individual differences in visuo-spatial working memory. In: Denis, M., Logie, R.H., Cornoldi, C., De Vega, M., Engelkamp, J. (Eds.), Imagery, Language and Visuospatial Thinking. Psychology Press, Hove, pp. 29–58.

Vecchi, T., Tinti, C., Cornoldi, C., 2004. Spatial memory and integration processes in congenital blindness. Neuroreport 15, 2787–2790.

Veraart, C., De Volder, A.G., Wanet-Defalque, M.C., Bol, A., Michel, C., Goffinet, A.M., 1990. Glucose utilization in human visual cortex is abnormally elevated in blindness of early onset but decreased in blindness of late onset. Brain Res. 510, 115–121.

Wanet-Delfaque, M.C., Veraart, C., De Volder, A., Metz, R., Michel, C., Dooms, G., Goffinet, A., 1988. High metabolic activity in visual cortex of early blind subjects. Brain Res. 446, 369–373.

Weeks, R., Horwitz, B., Aziz-Sultan, A., Tian, B., Wessinger, C.M., Cohen, L.G., Hallett, M., Rauschecker, J.P., 2000. A positron emission tomographic study of auditory localization in the congenitally blind. J. Neurosci. 20, 2664–2672.

Wheeler, M.E., Petersen, S.E., Buckner, R.L., 2000. Memory's echo: vivid remembering reactivates sensory-specific cortex. Proc. Natl. Acad. Sci. U.S.A. 97, 11125–11129.

Wraga, M., Shephard, J.M., Church, J.A., Inati, S., Kosslyn, S.M., 2005. Imagined rotations of self versus objects: an fMRI study. Neuropsychologia 43, 1351–1361.

Young, A.W., Humphreys, G.W., Riddoch, M.J., Hellawell, D.J., De Haan, E.H.F., 1994. Recognition impairments and face imagery. Neuropsychologia 32, 693–702.

Zangaladze, A., Epstein, C.M., Grafton, S.T., Sathian, K., 1999. Involvement of visual cortex in tactile discrimination of orientation. Nature 401, 587–590.

Zimler, J., Keenan, J.M., 1983. Imagery in the congenitally blind: how visual are visual images? J. Exp. Psychol. Learn. Mem. Cogn. 9, 269–282.