

REVIEW

Reopening the Mental Imagery Debate: Lessons from Functional Anatomy

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Over the past few years, the neural bases of mental imagery have been both a topic of intense debate and a domain of extensive investigations using either PET or fMRI that have provided new insights into the cortical anatomy of this cognitive function. Several studies have in fact demonstrated that there exist types of mental imagery that do not rely on primary/early visual areas, whereas a consensus now exists on the validity of the dorsal/ventral-route model in the imagery domain. More importantly, these studies have provided evidence that, in addition to higher order visual areas, mental imagery shares common brain areas with other major cognitive functions, such as language, memory, and movement, depending on the nature of the imagery task. This body of recent results indicates that there is no unique mental imagery cortical network; rather, it reflects the high degree of interaction between mental imagery and other cognitive functions. © 1998 Academic Press

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INTRODUCTION

The ability to produce and to manipulate mental entities that can be used in place of their real counterparts is clearly mandatory for the most elaborate aspects of human psychic activity such as anticipation, reasoning, or creativity. Identification of the cognitive processes involved during visual mental imagery is one of the most active research areas in cognitive psychology (Rumelhart and Norman, 1988; Denis, 1991; Kosslyn and Koenig, 1992; Kosslyn, 1994). However, two decades ago, a powerful trend of thought postulated

that information in the brain was encoded by a unique system of representation whatever the sensory modality (Pylyshyn, 1973, 1981). According to this view, the mental images constituted an epiphenomenon of the mental activity and were thus taken out of a functional role in the elaboration and the progression of the thought. Numerous experimental data based on either experimental psychology or neuropsychological studies and, more recently, functional imaging studies have disparaged this hypothesis (Kosslyn, 1994). These different approaches replaced the mental imagery in the heart of the psychic activity, underlining its interaction with the other cognitive systems such as visual perception, language, and memory. In the present article, we review the results obtained in positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) dealing with the comprehension of the anatomofunctional basis of the relationships between mental imagery and the other cognitive systems.

VISUAL MENTAL IMAGERY AND VISUAL PERCEPTION: THE ANATOMOFUNCTIONAL POINT OF VIEW

Top-Down Processes and Mental Imagery: A Role for Primary Visual Areas?

Visual mental images are a peculiar kind of mental representations in that they preserve the structural and spatial properties of the object or scene they represent. It has been shown for example that the time it takes for one to move between two points of a mental image is proportional to their distance (Kosslyn *et al.*, 1978), similar to what happens in the visual perceptive domain. Similarly, mental rotation of 3D objects linearly depends on the rotation angle (Shepard and Metzler, 1971). Such results demonstrate that mental images are psychological entities that reproduce the physical world constraints and it is therefore legitimate

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to try to uncover the neural bases of such a similitude or, more specifically, to search for a possible network of cerebral structures on which both visual perception and mental imagery would rely.

The degree of involvement of visual perception areas during mental imagery activity has become one of the most debated issues in the human brain mapping community. On one side are the holders of a theory assuming that the invariance of structural and spatial properties of visual mental images is based on the involvement of topographically organized visual areas, including the primary visual area (PVA) (Kosslyn, 1994). According to this hypothesis, mental image generation would require PVA activation from a top-down flux of information coming from the visual association cortices (either occipitoparietal or occipitotemporal). On the other side are several authors who, on the basis of PET and fMRI studies, promote the idea that

the network of brain structures shared by visual perception and mental imagery is limited to the occipital and occipitotemporal cortices, thereby defining the concept of a top-down PVA activation of mental imagery (Roland and Gulyas, 1994).

At the origin of the debate is a study by Kosslyn *et al.* who compared cortical areas activated by mental imagery and by visual perception (Kosslyn *et al.*, 1993). In the first paradigm, subjects were presented with an achromatic grid containing a cross in one of its cells together with a lowercase letter located beneath the grid (Fig. 1A). The task the subjects had to perform was to generate a mental image of the uppercase version of the same letter, to mentally project it onto the grid and to decide if it would contain the cell with the cross. The control task was the perceptual equivalent of the mental imagery task, the subjects being presented with the grid, the cross, the lowercase

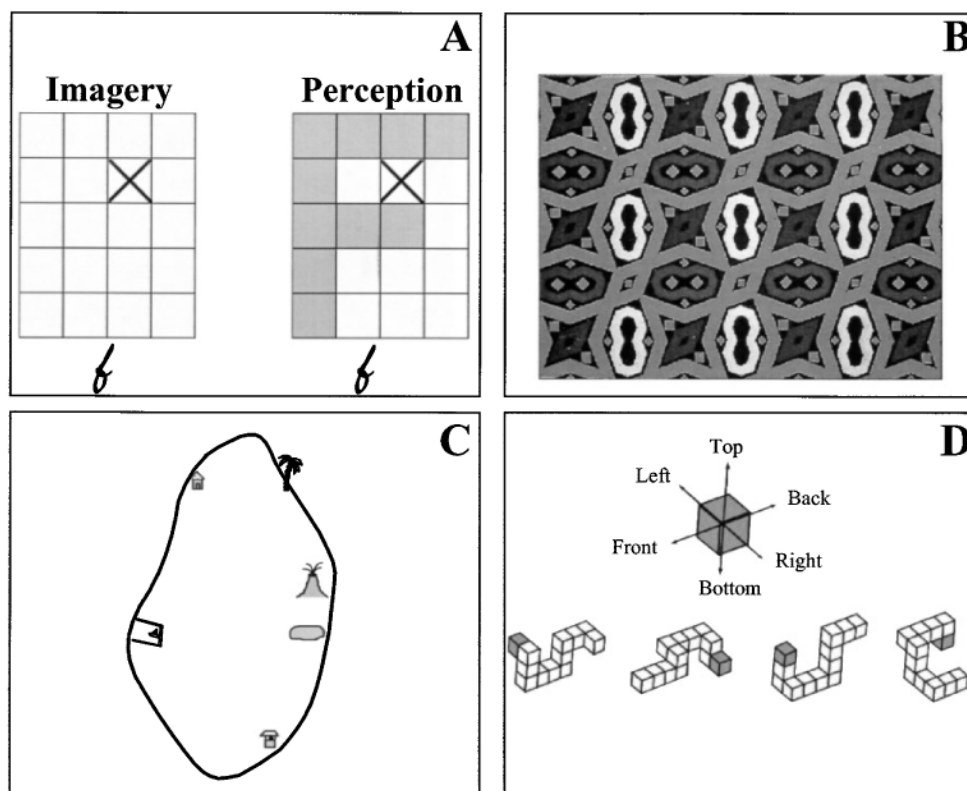


FIG. 1. (A) Stimuli used in the study of Kosslyn *et al.* (1993) (adapted from Podgorny and Shepard, 1978). In the imagery task (left), the subjects saw the grid and the X mark. They had to visualize the block letter that corresponded to the cue beneath the grid (presented in the opposite case) and to decide whether the letter would cover or the X. This condition was compared to a perception task (right) in which the subjects actually saw a letter in a grid and an X mark and had to decide whether the X mark was on or off the letter. (B) Example of 1 of the 10 patterns that the subjects had to learn in the study by Roland *et al.* (1995). In the imagery condition, the subjects were requested to visualize the 10 patterns in the order they had learned them. (C) One of the island maps that subjects had to mentally explore in Mellet *et al.* (1995). After a learning phase, they had to generate a mental image of the map with the landmarks and to move their "mind's eye" from landmark to landmark, pausing a few seconds on each one. (D) Stimuli used in the study of Mellet *et al.* (1996) (adapted from Shepard and Metzler, 1971). The subjects, eyes closed in total darkness, were first asked to mentally visualize a starting cube at the center of their field of view (shown in gray) and to add cubes according to a list of 11 directional words binaurally delivered by earphones at 0.5 Hz. For example, the first cube assembly corresponds to the list right, down, down, back, back, back, up, up, back, back, right. This condition was compared both to a passive listening task of words that phonetically matched the direction word and to a resting state.

letter beneath, and the uppercase letter actually positioned in the grid. The major result of the study was the activation of an area near the PVA when perception was subtracted from mental imagery, showing that PVA blood flow was larger when subjects imagined the uppercase letter than when they actually saw it. This finding constitutes a very strong argument in favor of a topographic organization of mental images and supports the hypothesis of a top-down process involved during mental imagery. Using fMRI, LeBihan *et al.* also reported PVA activation during visual recall of a diode pattern that the subjects had seen a few seconds before (Le Bihan *et al.*, 1993).

Quite divergent results have been reported by several other investigators who did not find PVA involvement during a variety of mental imagery tasks that were reviewed in a 1994 article (Roland and Gulyas, 1994). In their original PET study, Roland *et al.* asked subjects to mentally visualize the route they would follow from their home if they were asked to turn alternately left or right at each intersection (Roland *et al.*, 1987). Contrasting this task to a rest condition in darkness shows activation of the superior occipital and posterior parietal cortices but no activation of the PVA or nearby cortices. In a subsequent study (Roland and Gulyas, 1995), the same authors measured CBF during rest and three new conditions: (1) learning of 10 geometric colored figures visually presented on a screen, (2) visual mental recall of each figure, and (3) visual recognition of the learned figures among a set of visually presented figures (Fig. 1B). When compared to the resting state, both the learning and the recognition tasks activated the PVA, whereas the mental imagery task did not recruit the PVA nor the nearby cortices.

Within this framework, we have compared the brain areas involved during a visual perception and its mental equivalent (Mellet *et al.*, 1995). In this work, during the perceptual task, subjects had to move their gaze between landmarks of an island map visually presented during the PET acquisition, while during the mental imagery task they had to do the same task on a mental image of an island map they were presented with before the PET measurements (Fig. 1C). Comparing the mental imagery task to rest revealed significant activations of the occipitoparietal cortex without any activation of the PVA.

It has been argued by the supporters of PVA involvement during mental imagery that the discrepancies between the results of both sides could be due to the different natures of the control tasks. More specifically, it has been hypothesized that PVA activation could be masked because of high blood flow value in this region during the resting state (Kosslyn and Ochsner, 1994). This issue was raised following the report of PVA activation when mental imagery of objects from their name was contrasted to passive word listening, the

activation being posteriorly located for small objects and lying more anteriorly from large objects, thereby fitting with PVA topographic organization. In contrast, no PVA activation was noted when mental imagery was compared to rest, and PVA blood flow was higher during the former condition than during passive word listening (Kosslyn *et al.*, 1995).

These findings were challenged by that of a recent work we conducted, investigating brain regions involved in mental construction of an object from verbal instructions (Mellet *et al.*, 1996). In this latter study, both the rest condition and a passive listening to words were used as controls (Fig. 1D). No PVA activation was detected whether it was the rest or the passive-listening condition that was subtracted from the mental imagery task, thereby providing a strong argument against the masking effect as the cause of the divergent results.

One could still try to reconcile these results if one assumes that it is the type of mental imagery involved in the task that determines PVA activation or not. In this framework, visual mental imagery of objects would require access to topographically organized visual areas, including PVA, whereas spatial mental imagery would not. This hypothesis, however, is not supported by two recent studies that reported an absence of PVA activation during generation of mental images of animals or objects (D'Esposito *et al.*, 1997; Mellet *et al.*, 1998).

The debate also concerns very specific forms of mental images such as those occurring during dreaming: a recent study described an rCBF increase in the visual associative regions of the ventral pathway during the dream (compared to an awake/rest condition), while the primary visual area showed a significant rCBF decrease (Braun *et al.*, 1998).

Visual hallucinations are another "visual-like" activity that has been sometimes defined as mental images of an extreme vivacity (Mintz and Alpert, 1972). However, the hallucinatory activity did not induce an increased activity in the primary visual area while visual associative regions were activated (Silbersweig *et al.*, 1995).

Because of such divergent results reported in the literature, the debate on the exact role of the PVA in mental imagery remains open. There is, however, a general consensus that methodological arguments such as method sensitivity, data analysis strategies, and control task choice are unlikely to resolve the controversy by themselves alone. Rather, investigators are now focusing on trying to define more precisely the type of mental imagery tasks that activate the PVA (Kosslyn *et al.*, 1998). In other words, PVA engagement during mental imagery may depend on the mental image resolution. Experimental protocols testing this hypothesis are currently under construction.

Ventral and Dorsal Routes in Mental Imagery

Contrasting with the PVA debate, there is a general consensus on the role of associative visual areas in mental imagery. Recall first that visual perceptual information processing schematically follows two major neuroanatomical routes, as first demonstrated in the monkey (Mishkin *et al.*, 1983) and then in humans (Haxby *et al.*, 1991). The so-called ventral or occipitotemporal route that goes from the occipital cortex down to the inferior temporal gyrus is specialized in the processing of object form and, more generally, of object figurative aspects, including face processing (Sergent *et al.*, 1992). This is the identification route by which one answers the "what?" question. The so-called dorsal or occipitoparietal route goes from the occipital cortex up to the superior parietal lobule. It is recruited by object localization and spatial attribute processing. Actually, this route seems to have rather extensive competence since it has been reported to be involved in object localization (Haxby *et al.*, 1991, 1994), shift of spatial attention (Corbetta *et al.*, 1993), and spatial working memory (Jonides *et al.*, 1993). It is used to answer to the "where?" question.

The existence of such a dichotomy in the mental imagery domain was first suggested by neuropsychological studies (Levine *et al.*, 1985; Farah *et al.*, 1988) and is nowadays a topic of intensive investigation with functional imaging.

On the one hand, several recent PET studies have indeed demonstrated that the dorsal route 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 activates the right superior occipital cortex, the left intraparietal sulcus, and the precuneus (Mellet *et al.*, 1995, 1996). Similar results have been obtained during mental navigation along routes previously memorized through a walk in the real environment (Ghaëm *et al.*, 1997). Compared to rest, this task activated the occipitoparietal cortex, including the middle occipital gyrus and the precuneus. Also consistent with these results were those of a visuomotor study in which subjects had to mentally visualize and point at targets the spatial location of which they had previously learned. When compared to rest again, this task bilaterally involved the dorsal route (Kawashima *et al.*, 1995). In another PET study including a spatial imagery task, subjects had to mentally assemble 3D structures according to direction that was auditorily delivered (Fig. 1D). When compared either to a rest or to a passive listening condition, this spatial imagery task bilaterally activated the superior occipital gyrus as well as the inferior and superior parietal lobules (Fig. 2) (Mellet *et al.*, 1996). In summary, there is now strong evidence that the dorsal route, specialized in visuospatial informa-

tion processing, is also involved in spatial mental imagery, even in the absence of previous visual inputs.

On the other hand, the ventral route is known to be involved in object and face recognition and more generally in the encoding and retrieval of the figurative properties of visual representations (Martin *et al.*, 1996). In that respect, it is noteworthy that most of the functional imaging studies dealing with mental image generation have reported inferior temporal and/or fusiform gyrus activations. Note that ventral visual areas of activation have been observed during the generation of the mental image of usual objects either visually recalled or named (Ghaëm *et al.*, 1997; D'Esposito *et al.*, 1997; Mellet *et al.*, 1998), of letters (Kosslyn *et al.*, 1993), and of unusual objects (Mellet *et al.*, 1996). To our knowledge, no functional distinction within the ventral route between fusiform gyrus and inferior temporal gyrus activations has been made at this time. The lateralization of these activations will be discussed later in this article.

In conclusion, the anatomofunctional dichotomy between the dorsal and the ventral pathways according to the spatial or object nature of the imagery task appears to closely match the one evidenced in the visual perception domain. This community of structure materializes the kinship between mental imagery and visual perception as previously emphasized in experimental psychology. However, as mentioned above for the primary visual area, all regions recruited by visual sensory processing are not systematically involved in mental imagery.

MENTAL IMAGERY AND LANGUAGE

Creating Visual Mental Images from Verbal Descriptions

In most of the previously presented studies, subjects first memorized visual percepts and later generated a mental image based on the reactivation of their representations in long-term memory. It is possible, however, to generate the mental image of an object or a scene solely on the basis of a verbal description. It has been shown that such images exhibit properties similar to those of images based on perceptual experience. In particular, cognitive operations such as mental scanning or distance comparison show chronometric patterns similar to those executed on an image that reactivates stored visual information (Denis *et al.*, 1995; De Vega *et al.*, 1996). These findings raise the following question: Do operations on mental visual images that do not arise from a visual experience recruit visual areas? In a study quoted above (Mellet *et al.*, 1996), subjects had to construct mental objects, made of cube assemblies, that they had never seen. Adding cubes to the construction was done upon auditory spatial instructions (i.e., left, right, up, down, back, or front) (Fig. 1D). This operation implied on-line

translation of the semantic content of the verbal stimuli into picture-like representations. The bilateral activations of the superior temporal gyrus that accompanied the dorsal route activation observed in this study support the hypothesis that temporal language areas can convey the information directly to the associative visual areas, both structures being necessary and sufficient for changing the nature of the information (Fig. 2).

By contrast, deactivation in inferior occipital and parietal areas has been reported during mental evocation of memories, a task very likely to be accompanied by visual images (Fink *et al.*, 1996b). Another study also reported rCBF decreases during visual imagery of previously learned objects, compared to rest, in superior and inferior occipital, in superior and inferior parietal, and in inferior temporal cortices (Buckner *et al.*, 1996). The authors of this last study claimed that this fact could be explained by a cross-modal inhibition, given the auditorily directed attention paid to the stimuli. These results obscured the nature of the anatomofunctional interaction between language and mental imagery, although further studies have reported visual areas activation during imagery tasks cued from words (Kosslyn *et al.*, 1995; Ghaëm *et al.*, 1997; D'Esposito *et al.*, 1997). However, one must note that, in all these studies, the language stimulus was restricted to single words or simple verbal instructions, making it quite different from usual speech. In addition, these studies were designed in such a way that listening to the language stimulus and mental image generation were subsequent to one another rather than simultaneous. In a recent PET study we investigated the cerebral areas involved in a task that closely intermingled language and visual mental imagery (Mellet *et al.*, 1998). In this protocol, the subjects, while listening to concrete words and their definition, had to generate the mental image of the corresponding object or animal and to adjust this image to the definition. Compared to rest, this condition elicited bilateral activations in superior temporal sulcus, related to the language comprehension, together with bilateral activations in the fusiform and inferior temporal gyri reflecting, as suggested earlier, the involvement of the ventral route during the mental imagery of objects (Fig. 3). This study confirms that higher order visual areas can be activated when an imagery and a language comprehension task are performed simultaneously. Although verbal representation and visual mental images are distinct cognitive entities (Paivio, 1986), the so-called cross-modal inhibition does not prevent a coactivation of visual and language areas. Moreover, in the mental construction study, no activation in Broca's area was detected when subjects listened to spatial words and used them to assemble the mental image. On the contrary, this area was found activated when they listened to phonetically matched nonspatial words with no instruction of imag-

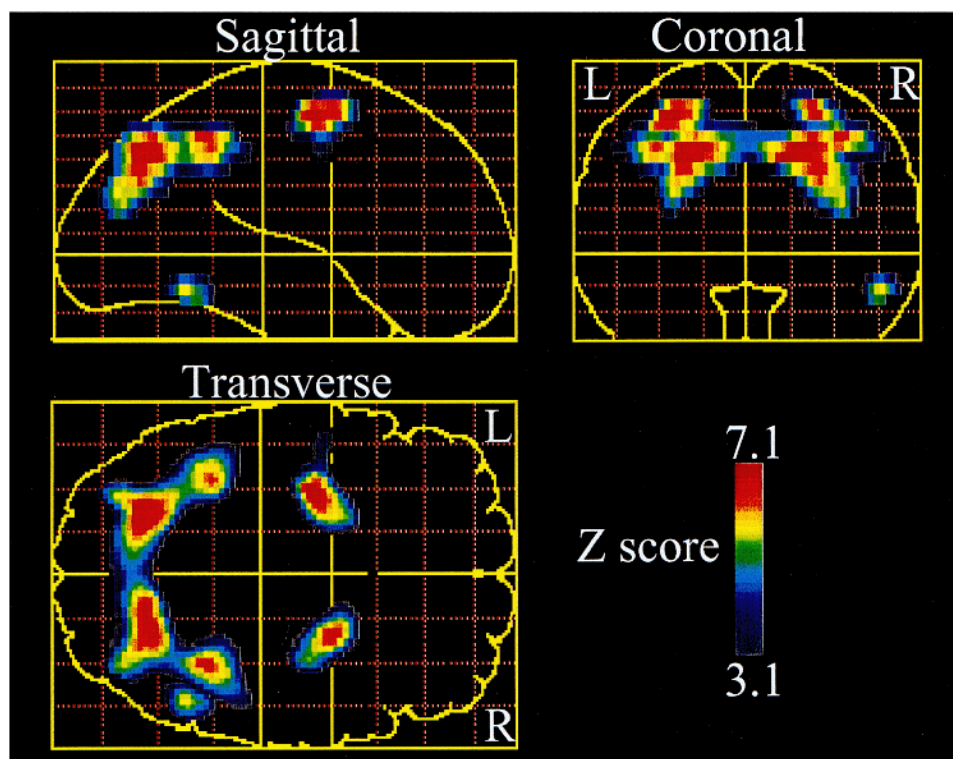
ery (Mellet *et al.*, 1996). In the same vein, the temporal language areas appear less activated in the concrete-definition than in the abstract-definition listening task (Mellet *et al.*, 1998), suggesting that language areas could be solicited more to address a representation when language is the only source of information than when imagery and language are used in conjunction.

Hemispheric Lateralization of Mental Imagery

While it is well established that ventral visual areas, such as the left inferior temporal and fusiform gyri, are involved in object mental imagery, whether a functional hemispheric asymmetry exists remains under debate. In that respect, a recent fMRI study has reported left lateralized activations of the inferior temporal and fusiform gyri during mental image generation of an object or animal upon listening to its name, the control task being to listen to an abstract word (D'Esposito *et al.*, 1997). According to the authors, this finding reflects the specific role of the left hemisphere in mental image generation, an interpretation 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. Moreover, bilateral activations of these ventral areas were also observed in a recent PET study in which subjects were asked to generate the mental image of an animal or object while listening to its dictionary definition (Fig. 3) (Mellet *et al.*, 1998).

It seems thus difficult to conclude the exclusive participation of either one of the hemispheres in mental image generation. Rather, a bilateral participation appears more likely, which does not imply that the two hemispheres play identical roles. Similar to what has been described in the perceptive domain (Fink *et al.*, 1996a), the right hemisphere could be specialized in the processing of the global attributes of a mental image, whereas the left hemisphere could process the local ones. There is, however, little evidence of such a dichotomy in the literature. Another factor that could play a role in functional lateralization is the image complexity. In the visual perception domain, activations of the right inferior temporal and fusiform gyri have been reported during complex form discrimination (Schacter *et al.*, 1995; Faillenot *et al.*, 1997). Similar findings have been observed during the mental imagery of complex objects (Mellet *et al.*, 1996), letters (Kosslyn *et al.*, 1993), or schematic objects (Mellet *et al.*, 1996). A right ventral activation has also been found during mental imagery of concrete words upon listening to their definitions: in this latter study, the definitions contained a detailed description of the object/animal, allowing the generation of a complex mental image (Mellet *et al.*, 1998). Accordingly, the absence of a right ventral activation in the fMRI study of D'Esposito

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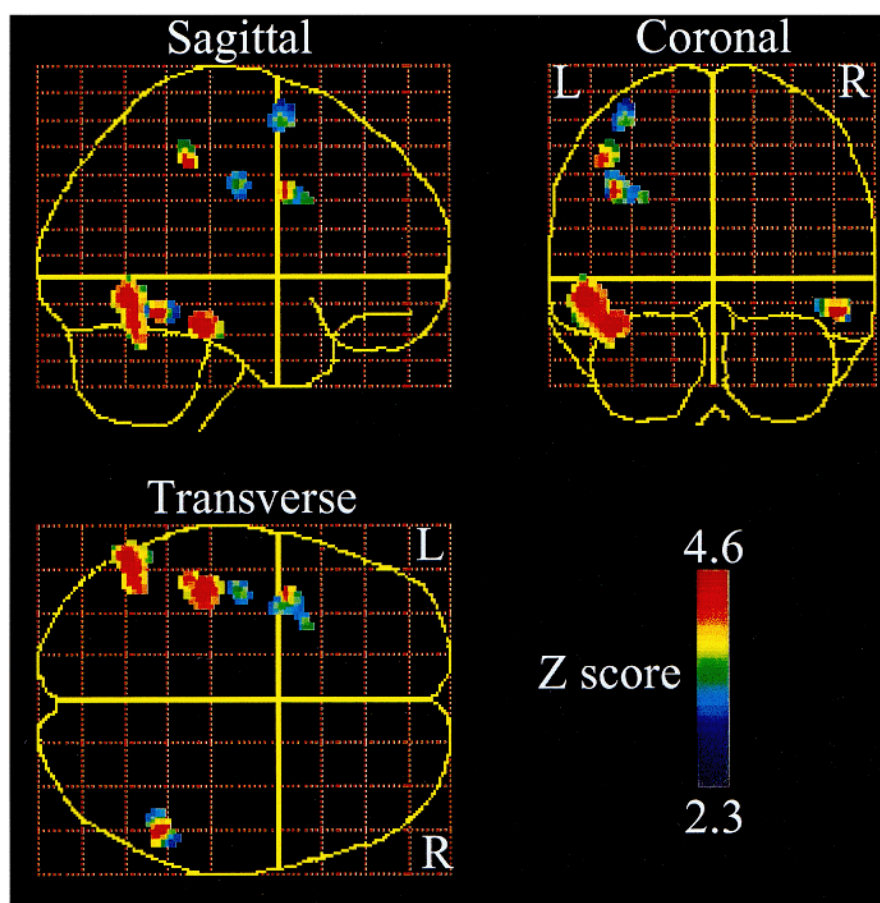


FIG. 2. Statistical parametric maps resulting from the comparison of (1) mental construction of 3D cube assemblies according to verbally delivered directional words (see Fig. 1D) and (2) passive listening of words without any visual imagery activity. Note the bilateral activation of occipitoparietal regions (the dorsal route) as well as the prefrontal activity which is likely to reflect the working-memory

et al. could be due to the high frequency at which the subjects had to generate mental images (1 Hz), which limited their complexity.

Concerning the left hemisphere, the inferior temporal and nearby fusiform gyri seem to be recruited by the perception of forms that can be named, e.g., for which a lexical entry exists (Sergent *et al.*, 1992; Kosslyn *et al.*, 1994b). The same finding seems to be valid in the visual mental imagery domain: these left ventral areas were activated when subjects were asked to generate mental images of objects (Mellet *et al.*, 1996, 1998; Ghaëm *et al.*, 1997; D'Esposito *et al.*, 1997) or even of letters (Kosslyn *et al.*, 1993) and in the transcription of phonemes in visualized graphemes (Démonet *et al.*, 1994). Functional lateralization during mental imagery could thus depend on two different characteristics of the mental images to be generated: complexity, which would modulate the degree of involvement of the right hemisphere ventral route, and "lexicality," which would drive the left hemisphere participation. Within this framework, the finding of bilateral activations in several studies could reflect the simultaneous contribution of both components in the proposed tasks (Kosslyn *et al.*, 1993; Mellet *et al.*, 1998).

MENTAL IMAGERY AND MEMORY

Mental Imagery and Visual Working Memory

Visual working memory allows one to maintain a piece of visual information for a short period of time and it is likely that it is engaged by the generation, the upholding, and the transformation of visual mental images. Several neuroimaging studies have emphasized the role of the prefrontal cortex in visual working memory (Jonides *et al.*, 1993; Courtney *et al.*, 1996, 1997, 1998; Cohen *et al.*, 1997) or delayed visuomotor tasks (Deiber *et al.*, 1997). Similarly, several mental imagery studies have reported activations located on the lateral surface of the superior and median frontal gyri, in the vicinity of the precentral sulcus, that are likely to reflect the involvement of working memory (Kosslyn *et al.*, 1993; Mellet *et al.*, 1996, 1998; Ghaëm *et al.*, 1997). Amazingly, at least two distinct anatomical areas seem to be involved depending on the nature of the mental imagery task, a finding to be interpreted in the light of recent studies demonstrating that spatial and object visual working memory are subserved by distinct frontal areas (Courtney *et al.*, 1996, 1998).

The first area, lying in a dorsal position in the superior frontal gyrus near the precentral sulcus, seems to be activated whenever the mental imagery task is of "dynamic" nature (Paivio and Clark, 1991), meaning that it requires a spatial transformation of the mental image (Mellet *et al.*, 1996, 1998) and thus the involvement of the spatial working memory. As a matter of fact, several recent functional imaging studies have reported activations of this region during spatial working memory tasks (Jonides *et al.*, 1993; Smith *et al.*, 1995, 1996; Courtney *et al.*, 1996). Recently, Courtney *et al.* have identified a frontal area specialized for spatial working memory located in the superior frontal sulcus, just anterior to the precentral location of the frontal eye field (Courtney *et al.*, 1998). The second area is located in a more ventral position, in the middle frontal gyrus at the intersection of the precentral and middle frontal sulci. It appears to be recruited when the mental imagery task is of the "figurative" kind, e.g., when it relies on "object" type characteristics of the image (Kosslyn *et al.*, 1993; Mellet *et al.*, 1998). The same area has been found activated during working memory tasks dealing with object form (Smith *et al.*, 1995; Cohen *et al.*, 1997) or faces (Courtney *et al.*, 1997, 1998), suggesting that its activation during mental imagery reflects the involvement of a specialized working-memory component.

Therefore, the double anatomofunctional dissociation in visual working memory appears to hold also in visual mental imagery. As higher order visual areas, these regions belong to the common set of areas involved in both visual perception and mental imagery.

Mental Imagery and Episodic Memory

Mental images are one of the major components of episodic memory recall (Tulving, 1983). In the imagery domain, the precuneus seems to be specifically recruited whenever the generation of the mental image relies on the reactivation of a memorized percept (Kosslyn *et al.*, 1993; Mellet *et al.*, 1995; Roland and Gulyas, 1995; Ghaëm *et al.*, 1997). In the memory domain, numerous studies have reported precuneus activation during episodic memory recall (Tulving *et al.*, 1994; Andreasen *et al.*, 1995a,b,c; Buckner *et al.*, 1996; Fink *et al.*, 1996b). In another study, the precuneus was specifically activated by the perception of degraded images of object or faces previously seen in an undegraded version, emphasizing the role of this area

activity. Also note the right inferior temporal gyrus activation that may translate the object-processing component of the task (adapted from Mellet *et al.*, 1996).

FIG. 3. Statistical parametric maps resulting from the comparison of (1) listening to concrete words and their definitions that elicited, in addition to language processing, a visual imagery activity and (2) listening to abstract words and their definitions that resulted in language processing only. Note the bilateral activation of the inferior temporal/fusiform gyri (the ventral route), specific of the mental imagery activity as well as the prefrontal activity that may reflect the involvement of working memory (adapted from Mellet *et al.*, 1998).

in facilitating recognition by the use of previously stored visual information (Dolan *et al.*, 1997). It is still not clear whether this region is specific for the visual component of memory retrieval, i.e., is involved in the imagery process that accompanies the recollection (Fletcher *et al.*, 1995), or whether it is independent of this process (Buckner *et al.*, 1996). Indeed, even the retrieval of pure verbal material may be accompanied by visual mental imagery because of the potential imageability of the words or sentences used as targets to recall. In any case, the precuneus, at the internal part of the parietal lobe, appears to be a likely candidate as an area common to mental imagery and memory recall.

VISUAL IMAGERY AND MOTOR IMAGERY: SIMILARITIES AND DIFFERENCES

Motor imagery may be defined as the mental rehearsal of simple or complex motor acts that is not accompanied by overt body movement. Using motor imagery as a means of analyzing covert processes is justified by previous work on mental imagery of other modalities, including visual imagery. Although motor imagery has some similarity to the mental manipulation of visual images, as in mental rotation (Shepard and Metzler, 1971) or mental scanning (Kosslyn *et al.*, 1978), a distinction can be made between the dynamic aspect of visual imagery, which allows us to imagine scenes in which objects or people (including ourselves) are seen as moving (Paivio and Clark, 1991), and motor imagery. This distinction is based on two types of mental representations of motor acts generated by normal subjects: an "external" or third-person process involving a visuospatial representation of actions and an "internal" (or kinesthetic) or first-person process in which subjects feel themselves executing movements. In this section, we review the functional imaging studies of motor imagery dealing with the first-person perspective.

Interestingly, as in the visual imagery, the question whether motor images share the same neural mechanisms that are also responsible for preparation and programming of actual movements has been highly debated (Jeannerod, 1994; Annett, 1995). The functional equivalence between motor imagery and motor preparation has been supported by physiological correlates of motor imagery. The timing of mentally simulated actions closely mimics actual movement times (Decety *et al.*, 1989) and it is possible to characterize motor imagery by changes in heart and respiration rates that are related to the degree of mental effort (Decety *et al.*, 1991; Wang and Morgan, 1992). In addition, imagined movements seem to obey the same psychophysical constraints as executed movements (Sirigu *et al.*, 1996).

Pioneering studies using SPECT or PET have emphasized the activity of several brain areas during imagination of various types of fingers movements such as the SMA, the lateral premotor cortex, the prefrontal cortex, the basal ganglia, and the cerebellum (Ingvar and Philipson, 1977; Roland *et al.*, 1980). More recent PET studies (Decety *et al.*, 1994; Stephan *et al.*, 1995; Stephan and Frackowiak, 1996) and fMRI studies (Rao *et al.*, 1993; Tyszka *et al.*, 1994; Roth *et al.*, 1996, 1996) revealed activation of a number of cortical and subcortical areas, including the SMA, the anterior cingulate cortex, the bilateral premotor cortex, the bilateral superior and inferior parietal cortex, and the posterior cerebellar cortex, most of these regions being also involved in the preparation of movement (Deiber *et al.*, 1996). In addition, imagination of horizontal saccadic eye movements activated cortical regions also involved during the actual execution of saccades, namely both frontal and supplementary eye fields and the median cingulate cortex (Lang *et al.*, 1994), these PET results being confirmed by recent fMRI study (Bodis-Wollner *et al.*, 1997).

Thus, these previous functional imaging studies have demonstrated that most of the regions that are active during overt hand and eye movement execution are active during motor imagery as well, except for the primary motor cortex. However, the most recent fMRI studies have reported involvement of the primary motor cortex during imagined movements (Hallett *et al.*, 1994; Leonardo *et al.*, 1995; Sabbah *et al.*, 1995; Porro *et al.*, 1996; Roth *et al.*, 1996). Levels of activation during imagery have been described as relatively low compared with actual movement which may explain why primary motor activations were undetected by imaging techniques with lesser spatial resolution, particularly when activation from the adjacent premotor areas could not be clearly separated. Interestingly, some activity over the primary sensorimotor area can also be detected with time-sensitive techniques such as EEG (Beisteiner *et al.*, 1995) and, more recently, MEG (Schnitzler *et al.*, 1997) during both motor performance and motor imagery. Altogether, these studies endorse the participation of the primary motor cortex in the mental representation of motor acts. Moreover, these studies showed that MR signal changes in the primary motor cortex during motor imagery largely overlapped the changes observed during motor execution. Thus, contrary to visual mental imagery for which the question of primary area involvement is still open, it seems that, in addition to the associative motor areas, the primary motor area is involved in motor imagery.

As in motor imagery, activation in the SMA has been reported in most of visual imagery studies (Kosslyn *et al.*, 1993; Mellet *et al.*, 1995, 1996; Roland and Gulyas, 1995; Ghaëm *et al.*, 1997). Eye movements are an unlikely explanation for these later findings in visual

imagery since they did not differ between conditions in the studies in which they were recorded. More often than not, SMA activations observed during visual mental imagery are located in front of the anterior commissure vertical plane (VAC) and are thus likely to correspond to the pre-SMA area as recently defined (Picard and Strick, 1996). Interestingly, similar pre-SMA activations have been described in spatial (Goldberg *et al.*, 1996; Petit *et al.*, 1997) and nonspatial (Paulesu *et al.*, 1993; Fiez *et al.*, 1996; Smith *et al.*, 1996; Coull *et al.*, 1996; Braver *et al.*, 1997; Klingberg *et al.*, 1997) working memory studies. These studies showed a nonspecific pre-SMA activation in visual working memory which is also observed in mental imagery since both dynamic (Kosslyn *et al.*, 1993; Mellet *et al.*, 1995, 1996, 1998; Roland and Gulyas, 1995; Ghaëm *et al.*, 1997) and static (Kosslyn *et al.*, 1993; Roland and Gulyas, 1995) mental imagery led to similar pre-SMA activation. Thus, as acknowledged with the dorsal and the ventral prefrontal cortex, visual mental imagery appears to engage the pre-SMA in the same way as visual working memory does.

On the contrary, the SMA proper, posterior to VAC and known to be involved in simple motor tasks (Picard and Strick, 1996), is the part of the SMA activated in motor imagery. Using both PET and fMRI techniques, functionally distinct rostral and caudal activation in this part of the SMA have been described during imagined and executed finger movements, respectively (Tyszka *et al.*, 1994; Stephan *et al.*, 1995; Roth *et al.*, 1996). It has been suggested that the rostral part of the posterior SMA activated during motor imagery may subserve the funneling of thoughts about movement into motor executor areas, whereas the most caudal part of the SMA is commonly related to the execution of motor behavior (Tyszka *et al.*, 1994; Picard and Strick, 1996).

It has been shown that motor imagery and overt movements activate nearly the same structures, including the primary motor area, while seeing someone else executing the same movement involved mainly visual areas (Decety *et al.*, 1994). As argued in a recent review, this emphasized that motor imagery is distinct from visual representation of movement (Crammond, 1997). Crammond claimed that the former results from the utilization of stored actions that are constrained in the same way as actual movements, allowing only the simulation of possibly achievable movements. On the contrary, visual mental images allow the human mind to partly escape the constraints of the physical world. Indeed, if visual mental images are able to represent an interpretation of reality, they can also wander from it and allow the creation of "chimera" with no equivalence in the real world. The anatomofunctional counterpart could be explained by the fact that the primary motor area is activated during an imagined movement, while

the primary visual area is not mandatory for the visualization of an object or a scene which could be then detached from the reality.

CONCLUSION

Although visual mental imagery is supported by high order visual areas, the regions and the networks engaged in this activity are partly shared by language and memory, depending on the nature of the mental imagery task. This reflects the high level of interaction between visual imagery and the most elaborated cognitive functions, providing thus an anatomofunctional substrate to the very early assumption that mental imagery is at the crossroads of most of human cognitive activities.

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