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Neural Underpinning of Object Mental Imagery, Spatial Imagery, and Motor Imagery

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[–] Abstract and Keywords

Mental imagery is one of the cognitive functions that has received a lot of attention in the past 40 years both from philosophers and cognitive psychologists. Recently, researchers started to use neuroimaging techniques in order to tackle fundamental properties of mental images such as their depictive nature—which was fiercely debated for almost 30 years. Results from neuroimaging, brain-damaged patients, and transcranial magnetic stimulation studies converged in showing that visual, spatial and motor mental imagery relies on the same basic brain mechanisms used respectively in visual perception, spatial cognition, and motor control. Thus, neuroimaging and lesions studies have proved critical to answer the imagery debate between depictive and propositionalist theorists. Partly because of the controversy that surrounded the nature of mental images, the neural bases of mental imagery are probably more closely defined than those of any other higher cognitive functions.

Keywords: visual mental imagery, spatial mental imagery, motor mental imagery, visual perception, neuroimaging, brain-damaged patients, transcranial magnetic stimulation

When we think of the best way to load luggage in the trunk of a car, of the fastest route to go from point A to point B, or of the easiest way to assemble bookshelves, we generally rely on our abilities to simulate those events by visualizing them instead of actually performing them. When we do so, we experience "seeing with the mind's eye," which is the hallmark of a specific type of representation processed by our brain, namely, visual mental images. According to Kosslyn, Thompson, and Ganis (2006), mental images are representations that are similar to those created on the initial phase of perception but that do not require an external stimulation to be created. In addition, those representations preserve the perceptible properties of the stimuli they represent.

Early Studies of Mental Imagery and the Imagery Debate

Visual mental imagery has a very specific place in the study of human mental activity. In fact, dating back to early theories of mental activity, Greek philosophers such as Plato proposed that memory might be analogous to a wax tablet into which our perception and thoughts stamp images of themselves, as a signet ring stamps impressions in wax. According to this view, seeing with the mind's eye is considered a phenomenon closely related to perceptual activities. Thus, the idea of an analogy between mental imagery and perception is not new. However, because of the inherent private and introspective nature of mental imagery, garnering objective empirical evidence of the nature of these representations has been a great challenge for psychology researchers. The introspective nature of imagery led behaviorists (who championed the idea that psychology should focus on observable stimuli and the responses to these stimuli) such as Watson (1913) to deny the existence of mental images by asserting that thinking was solely constituted by subtle movements of the vocal apparatus. Behaviorism has had a (p. 75) long-lasting negative impact on the legitimacy of studying mental imagery. In fact, neither the cognitive revolution of the 1950s—during which the human mind started to be conceived of as like computer software—nor the first results of

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Paivio (1971) showing that mental imagery improves the memorization of words were sufficient to legitimize the study of mental imagery.

The revival of mental imagery was driven not only by empirical evidence that mental imagery was a key part of memory, problem solving, and creativity but also by the type of questions and methodologies researchers used. Researchers shifted from phenomenological problematic and introspective methods and started to focus on refining the understanding of the nature of the representations involved in mental imagery and of the cognitive processes that interpret those representations. The innovative idea was to use chronometric data as a "mental tape measure" of the underlying cognitive processes that interpret mental images in order to characterize the properties of the underlying representations and cognitive processes. One of the most influential works that helped mental imagery to regain its respectability was proposed by Shepard and Metzler (1971). In their mental rotation paradigm, participants viewed two three-dimensional (3D) objects with several arms, each consisting of small cubes, and decided whether the two objects had the same shape, regardless of difference in the orientations of the objects. The key finding was that response times increased linearly with increasing angular disparity between the two objects. The results demonstrated for the first time that people mentally rotated one of the objects in congruence with the orientation of the other object. Other paradigms, such as the image scanning paradigm (e.g., Finke & Pinker, 1982; Kosslyn, Ball, & Reiser, 1978), allowed researchers to characterize not only the properties of the cognitive processes at play in visual mental imagery but also the nature of visual mental images. Critically, the data of these experiments suggested that visual mental images are depictive representations. By depictive, researchers mean that (1) each part of the representation corresponds to a part of the represented object, such that (2) the distances between representations of the parts (in a representational space) correspond to the distances between the parts on the object itself (see Kosslyn et al., 2006).

However, not all researchers interpreted behavioral results in mental imagery studies as evidence that mental images are depictive. For example, Pylyshyn (1973, 2002, 2003a, 2003b, 2007) proposed a propositional account of mental imagery. According to this view, results obtained in mental imagery experiments can be best explained by the fact that participants rely not on visuo-spatial mental images, but instead on descriptive representations (the sort of representations that underlie language). Pylyshyn (1981) championed the idea that the conscious experience of visualizing an object is purely epiphenomenal, as is the power light on an electronic device—the light does not plays a functional role in the way the electronic device works. Thus, it became evident that behavioral data would not be sufficient to resolve the mental imagery debate between propositional and depictive researchers. In fact, Anderson (1978) demonstrated that any behavioral data collected in a visual mental imagery experiment could be explained equally well by inferring that depictive representations were processed or that a set of propositions were processed.

As cognitive neuroscience started to elicit the neural underpinning of a number of higher cognitive functions and of visual perception started, it became evident that neuroimaging data could resolve the imagery debate initiated in the 1970s. The rationale of using neuroimaging to characterize the nature of visual mental images followed directly on the heels of the functional and structural equivalence documented in behavioral studies between visual mental imagery and visual perception (see Kosslyn, 1980). Researchers reasoned that if visual mental imagery relies on representations and cognitive processes similar to those involved during visual perception, then visual mental imagery should rely on the same brain areas that support visual perception (Kosslyn, 1994).

In this chapter we report results collected in positron tomography emission (PET), functional magnetic resonance imagery (fMRI), transcranial magnetic stimulation (TMS), and brain lesions studies, which converged in showing that visual mental imagery relies on the same brain areas as those elicited when one perceives the world or initiates an action. The different methods serve different means. For example, fMRI allows researchers to monitor the whole brain at work with a good spatial resolution—by contrasting the mean blood oxygen level–dependent signal (BOLD) in a baseline condition to the BOLD signal in an experimental condition. However, fMRI provides information on the correlations between the brain areas activated and the tasks performed but not on the causal relations between the two. In contrast, brain-damaged patients and TMS studies can provide such causal (p. 76) relations. In fact, if a performance in a particular task is selectively impaired following a virtual lesion (TMS) or an actual brain lesion, this specific brain area plays a causal role in the cognitive processes and representations engaged in that particular task. However, researchers need to rely on previous fMRI or PET studies to decide what specific brain areas to target with TMS or which patients to include in their study. Thus, a comprehensive view of the neural underpinning of any cognitive function requires taking into account data from all of these approaches.

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In this chapter, we first discuss and review the results of studies that document an overlap of the neural circuitry in the early visual cortex between visual mental imagery and visual perception. Then, we present studies that specifically look at the neural underpinning of shape-based mental imagery and spatial mental imagery. Finally, we report studies on the neural bases of motor imagery and how they overlap with those recruited when ones initiates an action.

Visual Mental Imagery and the Early Visual Areas

The early visual cortex comprises Brodmann areas 17 and 18, which receive input from the retina. These visual areas are retinotopically organized: Two objects located close to each other in a visual scene activate neurons in areas 17 and 18 relatively close to each other (Sereno et al., 1995). Thus, visual space is represented topographically in the visual cortex using two dimensions: eccentricity and polar angle. "Eccentricity" is the distance from the fovea (i.e., high-resolution central region of the visual field) of a point projected on the retina. Crucially, the farther away a point is located from the fovea, the more anterior the activation is observed in the early visual cortex. Bearing on the way eccentricity is represented on the cortex, Kosslyn and collaborators (1993) used PET to study whether area 17 was recruited during visual mental imagery of letters. In their task, participants visualized letters, maintained the mental images of the letters for 4 seconds, and then were asked to make a judgment about a visual property of the letters—such as whether the letters possess a straight line. Blood flow was monitored through PET. The hypothesis was that if visual mental images were depictive and recruited topographical areas of the visual cortex, then when participants were asked to visualize letters as small as possible (while remaining visible), the activation of area 17 should be more anterior than when participants visualized letters as large as possible (while being entirely visible). The results were consistent with their hypothesis: Large visualized letters activated posterior regions of area 17, whereas small visualized letters recruited anterior regions of area 17. Kosslyn, Thompson, Kim, and Alpert (1995) replicated the results in a PET study in which participants visualized line drawings of objects previously memorized in boxes of three different sizes. These two studies used a neuroimaging technique with limited spatial resolutions, which led some to raise doubt about these results.

However, similar findings were reported when fMRI was used—a technique that provides a better spatial resolution of the brain areas activated. For example, Klein, Paradis, Poline, Kosslyn, and Lebihan (2000) in an event-related fMRI study documented an activation of area 17 that started 2 seconds after the auditory cue prompting participants to form a mental image, peaked around 4 to 6 seconds, and dropped off after 8 seconds or so. In a follow-up experiment, Klein et al. (2004) demonstrated that the orientation with which a bowtie shape stimulus was visualized modulated the activation of the visual cortex. The activation elicited by visualizing the bowtie vertically or horizontally matched the cortical representations of the horizontal and vertical meridians. Moreover, in a fMRI study, Slotnick, Thompson, and Kosslyn (2005) found that the retinotopic maps produced by the visual presentation of rotating and flickering checkerboard wedges were similar to the ones produced when rotating and flickering checkerboard wedges were visualized. And to some extent, those maps were more similar than the maps produced in an attention-based condition. Finally, Thirion and colleagues (2006) adopted an "inverse retinotopy" approach to infer the content of visual images based on the brain activations observed. Participants were asked in a perceptual condition to fixate rotating Gabor patches and in the mental imagery condition to visualize one of the six Gabor patches rotating right or left of a fixation point. Authors were able to predict accurately the stimuli participants had seen and to a certain degree the stimuli participants had visualized. Crucially, most of the voxels leading to a correct prediction of the stimuli visualized or presented visually were located in area 17 and 18.

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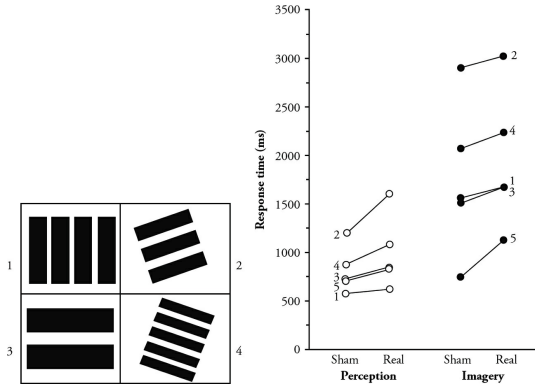

Click to view larger

Figure 5.1 Set of stimuli (*left*) and mean response times for each participant (noted 1 to 5) in the two experimental conditions (perception vs. mental imagery) as a function of the repetitive transcranial magnetic stimulation (rTMS) condition (real vs. sham).

Taken together, results from fMRI and PET studies converge in showing that visual mental imagery activates the early visual areas and that the spatial structure of the activations elicited by the mental imagery task is accounted for by standard (p. 77) retinotopic mapping. Nevertheless, the questions remained as to whether activation of the early visual areas plays any functional role in visual imagery. In order to address this question, Kosslyn et al. (1999) designed a task in which participants first memorized four patterns of black and white stripes (which varied in length, width, orientation, and spacing of the stripes; Figure 5.1) in four quadrants, and then were asked to visualize two of the patterns and to compare them on a given visual attribute (such as the orientation of the stripes). The same participants performed the task in a perceptual condition on which their judgments were based on patterns of stripes displayed on the screen. In both conditions, before comparing two patterns of stripes, repetitive TMS (rTMS) was delivered to the early visual cortex—which had been shown to be activated using PET. In rTMS studies, a coil is used to deliver low-frequency magnetic pulses, which decrease cortical excitability for several minutes in the cortical area targeted (see Siebner et al. 2000). This technique has the advantage that the disruption is reversible and lasts for a few minutes. In addition, because the disruption is transient, there are no compensatory phenomena as with real lesions. When stimulation was delivered to the posterior occipital lobe (*real* rTMS condition), participants required more time to compare two patterns of stripes than when stimulations were delivered away from the brain (in a *sham* rTMS). The effect of real rTMS (as denoted by the difference between the sham and real stimulations; see Figure 5.1) was similar in visual mental imagery and visual perception, which makes sense if area 17 is critical for both.

Sparing et al. (2002) used another TMS approach to determine whether visual mental imagery modulates cortex excitability. The rationale of their approach was to use the *phosphene threshold* (PT; i.e., the minimum TMS intensity that evokes phosphenes) to determine the cortical excitability of the primary visual areas of the brain. A single-pulse TMS was delivered on the primary visual cortex to produce phosphenes in the right lower quadrant of the visual field. Concurrently, participants performed either a visual mental imagery task or an auditory control task. For each participant, the PT was determined by increasing TMS intensity on each trial until participants reported experiencing phosphenes. Visual mental imagery decreased the PT compared with the baseline condition, whereas the auditory task had no effect on the PT. The results indicate that visual mental imagery enhances cortex excitability in the visual cortex, which supports the functional role of the primary visual cortex in visual mental imagery. Consistent with the role of area 17 in visual mental imagery, the apparent horizontal (p. 78) size of visual mental images of a patient who had the occipital lobe surgically removed in one hemisphere was half the apparent size of mental images in normal participants (Farah, Soso, & Dasheiff, 1992).

However, not all studies reported a functional role of area 17 in visual mental imagery. In fact, neuropsychological studies offered compelling evidence that cortically blind patients could have spared visual mental imagery abilities (see Bartolomeo, 2002, 2008). Anton (1899) and Goldenberg, Müllbacher, and Nowak (1995) reported cortically blind patients who seemed to be able to form visual mental images. In addition, Chatterjee and Southwood (1995) reported two cortically blind patients resulting from medial occipital lesions with no impairment of their capacity to imagine object forms—such as capital letters or common animals. These two patients could also draw a set of common objects from memory.

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Finally, Kosslyn and Thompson (2003), reviewed more than 50 neuroimaging studies (fMRI, PET, and single-photon emission computer tomography, or SPECT) and found that in nearly half, there was no activation of the early visual cortex. A meta-analysis of the neuroimaging literature of visual mental imagery revealed that three factors accounted for the probability of activation in area 17. Sensitivity of the technique is one of the factors, and 19 fMRI studies out of 27 reported activation in area 17, compared with only 2 SPECT studies out of 9 reporting such activation. The degree of detail of the visual mental images that needs to be generated is also important, with high-resolution mental images more likely to elicit activation in area 17. Finally, the type of judgment accounts for the probability of activation in area 17: If spatial judgment is required, activation in area 17 is less likely. Thus, activation in area 17 most likely reflects the computation needed to generate the visual images, at least for certain types of mental images, such as high-resolution, shape-based mental images.

Visual Mental Imagery and Higher Visual Areas

The overlap of the brain areas elicited by visual perception and mental imagery was studied not only in early visual areas but also in higher visual areas. The visual system is organized hierarchically, with early visual cortical areas (areas 17 and 18) located on the lowest level (see Felleman & Van Essen, 1991). Brain lesions and neuroimaging studies document that the visual system is then organized in two parallel streams with different functions (e.g., Goodale & Milner, 1992; Haxby et al., 1991; Ungerleider & Mishkin, 1982). The ventral stream (running from the occipital lobes down to the inferior temporal lobes) is specialized in processing object properties of percepts (such as shape, color, and texture), whereas the dorsal stream (running from the occipital lobes up to the posterior parietal lobes) is specialized in processing spatial properties of percepts (such as orientation and location) and action (but see for a discussion Borst, Thompson, and Kosslyn, 2011). A critical finding is that parallel deficits occur in visual mental imagery (e.g., Levine, Warach, & Farah, 1985): Damages to the ventral stream disrupt the ability to visualize the shape of objects (such as the shape of a stop sign), whereas damages to the dorsal stream disrupt the ability to create a spatial mental image (such as the locations of landmarks on a map).

In the next section, we review neuroimaging and brain-damaged patient studies showing that shape-based mental imagery (including mental images of faces) and visual perception engage most of the same higher visual areas in the ventral stream and that spatial mental imagery and spatial vision recruit most of the same areas in the dorsal stream.

Ventral Stream, Shape-Based Mental Imagery and Color Imagery

Brain imaging and neuropsychological data document a spatial segregation of visual object representations in the higher visual areas. For example, Kanwisher and Yovel (2006) demonstrated that the lateral fusiform gyrus responds more strongly to pictures of faces than other categories of objects, whereas the medial fusiform gyrus and the parahippocampal gyri respond selectively to pictures of buildings (Downing, Chan, Peelen, Dodds, & Kanwisher, 2006).

To demonstrate the similarity between the cognitive processes and representations in vision and visual mental imagery, researchers investigated whether the spatial segregation of visual objects in the ventral stream can be found during shape-based mental imagery. Bearing on this logic, O'Craven and Kanwisher (2000) asked a group of participants either to recognize pictures of familiar faces and buildings or to visualize those pictures in an fMRI study. In the perceptual condition, a direct comparison of activation elicited by the two types of stimuli (buildings and faces) revealed a clear segregation within the ventrotemporal cortex—with activation found in the fusiform face area (FFA) for faces and in the parahippocampal place area for buildings (PPA). In the visual mental imagery condition, (p. 79) the same pattern was observed but with weaker activation and smaller patches of cortex activated. Crucially, there was no hint of activation of the FFA when participants visualized faces, nor of the PPA when they visualized buildings. The similarity between vision and mental imagery in the higher visual areas was further demonstrated by the fact that more than 84 percent of the voxels activated in the mental imagery condition were activated in the perceptual condition.

These results were replicated in another fMRI study (Ishai, Ungerleider, & Haxby, 2000). In this study, participants were asked either to view passively pictures of three objects categories (i.e., faces, houses, and chairs), to view scrambles version of these pictures (perceptual control condition), to visualize the pictures while looking at a gray

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background, or to stare passively at the gray background (mental imagery control condition). When activation elicited by the three object categories were compared in the perceptual condition—after removing the activation in the respective control condition—different regions in the ventral stream showed differential responses to faces (FFA), houses (PPA), and chairs (inferior temporal gyrus). Fifteen percent of the voxels in these three ventral stream regions showed a similar pattern of activation in the mental imagery condition. Mental images of the three categories of objects elicited additional activation in the parietal and the frontal regions that were not found in the perceptual condition.

In a follow-up study, Ishai, Haxby, and Ungerleider (2002) studied the activation elicited by famous faces either presented visually or visualized. In the mental imagery condition, participants studied pictures of half of the famous faces before the experiment. For the other half of the trials, participants had to rely on their long-term memory to generate the mental images of the faces. In the mental imagery and perceptual conditions, the FFA (lateral fusiform gyrus) was activated, and 25 percent of the voxels activated in the mental imagery condition were within regions recruited during the perceptual condition. The authors found that activation within the FFA was stronger for faces studied before the experiment than for faces generated on the basis of information stored in long-term memory. In addition, given that visual attention did not modulate the activity recorded in higher visual areas, Ishai and colleagues argued that attention and mental imagery are dissociated to some degree.

Finally, although mental imagery and perception recruit the same category-selective areas in the ventral stream, these areas are activated predominantly through bottom-up inputs during perception and through top-down inputs during mental imagery. In fact, a new analysis of the data reported by Ishai et al. (2000) revealed that the functional connectivity of ventral stream areas was stronger with the early visual areas in visual perception; whereas during visual mental imagery, stronger functional connections were found between the higher visual areas and the frontal and parietal areas (Mechelli, Price, Friston, & Ishai, 2004).

A recent fMRI study further supported the similarity of the brain areas recruited in the ventral stream during visual mental imagery and visual perception (Stokes, Thompson, Cusack, & Duncan, 2009). In this study, participants were asked to visualize an “X” or an “O” based on an auditory cue, or to view passively the two capital letters displayed on a computer screen. During both conditions (i.e., visual mental imagery and visual perception), the visual cortex was significantly activated. Above-baseline activation was recorded in the calcarine sulcus, cuneus, and lingual gyrus, and it extended to the fusiform and middle temporal gyri. In addition, in both conditions, a multivoxel pattern analysis restricted to the anterior and posterior regions of the lateral occipital cortex (LOC) revealed that different populations of neurons code for the two types of stimuli (“X” and “O”). Critically, a perceptual classifier trained on patterns of activation elicited by the perceptual presentation of the stimuli was able to predict the type of visual images generated in the mental imagery condition. The data speak to the fact that mental imagery and visual perception activate shared content-specific representations in high-level visual areas, including in the LOC.

Brain lesions studies generally present converging evidence that mental imagery and perception rely on the same cortical areas in the ventral stream (see Ganis, Thompson, Mast, & Kosslyn, 2003). The logic underlying the brain lesions studies is that if visual mental imagery and perception engage the same visual areas, then the same pattern of impairment should be observe in the two functions. Moreover, given that different visual mental images (i.e., houses vs. faces) selectively elicit activation in different areas of the ventral stream, the impairment in one domain of mental imagery (color or shape) should yield parallel deficit in this specific domain in visual perception. In fact, patients with impairment in face recognition (i.e., prosopagnosia) are impaired in their ability to visualize faces (Shuttleworth, Syring, & Allen, 1982; (p. 80) Young, Humphreys, Riddoch, Hellawell, & De Haan, 1994). Selective deficit to identify animals in a single case study was accompanied by similar deficit to describe animals or to draw them from memory (Sartori & Job, 1988). In addition, as revealed by an early review of the literature (Farah, 1984), object agnosia was generally associated with deficit in the ability to visualize objects. Even finer parallel deficits can be observed in the ventral stream. For example, Farah, Hammond, Mehta, and Ratcliff (1989) reported the case of a prosopagnosic patient with specific deficit in his ability to visualize living things (such as animals or faces) but not in his ability to visualize nonliving things. In addition, some brain-damaged patients cannot distinguish colors perceptually and present similar deficits in color imagery (e.g., Rizzo, Smith, Pokorony, & Damasio, 1993). Critically, patients with color perception deficits have good general mental imagery abilities but are specifically impaired in color mental imagery tasks (e.g., Riddoch & Humphreys, 1987).

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However, not all neuropsychological findings report parallel deficits in mental imagery and perception. Cases of patients were reported who had altered perception but preserved imagery (e.g., Bartolomeo et al., 1998; Behrmann, Moscovitch, & Winocur, 1994; Servos & Goodale, 1995). For example, Behrmann et al. (1994) reported the case of C.K., a brain-damaged patient with a left homonymous hemianopia and a possible thinning of the occipital cortex (as revealed by a PET and MRI scan) who was severely impaired at recognizing objects but who had no apparent deficit in shape-based mental imagery. In fact, C.K. could draw objects with considerable detail from memory and could use information derived from visual images in a variety of tasks. Conversely, he could not identify objects presented visually, even those he drew from memory. A similar dissociation between perceptual impairments and relative spared ability in mental imagery was observed in Madame D. (Bartolomeo et al., 1998). Following bilateral brain lesions to the extrastriate visual areas (i.e., Brodmann areas 18, 19 bilaterally and 37 in the right hemisphere), Madame D. developed severe alexia, agnosia, prosopagnosia, and achromatopsia. Her ability to recognize objects presented visually was severely impaired except for very simple shapes like geometric figures. In contrast, she could draw objects from memory, but she could not identify them. She performed well on an object mental imagery test. Her impairment was not restricted to shape processing. In fact, she could not discriminate between colors, match colors, or point to the correct color. In sharp contrast, she presented no deficit in color imagery, being able, for example, to determine which of two objects had a darker hue when presented with a pair of objects names.

In some instances, studies reported the reverse pattern of dissociation with relatively normal perception associated with deficits in visual mental imagery (e.g., Goldenberg, 1992; Guariglia, Padovani, Pantano, & Pizzamiglio, 1993; Jacobson, Pearson, & Robertson, 2008; Moro, Berlucchi, Lerch, Tomaiuolo, & Aglioti, 2008). For example, two patients who performed a battery of mental imagery tests in several sensory domains (visual, tactile, auditory, gustatory, olfactory, and motor) showed pure visual imagery deficit for one and visual and tactile imagery deficit for the other. Critically, the two patients had no apparent perceptual, language, or memory deficits (Moro et al., 2008). Lesions were located in the middle and inferior temporal gyri of the left hemisphere in one patient and in the temporo-occipital area and the left medial and superior parietal lobe in the other patient.

The fact that some brain-damaged patients can present spared mental imagery with deficit in visual perception or spared visual perception with deficit in mental imagery could reveal a double dissociation between shape- and color-based imagery and visual perception. In fact, visualizing an object relies on top-down processes that are not always necessary to perceive this object, whereas perceiving an object relies on bottom-up organizational processes not required to visualize it (e.g., Ganis, Thompson, & Kosslyn, 2004; Kosslyn, 1994). This double dissociation is supported by the fact that not all of the same brain areas are activated during visual mental imagery and visual perception (Ganis et al., 2004; Kosslyn, Thompson, & Alpert, 1997). In an attempt to quantify the similarity between visual mental imagery and visual perception, Ganis et al. (2004) in an fMRI study asked participants to judge visual properties of objects (such as whether the object was taller than wide) based either on a visual mental image of that object or on a picture of that object presented visually. Across the entire brain, the amount of overlap of the brain regions activated during visual mental imagery and visual perception reached 90 percent. The amount of overlap in activation was smaller in the occipital and temporal lobes than in the frontal and parietal lobes, which suggests that perception relies in part on bottom-up organizational processes that are not used as extensively during mental imagery. However, visual imagery elicited activation in regions that were a (p. 81) subset of the regions activated during the perceptual condition.

Dorsal Stream and Spatial Mental Imagery

In the same way that researchers have studied brain areas in the ventral stream involved in shape- and color-based mental imagery, researchers have identified brain areas recruited during spatial mental imagery in the dorsal stream. A number of neuroimaging studies used a well-understood mental imagery phenomenon to investigate the brain areas elicited during spatial mental imagery, namely, the image scanning paradigm.

In the image scanning paradigm, participants first learn a map of an island with a number of landmarks, then they mentally scan the distance between each pair of landmarks after hearing the names of a pair of landmarks (e.g., Denis & Cocude, 1989; Kosslyn et al., 1978). The landmarks are positioned in such a way that distances between each pair of landmarks are different. The classic finding is a linear increase of response times with increasing distance between landmarks (see Denis & Kosslyn, 1999). The linear relationship between distance and scanning

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times suggests that spatial images incorporate the metric properties of the objects they represent—which constitutes some of the evidence that spatial images depict information. In a PET study, Mellet, Tzourio, Denis, and Mazoyer (1995) investigated the neural basis of image scanning. After learning the map of a circular island, participants were asked either to scan between each landmark on a map presented visually in clockwise or counterclockwise direction or to scan a mental image of the same map in the same way. When compared with a rest condition, both conditions elicited brain activation in the bilateral superior external occipital regions and in the left internal parietal region (precuneus). However, primary visual areas were activated only in the perceptual condition.

fMRI studies provided further evidence that spatial processing of spatial images and spatial processing of the same material presented visually share the same brain areas in the dorsal stream (e.g., Trojano et al., 2000, 2004). For example, Trojano et al. (2000) asked participants to visualize two analogue clock faces and then to decide on which of them the clock hands form the greater angle. In the perceptual task, the task of the participants was identical, but the two clock faces were presented visually. When compared with a control condition (i.e., participants judged which of the two times was numerically greater), the mental imagery condition elicited activation in the posterior parietal cortex and several frontal regions. In both conditions, brain activation was found in the inferior parietal sulcus (IPS). Critically, when the two conditions (imagery and perception) were directly contrasted, the activity in the IPS was no longer observed. The neuroimaging data suggest that the IPS supports spatial processing of mental images and of visual percepts. In a follow-up study using the clock-face mental imagery task in an event-related fMRI study, Formisano et al. (2002) found similar activation of the posterior parietal cortex with a peak of activation in the IPS 2 seconds after the auditory presentation of the hours to visualize.

Interestingly, the frontoparietal network at play during spatial imagery is not restricted to the processing of static spatial representation. In fact, Kaas, Weigelt, Roebroeck, Kohler, and Muckli (2010) studied the brain areas recruited when participants were imagining objects in movement using fMRI. In the motion imagery task, participants were asked to visualize a blue ball moving back and forth within either the upper right corner or the lower left corner of a computer screen. Participants imagined the motion of the ball at different speeds—adjusted in the function of duration of an auditory cue. To determine whether participants visualized the ball at the correct speed, participants were required upon hearing a specific auditory cue to decide which of two visual targets was closer to the imagined blue ball. The motion imagery task elicited activation in a parietofrontal network comprising bilaterally the superior and inferior parietal lobules (areas 7 and 40) and the superior frontal gyrus (area 6), in addition to activation in the left middle occipital gyrus and hMT/V5+. Finally, in V1, V2, and V3, a negative BOLD response was found. Kass and colleagues argue that this negative BOLD signal might reflect an inhibition of these areas to prevent visual inputs to interfere with motion imagery in higher visual areas such as hMT/V5+.

The recruitment of the dorsal route for spatial imagery is not restricted to the modality in which information is presented. Mellet et al. (2002) found similar activation in a parietofrontal network (i.e., intraparietal sulcus, presupplementary motor area, and superior frontal sulcus) when participants mentally scan an environment described verbally or an environment learned visually. Activation of similar brain areas in the dorsal route is also observed when participants generate spatial images of cubes assembled on the basis of verbal information (Mellet et al., 1996). In addition, neuroimaging studies on (p. 82) blind participants suggest that representations and cognitive processes in spatial imagery are not visuo-spatial. For example, during a spatial mental imagery task, the superior occipital (area 19), the precuneus, and the superior parietal lobes (area 7) were activated in the same way in sighted and early blind participants (Vanlierde, de Volder, Wanet-Defalque, & Veraart, 2003). The task required participants to generate a pattern in a 6 × 6 grid by filling in cells based on verbal instructions. Once they generated the mental image of the pattern, participants judged the symmetry of this pattern. The fact that vision is not necessary to form and to process spatial images was further demonstrated in an rTMS study. Aleman et al. (2002) found that participants required more time to determine whether a cross presented visually "fell" on the uppercase letter they visualized in a *real* rTMS condition (compared with a *sham* rTMS condition) only when repetitive pulses were delivered on the posterior parietal cortex (P4 positions) but not when delivered on the early visual cortex (Oz position).

The functional role of the dorsal route in spatial mental imagery is supported by results collected on brain-damaged patients (e.g., Farah et al., 1988; Levine et al., 1985; Luzzatti, Vecchi, Agazzi, Cesa-Bianchi, & Vergani, 1998; Morton & Morris, 1995). For example, Morton and Morris (1995) reported a patient called M.G. with a left parieto-occipital lesion who was selectively impaired in visuo-spatial processing. M.G. had no deficit in face recognition

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and visual memory tests nor in an image inspection task. In contrast, she was not only impaired on a mental rotation task but also on an image scanning task. She could learn the map of the island and indicate the correct positions of the landmarks, but she was not able to mentally scan the distance between the landmarks. She presented similar deficit when asked to scan the contour of block letters.

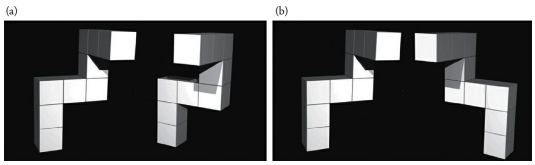
Motor Imagery

In the previous sections, we presented evidence that visual mental imagery and spatial imagery rely on the same brain areas as the ones elicited during vision and spatial vision, respectively. Given that motor imagery occurs when a movement is mentally simulated, motor imagery should recruit brain areas involved in physical movement. And in fact there is a growing number of evidence that motor areas are activated during motor imagery. In the next section, we review evidence that motor imagery engages the same brain areas as the ones recruited during a physical movement, including in some instances the primary motor cortex, and that motor imagery is one of the strategies used to transform mental images.

Motor Imagery and Physical Movement

Decety and Jeannerod (1995) demonstrated that if one is asked to mentally walk from point A to point B, the time to realize this "mental travel" is similar to the time one would take to walk that distance. This mental travel effect (i.e., similarity of the time to imagine an action and the time to perform that action) constitutes strong evidence that motor imagery is crucial to simulating actual physical movements. Motor imagery is a particular type of mental imagery and differs from visual imagery (and to a certain extent from spatial imagery). In fact, a number of studies have documented that visual mental imagery and motor imagery rely on distinct mechanisms and brain areas (Tomasino, Borroni, Isaja, & Rumiati, 2005; Wraga, Shepard, Church, Iniati, Kosslyn, 2005; Wraga, Thompson, Alpert, & Kosslyn, 2003). A single-cell recoding of the motor strip of monkeys first demonstrated that motor imagery relies partially on areas of the cortex that carry motor control: Neurons in the motor cortex fired in sequence depending of their orientation tuning while monkeys were planning to move a lever along a specific arc (Georgopoulos, Lurito, Petrides, Schwartz, & Massey, 1989). Crucially, the neurons fired when the animals were preparing to move their arms, not actually moving them.

To study motor imagery in humans, researchers often used mental rotation paradigms. In the seminal mental rotation paradigm designed by Shepard and Metzler (1971), a pair of 3D objects with several arms (each consisting of small cubes) is presented visually (Figure 5.2). The task of the participants is to decide whether the two objects have the same shape, regardless of difference in their orientation. The key finding is that the time to make this judgment increases linearly as the angular disparity between the two objects increases (i.e., mental rotation effect). Subsequent studies showed that the mental rotation effect is found with alphanumerical stimuli (e.g., Cooper & Shepard, 1973, Koriat & Norman, 1985), two-dimensional line drawings of letter-like asymmetrical characters (e.g., Tarr & Pinker, 1989), and pictures of common objects (e.g., Jolicoeur, 1985).



Click to view larger

Figure 5.2 Example of a pair of Shepard and Metzler–like three-dimensional objects with **(a)** identical and **(b)** different shapes with a 50-degree rotation of the object on the right.

Richter et al. (2000) in an fMRI study found that mental rotation of Shepard and Metzler stimuli elicited activation in the superior parietal lobes bilaterally, the supplementary motor cortex, and the left (p. 83) primary motor cortex. Results from a hand mental rotation study provided additional evidence that motor processes were involved during image transformation (Parsons et al., 1995). Pictures of hands were presented in the right or left visual field with different orientations, and participants determined whether each picture depicted a left or right hand. Parsons and colleagues reasoned that the motor cortex would be recruited if participants mentally rotated their own hand in congruence with the orientation of the stimulus presented to make their judgment. Bilateral activation was found in the supplementary motor cortex, and critically, activation in the prefrontal and the insular premotor areas occurred

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in the hemisphere contralateral to the stimulus handedness. Activation was not restricted to brain areas that implemented motor functions; significant activation was also reported in the frontal and parietal lobes as well as in area 17.

According to Decety (1996), image rotation occurs because we anticipate what we would see if we manipulate an object, which implies that motor areas are recruited during mental rotation regardless of the category of objects rotated. Kosslyn, DiGirolamo, Thompson, and Alpert (1998) in a PET study directly tested this assumption by asking participants either to mentally rotate inanimate 3D armed objects or pictures of hands. In both conditions, the two objects (or the two hands) were presented with different angular disparities, and participants judged whether the two objects (or hands) were identical. To determine the brain areas specifically activated during mental rotation, each experimental conditions was compared with a baseline condition in which the two objects (or hands) were presented in the same orientation. The researchers found activation in the primary motor cortex (area M1), premotor cortex, and posterior parietal lobe when participants rotated hands. In contrast, none of the frontal motor areas was activated when participants mentally rotated inanimate objects. The findings suggest that there are at least two ways objects in images can be rotated: one that relies heavily on motor processes, and one that does not. However, the type of stimuli rotated might not predict when the motor cortex is recruited. In fact, Cohen et al. (1996) in an fMRI study found that motor areas were activated in half of the participants in a mental rotation task using 3D armed object similar to the one used in the Kosslyn et al. (1998) study.

Strategies in Mental Rotation Tasks

The fact that mental rotation of inanimate objects elicits activation in frontal motor areas in some participants but not others suggests that there might be more than one strategy to rotate this type of object. Kosslyn, Thompson, Wraga, and Alpert (2001) tested whether in a mental rotation task of 3D armed objects participants could imagine the rotation of objects in two different ways: as if an external force (such as a motor) was rotating the objects (i.e., external action condition), or as if the objects were being physically manipulated (i.e., internal action condition). Participants received different sets of instructions and practice procedures to prompt them to use one of the two strategies (external action vs. internal action). In the practice of the external action condition, a wooden model of a typical Shepard and Metzler object was rotated by an electric motor. In contrast, in the internal condition, participants rotated the wooden model physically. The object used during practice was not used on the experimental trials. On each new set of trials, participants were instructed to mentally rotate the object in the exact same way the wooden model was rotated in the preceding practice session. The crucial finding was that area M1 was activated when participants mentally rotated the object on the internal action trials but not on the external action trials. However, posterior parietal and secondary motor (p. 84) areas were recruited in both conditions. The results have two implications: First, mental rotation in general (independently of the type of stimuli) can be achieved by imagining the physical manipulation of the object. Second, participants can adopt one or the other strategy voluntarily regardless of their cognitive styles or cognitive abilities.

However, the previous study left open the question of whether one can spontaneously use a motor strategy to perform a mental rotation task of inanimate objects. Wraga et al. (2003) addressed this issue in a PET study. In their experiment, participants performed either a mental rotation task of pictures of hands (similar to the one used by Kosslyn et al., 1998) and then a Shepard and Metzler rotation task or two Shepard and Metzler tasks. The authors reasoned that for the group that started with the mental rotation task of hands, motor processes involved in the hand rotation task would covertly transfer to the Shepard and Metzler task. In fact, when the brain activation in the two groups of participants were compared in the second mental rotation task (Shepard and Metzler task in both groups), activation in the motor areas (areas 6 and M1) were found only in the group that performed a hand rotation task before the Shepard and Metzler task (Figure 5.3). The results clearly demonstrate that motor processes can be used spontaneously to mentally rotate objects that are not body parts.

Functional Role of Area M1

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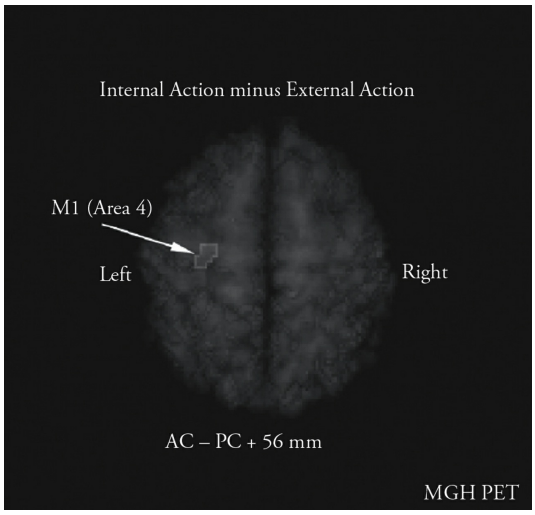

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Figure 5.3 Brain activations observed in the internal action minus the external action conditions.

The studies we reviewed suggest that area M1 plays a role in the mental transformation of objects. However, none addressed whether M1 plays a functional role in mental transformation and more specifically in mental rotation of objects. To test this issue, Ganis, Keenan, Kosslyn, and Pascual-Leone (2000) administered single-pulse TMS to the left primary motor cortex of participants while they performed mental rotations of line drawings of hands or feet presented in their right visual field. Single-pulse TMS was administered at different time intervals from the stimulus onset (400 or 650 ms) to determine when primary motor areas are recruited during mental rotation. In addition, to test whether mental rotation of body parts is achieved by imagining the movement of the corresponding part of the body, single-pulse TMS was delivered specifically to the hand area of M1. Participants required more time and made more errors when a single-pulse TMS was delivered to M1, when the single-pulse TMS was delivered 650 ms rather than 400 ms after stimulus onset, and when participants mentally rotated hands rather than feet. Within the limits of the spatial resolution of the TMS methodology, the results suggest that M1 is required to perform mental rotation of body parts by mapping the movement on one's own body part but only after the visual and spatial relations of the stimuli have been encoded. Tomasino et al. (2005) reported converging data supporting the functional role of M1 in mental rotation by using a mental rotation task of hands in a TMS study.

However, the data are not sufficient to claim that the computations are actually taking place in M1. It is possible that M1 relays information computed elsewhere in the brain (such as in the posterior parietal cortex). And in fact, Sirigu, Duhamel, Cohen, Pillon, Dubois, and Agid (1996) demonstrated that the parietal cortex, not the motor cortex, is critical to generate mental movement representations. Patients with lesions restricted to the parietal cortex showed deficit in predicting the time necessary to perform specific finger movements, whereas no such deficit was reported for a patient with lesions restricted to M1.

Conclusion

Some remain dubious that mental imagery can be functionally meaningful and can constitute a topic of research on its own. However, by drifting away from a purely introspective approach of mental imagery to embrace more objective approaches, and notably by using neuroimaging, researchers have collected evidence that mental images are depictive representations interpreted by cognitive processes at play in other systems—like the perceptual and the (p. 85) motor systems. In fact, we hope that this review of the literature has made clear that there is little evidence to counter the concepts that most of the same neural processes underlying perception are also used in visual mental imagery and that motor imagery can recruit the motor system in a similar way that physical action does. Researchers now rely on what is known of the organization of the perceptual and motor systems and of the key features of the neural mechanisms in those systems to refine the characterization of the cognitive mechanisms at play in the mental imagery system. The encouraging note is that each new characterization of the perceptual and motor systems brings a chance to better understand neural mechanisms at play in mental imagery.

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Finally, with the ongoing development of more elaborate neuroimaging techniques and analyses of the BOLD signal, mental imagery researchers have an increasing set of tools at their disposal to resolve complicate questions about mental imagery. A number of questions remain to be answered in order to achieve a full understanding of the neural mechanisms carrying shape, color, spatial, and motor imagery. For example, although much evidence points toward an overlapping of perceptual and visual mental imagery processes in high-level visual cortices—temporal and parietal lobes—evidence remains mixed at this point concerning the role of lower level processes in visual mental imagery. Indeed, we need to understand the circumstances under which the early visual cortex is recruited during mental imagery. Another problem that warrants further investigation is the neural basis of the individual differences observed in mental imagery abilities. As a prerequisite, we can develop objective methods to measure individual differences in those abilities.

References

Aleman, A., Schutter, D. J. L. G., Ramsey, N. F., van Honk, J., Kessels, R. P. C., Hoogduin, J. M., Postma, A., Kahn, R. S., & de Haan, E. H. F. (2002). Functional anatomy of top-down visuospatial processing in the human brain: Evidence from rTMS. *Cognitive Brain Research*, *14*, 300–302.

Anderson, A. K. (1978). Arguments concerning representations for mental imagery. *Psychological Review*, *85*, 249–277.

Anton, G. (1899). Über die Selbstwahrnehmungen der Herderkranungen des Gehirns durch den Kranken bei Rindenblindheit. *Archiv für Psychiatrie und Nervenkrankheiten*, *32*, 86–127.

Bartolomeo, P. (2002). The relationship between visual perception and visual mental imagery: A reappraisal of the neuropsychological evidence. *Cortex*, *38*, 357–378.

Bartolomeo, P. (2008). The neural correlates of visual mental imagery: An ongoing debate. *Cortex*, *44*, 107–108.

Bartolomeo, P., Bachoud-Levi, A. C., De Gelder, B., Denes, G., Dalla Barba, G., Brugieres, P., et al. (1998). Multiple-domain dissociation between impaired visual perception and preserved mental imagery in a patient with bilateral extrastriate lesions. *Neuropsychologia*, *36*, 239–249.

Behrmann, M., Moscovitch, M., & Winocur, G. (1994). Intact visual imagery and impaired visual perception in a patient with visual agnosia. *Journal of Experimental Psychology: Human Perception and Performance*, *20*, 1068–1087.

Borst, G., Thompson, W. L., & Kosslyn, S. M. (2011). Understanding the dorsal and ventral systems of the cortex: Beyond dichotomies. *American Psychologist*, *66*, 624–632.

Chatterjee, A., & Southwood, M. H. (1995). Cortical blindness and visual imagery. *Neurology*, *45*.

Cohen, M. S., Kosslyn, S. M., Breiter, H. C., DiGirolamo, G. J., Thompson, W. L., Bookheimer, S. Y., Belliveau, J. W., & Rosen, B. R. (1996). Changes in cortical activity during mental rotation: A mapping study using functional MRI. *Brain*, *119*, 89–100.

Cooper, L. A., & Shepard, R. N. (1973). Chronometric studies of the rotation of mental images. In W. G. Chase (Eds.), *Visual information processing* (pp. 75–176). New York: Academic Press.

Decety, J. (1996). Neural representation for action. *Reviews in the Neurosciences*, *7*, 285–297.

Decety, J., & Jeannerod, M. (1995). Mentally simulated movements in virtual reality: Does Fitts's law hold in motor imagery? *Behavioral Brain Research*, *72*, 127–134.

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

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

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Subscriber: Tufts University; date: 28 October 2014

Downing, P. E., Chan, A. W., Peelen, M. V., Dodds, C. M., & Kanwisher, N. (2006). Domain specificity in visual cortex. *Cerebral Cortex*, *16*, 1453–1461.

Farah, M. J. (1984). The neurological basis of mental imagery: A componential analysis. *Cognition*, *18*, 245–272.

Farah, M. J., Hammond, K. M., Mehta, Z., & Ratcliff, G. (1989). Category-specificity and modality-specificity in semantic memory. *Neuropsychologia*, *27*, 193–200.

Farah, M. J., Soso, M. J., & Dasheiff, R. M. (1992). Visual angle of the mind's eye before and after unilateral occipital lobectomy. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 241–246.

Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, *1*, 1–47.

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

Formisano, E., Linden, D. E. J., Di Salle, F., Trojano, L., Esposito, F., Sack, A. T., Grossi, D., Zanella, F. E., & Goebel, R. (2002). Tracking the mind's image in the brain I: Time-resolved fMRI during visuospatial mental imagery. *Neuron*, *35*, 185–194.

Ganis, G., Keenan, J. P., Kosslyn, S. M., & Pascual-Leone, A. (2000). Transcranial magnetic stimulation of primary motor cortex affects mental rotation. *Cerebral Cortex*, *10*, 175–180.

Ganis, G., Thompson, W. L., & Kosslyn, S. M. (2004). Brain areas underlying visual mental imagery and visual perception: An fMRI study. *Brain Research: Cognitive Brain Research*, *20*, 226–241.

(p. 86) Ganis, G., Thompson, W. L., Mast, F. W., & Kosslyn, S. M. (2003). Visual imagery in cerebral visual dysfunction. *Neurologic Clinics*, *21*, 631–646.

Georgopoulos, A. P., Lurito, J. T., Petrides, M., Schwartz, A. B., & Massey, J. T. (1989). Mental rotation of the neuronal population vector. *Science*, *243*, 234–236.

Goldenberg, G. (1992). Loss of visual imagery and loss of visual knowledge: A case study. *Neuropsychologia*, *30*, 1081–1099.

Goldenberg, G., Müllbacher, W., & Nowak, A. (1995). Imagery without perception: A case study of anosognosia for cortical blindness. *Neuropsychologia*, *33*, 1373–1382.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*, 20–25.

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

Haxby, J. V., Grady, C. L., Horwitz, B., Ungerleider, L. G., Mishkin, M., Carson, R. E., Herscovitch, P., Schapiro, M. B., & Rapoport, S. I. (1991). Dissociation of object and spatial visual processing pathways in human extrastriate cortex. *Proceedings of the National Academy of Sciences U S A*, *88*, 1621–1625.

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.

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

Jacobson, L. S., Pearson, P. M., & Robertson, B. (2008). Hue-specific color memory impairment in an individual with intact color perception and color naming. *Neuropsychologia*, *46*, 22–36.

Jolicoeur, P. (1985). The time to name disoriented natural objects. *Memory and Cognition*, *13*, 289–303.

Kaas, A., Weigelt, S., Roebroeck, A., Kohler, A., & Muckli, L. (2010). Imagery of a moving object: The role of

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occipital cortex and human MT/V5+. *NeuroImage*, *49*, 794–804.

Kanwisher, N., & Yovel, G. (2006). The fusiform face area: A cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society of London B*, *361*, 2109–2128.

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. *Brain Research: Cognitive Brain Research*, *22*, 26–31.

Klein, I., Paradis, A.-L., Poline, J.-B., Kosslyn, S. M., & Le Bihan, D. (2000). Transient activity in human calcarine cortex during visual imagery. *Journal of Cognitive Neuroscience*, *12*, 15–23.

Koriat, A., & Norman, J., (1985). Reading rotated words. *Journal of Experimental Psychology: Human Perception and Performance*, *11*, 490–508.

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

Kosslyn, S. M. (1994). *Image and brain*. Cambridge, MA: Harvard University Press.

Kosslyn, S. M., Alpert, N. M., Thompson, W. L., Maljkovic, V., Weise, S. B., Chabris, C., Hamilton, S. E., & Buonanno F. S. (1993). Visual mental imagery activates topographically organized visual cortex: PET investigations. *Journal of Cognitive Neuroscience*, *5*, 263–287.

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

Kosslyn, S. M., DiGirolamo, G., 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., Keenan, J. P., Thompson, W. L., Ganis, G., Sukel, K. E., & Alpert, N. M. (April 2, 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. (2003). When is early visual cortex activated during visual mental imagery? *Psychological Bulletin*, *129*, 723–746.

Kosslyn, S. M., Thompson, W. L., & Alpert, N. M. (1997). Neural systems shared by visual imagery and visual perception: A positron emission tomography study. *NeuroImage*, *6*, 320–334.

Kosslyn, S. M., Thompson, W. L., & Ganis, G. (2006). *The case for mental imagery*. New York: Oxford University Press.

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., Thompson, W. L., Wraga, M., & Alpert, N. M. (2001). Imagining rotation by endogenous versus exogenous forces: Distinct neural mechanisms. *NeuroReport*, *12*, 2519–2525.

Levine, D. N., Warach, J., & Farah, M. J. (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.

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

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

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

Mellet, E., Tzourio, N., Crivello, F., Joliot, M., Denis, M., & Mazoyer, B. (1996). Functional anatomy of spatial mental

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imagery generated from verbal instructions. *Journal of Neuroscience*, *16*, 6504–6512.

Mellet, E., Tzourio, N., Denis, M., & Mazoyer, B. (1995). A positron emission tomography study of visual and mental spatial exploration. *Journal of Cognitive Neuroscience*, *4*, 433–445.

Moro, V., Berlucchi, G., Lerch, J., Tomaiuolo, F., & Aglioti, S. M. (2008). Selective deficit of mental visual imagery with intact primary visual cortex and visual perception. *Cortex*, *44*, 109–118.

Morton, N., & Morris, R. G. (1995). Image transformations dissociated from visuo-spatial working memory. *Cognitive Neuropsychology*, *12*, 767–791.

O'Craven, K. M., & Kanwisher, N. (2000). Mental imagery of faces and places activates corresponding stimulus-specific brain regions. *Journal of Cognitive Neuroscience*, *12*, 1013–1023.

(p. 87) Paivio, A. (1971). *Imagery and verbal processes*. New York: Holt, Rinehart and Winston.

Parsons, L. M., Fox, P. T., Downs, J. H., Glass, T., Hirsch, T. B., Martin, C. C., Jerabek, P. A., Lancaster, J. L. (1995). Use of implicit motor imagery for visual shape discrimination as revealed by PET. *Nature*, *375*, 54–58.

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

Pylyshyn, Z. W. (1981). Psychological explanations and knowledge-dependent processes. *Cognition*, *10*, 267–274.

Pylyshyn, Z. W. (2002). Mental imagery: In search of a theory. *Behavioral and Brain Sciences*, *25*, 157–237.

Pylyshyn, Z. W. (2003a). Return of the mental image: Are there really pictures in the head? *Trends in Cognitive Sciences*, *7*, 113–118.

Pylyshyn, Z. W. (2003b). *Seeing and visualizing: It s not what you think*. Cambridge, MA: MIT Press.

Pylyshyn, Z. W. (2007). *Things and places: How the mind connects with the world*. Cambridge, MA: MIT Press.

Richter, W., Somorjai, R., Summers, R., Jarmasz, M., Tegeler, C., Ugurbil, K., Menon, R., Gati, J. S., Georgopoulos, A. P., & Kim, S.-G. (2000). Motor area activity during mental rotation studied by time-resolved single-trial fMRI. *Journal of Cognitive Neuroscience*, *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.

Sartori, G., & Job, R. (1988). The oyster with four legs: A neuropsychological study on the interaction of visual and semantic information. *Cognitive Neuropsychology*, *5*, 105–132.

Sereno, M. I., Dale, A. M., Reppas, J. B., Kwong, K. K., Belliveau, J. W., Brady, T. J., Rosen, B. R., & Tootell, R. B. H. (1995). Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science*, *268*, 889–893.

Servos, P., & Goodale, M. A. (1995). Preserved visual imagery in visual form agnosia. *Neuropsychologia*, *33* (11), 1383–1394.

Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, *171*, 701–703.

Shuttleworth, E. C., Jr., Syring, V., & Allen, N. (1982). Further observations on the nature of prosopagnosia. *Brain and Cognition*, *1*, 307–322.

Siebner, H. R., Peller, M., Willoch, F., Minoshima, S., Boecker, H., Auer, C., Drzezga, A., Conrad, B., & Bartenstein, P. (2000). Lasting cortical activation after repetitive TMS of the motor cortex: A glucose metabolic study. *Neurology*, *54*, 956–963.

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Sirigu, A., Duhamel, J.-R., Cohen, L., Pillon, B., Dubois, B., & Agid, Y. (1996). The mental representation of hand movements after parietal cortex damage. *Science*, *273* (5281), 1564–1568.

Slotnick, S. D., Thompson, W. L., & Kosslyn, S. M. (2005). Visual mental imagery induces retinotopically organized activation of early visual areas. *Cerebral 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 Research*, *938*, 92–97.

Stokes, M., Thompson, R., Cusack, R., & Duncan, J. (2009). Top-down activation of shape-specific population codes in visual cortex during mental imagery. *Journal of Neuroscience*, *29*, 1565–1572.

Tarr, M. J., & Pinker, S. (1989). Mental rotation and orientation-dependence in shape recognition. *Cognitive Psychology*, *21*, 233–282.

Thirion, B., Duchesnay, E., Hubbard, E., Dubois, J., Poline, J.-B., Lebihan, D., & Dehaene, S. (2006). Inverse retinotopy: Inferring the visual content of images from brain activation patterns. *Neuroimage*, *33*, 1104–1116.

Tomasino, B., Borroni, P., Isaja, A., & Rumiati, R. I. (2005). The role of the primary motor cortex in mental rotation: A TMS study. *Cognitive Neuropsychology*, *22*, 348–363.

Trojano, L., Grossi, D., Linden, D. E., Formisano, E., Hacker, H., Zanella, F. E., Goebel, R., & Di Salle, F. (2000). Matching two imagined clocks: The functional anatomy of spatial analysis in the absence of visual stimulation. *Cerebral Cortex*, *10*, 473–481.

Trojano, L., Linden, D. E., Formisano, E., Grossi, D., Sack, A. T., & Di Salle, F. (2004). What clocks tell us about the neural correlates of spatial imagery. *European Journal of Cognitive Psychology*, *16*, 653–672.

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

Vanlierde, A., de Volder, A. G., Wanet-Defalque, M. C., & Veraart C. (2003). Occipito-parietal cortex activation during visuo-spatial imagery in early blind humans. *NeuroImage*, *19*, 698–709.

Watson, J. B. (1913). Psychology as the behaviorist views it. *Psychological Review*, *20*, 158–177.

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.

Wraga, M. J., Thompson, W. L., Alpert, N. M., & Kosslyn, S. M. (2003). Implicit transfer of motor strategies in mental rotation. *Brain and Cognition*, *52*, 135–143.

Young, A. W., Humphreys, G. W., Riddoch, M. J., Hellawell, D. J., & de Haan, E. H. (1994). Recognition impairments and face imagery. *Neuropsychologia*, *32*, 693–702.

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