

# 62 The Neural Bases of Mental Imagery

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**ABSTRACT** What neural events underlie the generation of a visual mental image? This chapter reviews evidence from patients with brain damage and from measurements of regional brain activity in normal subjects. The answer emerging from these studies is that many of the same modality-specific cortical areas used in visual perception are also used in imagery. These areas include spatially mapped regions of occipital cortex. There is also evidence for a distinct imagery mechanism, not used under normal circumstances for perception, which is required for the generation of images from memory. Evidence concerning the localization of this process is not entirely consistent, but shows a trend toward regions of the posterior left hemisphere.

## *Introduction*

**THE STUDY OF IMAGERY IN COGNITIVE PSYCHOLOGY**  
The term "mental imagery" has been used in a number of different ways in psychology, from referring to the relatively specific act of forming a "picture in the head" to denoting a more general class of nonverbal thought processes in which spatial representations are actively recalled or manipulated. This chapter is primarily concerned with the first sense of mental imagery, the kind most readers will find themselves experiencing when they attempt to answer the question "What color are the stars on the American flag?" The distinctive phenomenology of imagery is probably its most salient characteristic feature as a form of mental representation. Most people report that images seem much like real percepts, although fainter, sketchier, and more effortful to maintain. However, a scientific psychology cannot allow distinctions among different forms of mental representation to rely entirely on phenomenology, and therefore much of the research on imagery in cognitive psychology and neuropsychol-

ogy has been devoted to characterizing imagery in more objective ways.

To most nonspecialists, it seems unbelievable that the existence of mental images, as a qualitatively different form of mental representation from verbal memory, could be doubted. Yet numerous psychologists did doubt this, in part because of the influence of the computer analogy in psychology and the conviction that cognition is symbol manipulation, and in part based on a preference for the parsimony of having fewer types of mental representations (see, e.g., Pylyshyn, 1973). Early imagery researchers devised many elegant and ingenious experimental paradigms to demonstrate the distinction between imagery and verbal thought, and to characterize imagery in objective information-processing terms (e.g., Paivio, 1971; Shepard, 1978; Kosslyn, 1980). Paivio (this volume) summarizes the research by himself and others on the role of imagery in memory. This research was important not only for our understanding of learning and memory, but also because it demonstrated the separate status of imagery as a distinct "code" or form of representation. Subsequent research by Kosslyn, Shepard, and others focused on the question of *how* imagery differed from verbal thought. This question was the subject of the so-called imagery debate.

**THE IMAGERY DEBATE** Starting in the late 1970s, two related issues concerning imagery came into focus. The first was whether mental imagery involved some of the same representations normally used during visual perception, or whether imagery involved only more abstract, postperceptual representations. This issue was discussed most explicitly by Finke (e.g., 1980) and Shepard (e.g., 1978). The second issue was whether mental images had a spatial, or array-like, format, or whether they were propositional in format. Much of Kosslyn's research was aimed at addressing this issue (e.g., Kosslyn, 1980). The two issues are in principle

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independent, although given the fact that much of visual representation is array-like (e.g., Maunsell and Newsome, 1987), they are closely related.

Although these issues are straightforwardly empirical in nature, they proved difficult to settle using the experimental methods of cognitive psychology. The classic image-scanning experiments of Kosslyn (e.g., Kosslyn, Ball, and Reiser, 1978) will be used to illustrate this point. Kosslyn and associates found that when subjects were instructed to focus their attention on one part of an image and then move it continuously, as quickly as possible, to some other part of the image, the time taken to scan between the two locations was directly proportional to their metric separation, just as if subjects were scanning across a perceived stimulus. This finding follows naturally from the view that images share representations with visual percepts, and that these representations have a spatial format. However, not all psychologists agreed with this interpretation. Various types of alternative explanations were proposed that accounted for the scanning findings, and many others, without hypothesizing shared representations for imagery and perception or a spatial format for imagery. These alternative explanations are discussed in detail by Farah (1988) as motivation for turning to neuropsychological evidence. Two examples will be mentioned briefly here.

Pylyshyn (1981) suggested that subjects in imagery experiments take their task to be simulating the use of visual-spatial representations, and that with their tacit knowledge of the functioning of their visual system subjects are able to perform this simulation using non-visual representations. Intons-Peterson (1983) suggested that subjects in imagery experiments may be responding to experimenter expectancies, and she has shown that at least certain aspects of the data in imagery experiments can indeed be shaped by the experimenters' preconceptions. Although these accounts strike many people as less plausible than the hypothesis that images are modality-specific visual representations that are intrinsically spatial in format, it has proven difficult to rule them out. In fact, Anderson (1978) has argued that no behavioral data (i.e., sets of stimulus inputs paired with subjects' responses to those stimuli and the latencies of the responses) can ever distinguish alternative, nonvisual theories of imagery from the visual-spatial theories. One of the incentives for studying the neuropsychology of mental imagery is

that it has the potential to be more decisive on these issues, because it provides more direct evidence on the internal processing stages intervening between stimulus and response in imagery experiments.

### *The brain bases of mental images: Modality specificity and format*

The neuropsychological studies relevant to the two issues of the imagery debate—are images visual, and do they have a spatial format?—include both studies of brain-damaged subjects and psychophysiological measures in normal subjects. These studies will be reviewed very briefly here; a more detailed review of some of this material can be found in Farah, 1988, and Farah, 1989.

**STUDIES OF BRAIN-DAMAGED PATIENTS** If forming a mental image consists of activating cortical visual representations, then patients with selective impairments of visual perception should manifest corresponding impairments in mental imagery. This is often the case. For example, DeRenzi and Spinnler (1967) investigated various color-related abilities in a large group of unilaterally brain-damaged patients and found an association between impairment on color-vision tasks, such as the Ishihara test of color blindness, and on color-imagery tasks, such as verbally reporting the colors of common objects from memory. Beauvois and Saillant (1985) studied the imagery abilities of a patient with a visual-verbal disconnection syndrome. The patient could perform purely visual color tasks (e.g., matching color samples) and purely verbal color tasks (e.g., answering questions such as "What color is associated with envy?") but could not perform tasks in which a visual representation of color had to be associated with a verbal label (e.g., color naming). On tasks that tested the patient's color imagery ability purely visually, such as selecting the color sample that represented the color of an object depicted in black and white, she did well. However, when the equivalent problems were posed verbally (e.g., "What color is a peach?") she did poorly. In other words, mental images interacted with other visual and verbal task components as if they were visual representations. More recently, De Vreese (1991) reported two cases of color imagery impairment, one of whom had left occipital damage and displayed the same type of visual-verbal

disconnection as the patient just described, and the other of whom had bilateral occipital damage and parallel color-perception and color-imagery impairments.

In another early study documenting the relations between imagery and perception, Bisiach and Luzzatti (1978) found that patients with hemispatial neglect for visual stimuli also neglected the contralesional sides of their mental images. Their two right-parietal-damaged patients were asked to imagine a well-known square in Milan, shown in figure 62.1. When they were asked to describe the scene from vantage point A in the figure, they tended to name more landmarks on the east side of the square (marked with lowercase as in the figure); that is, they named the landmarks on the right

side of the imagined scene. When they were then asked to imagine the square from the opposite vantage point, marked B on the map, they reported many of the landmarks previously omitted (because these were now on the right side of the image) and omitted some of those previously reported.

Levine, Warach, and Farah (1985) studied the roles of the "two cortical visual systems" (Ungerleider and Mishkin, 1982) in mental imagery, with a pair of patients. Case 1 had visual disorientation following bilateral parieto-occipital damage, and case 2 had visual agnosia following bilateral inferior temporal damage. We found that the preserved and impaired aspects of visual imagery paralleled the patients' visual abilities:

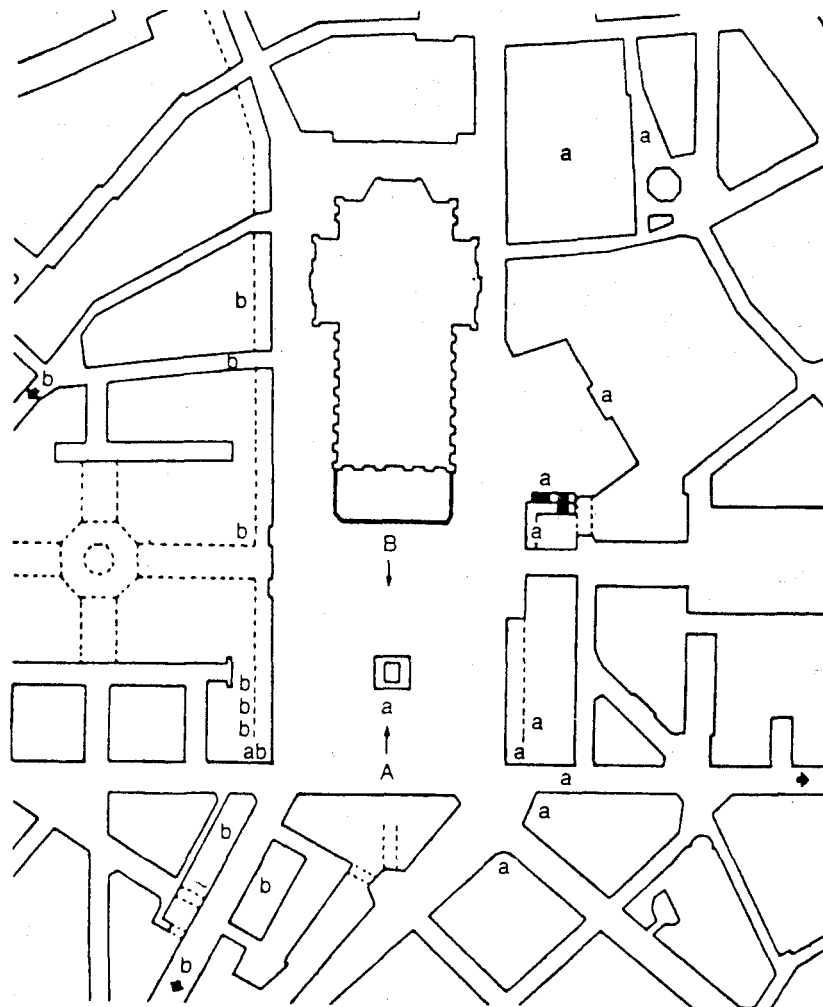


FIGURE 62.1 Map of the Piazza del Duomo in Milan, showing the two positions, A and B, from which patients were asked to imagine viewing the piazza, and the landmarks they

recalled from each imagined position, labeled "a" and "b" respectively.

Case 1 could neither localize visual stimuli in space nor accurately describe the locations of familiar objects or landmarks from memory. However, he was good at both perceiving object identity from appearance and describing object appearance from memory. Case 2 was impaired at perceiving object identity from appearance and at describing object appearance from memory, but was good at localizing visual stimuli and at describing their locations from memory.

Farah, Hammond, et al., (1988) carried out more detailed testing on the second patient, L. H. We adapted a large set of experimental paradigms from the cognitive psychology literature that had been used originally to argue for either the visual nature of imagery (i.e., "picture in the head" imagery) or for its more abstract spatial nature. Our contention was that both forms of mental imagery exist, contrary to much of the research in cognitive psychology aimed at deciding which of the two characterizations of imagery is correct. On the basis of the previous study, we conjectured that cognitive psychology's so-called visual imagery tasks would be failed by the patient with the damaged ventral temporo-occipital system, whereas cognitive psychology's so-called spatial imagery tasks would pose no problem for him because of his intact dorsal parieto-occipital system. Figure 62.2 shows the locations of his brain lesions, which spare the dorsal visual system.

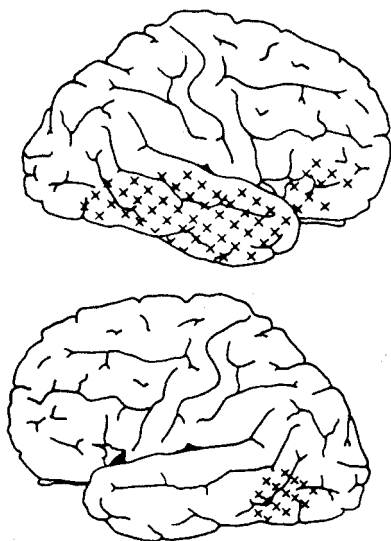


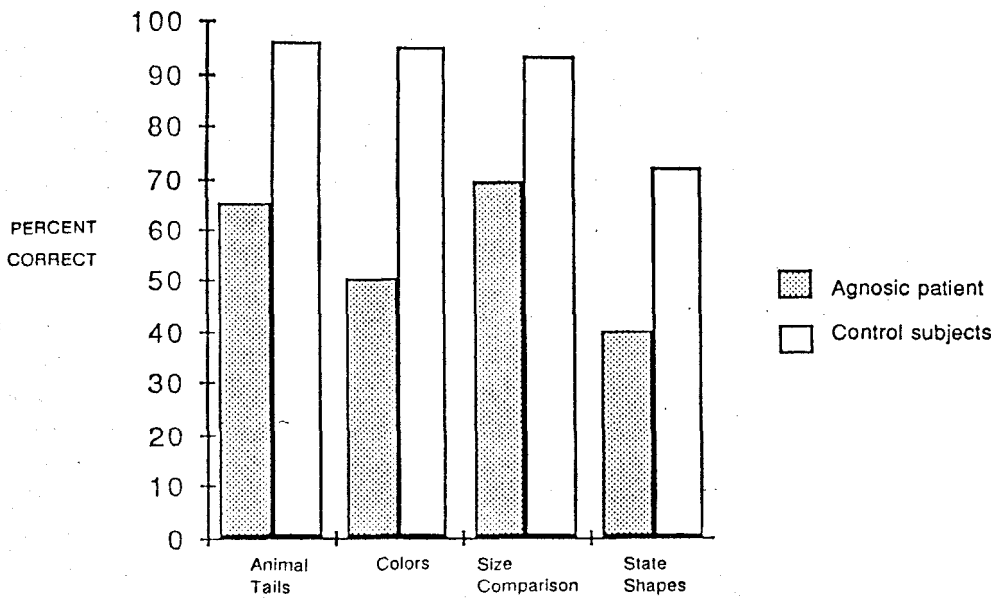
FIGURE 62.2 Diagram showing regions of damage in the brain of case L. H.

The visual imagery tasks included imagining animals and reporting whether they had long or short tails, imagining common objects and reporting their colors, and imagining triads of states within the United States and reporting which two are most similar in outline shape. The spatial imagery tasks included such mental image transformations as mental rotation, scanning, and size scaling, and imagining triads of shapes and reporting which two are closest to one another. As shown in figure 62.3, the patient was impaired relative to control subjects at the visual, pattern, and color imagery tasks, but entirely normal at the spatial imagery tasks.

Although the foregoing studies implicate modality-specific visual representations in imagery, they either are ambiguous as to the level of visual representation involved, or they implicate relatively high-level representation in the temporal and parietal lobes. In a recent study, Farah, Soso, and Dasheiff (1992) examined the role of the occipital lobe in mental imagery. If mental imagery consists of activating relatively early representations in the visual system, at the level of the occipital lobe, then it should be impossible to form images in regions of the visual field that are blind due to occipital lobe destruction. This predicts that patients with homonymous hemianopia should have a smaller maximum image size, or visual angle of the mind's eye. The maximum image size can be estimated using a method developed by Kosslyn (1978), in which subjects imagine walking toward objects of different sizes and report the distance at which the image just fills their mind's eye's visual field and is about to "overflow." The trigonometric relation between the distance, object size, and visual angle can then be used to solve for the visual angle.

We were fortunate to encounter a very high-functioning, educated young woman who could perform the rather demanding task of introspecting on the distance of imagined objects at "overflow." In addition, she could serve as her own control because she was about to undergo unilateral occipital lobe resection for treatment of epilepsy. We found that the size of her biggest possible image was reduced after surgery, as represented in figure 62.4. Furthermore, by measuring maximal image size in the vertical and horizontal dimensions separately, we found that only the horizontal dimension of her imagery field was significantly reduced. These results provide strong evidence for the use of occipital visual representations during imagery.

"VISUAL" IMAGERY TASKS



"SPATIAL" IMAGERY TASKS

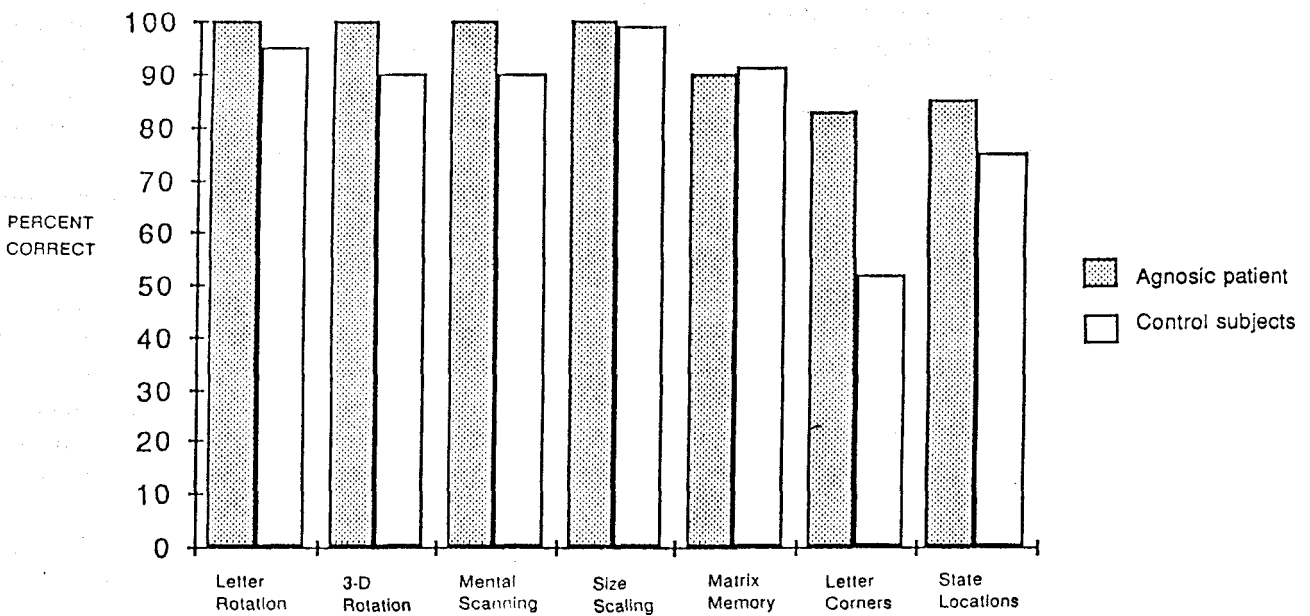
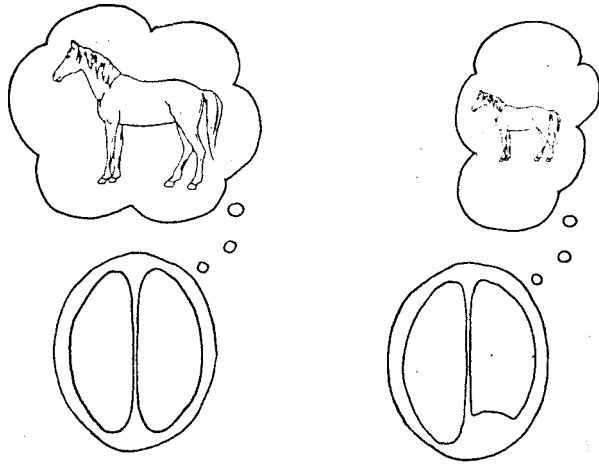


FIGURE 62.3 Performance of case L. H. and control subjects on mental imagery tasks requiring retrieval of visual (or "what") and spatial (or "where") information.



*"I can get to within 15 feet of the horse in my imagination before it starts to overflow"*

*"The horse starts to overflow at an imagined distance of about 35 feet"*

FIGURE 62.4 Representation of the effects of occipital lobectomy on the maximal mental image size of case M. G. S.

Although the results from brain-damaged patients are generally consistent with the hypothesis that mental imagery involves representations within the visual system proper—including relatively early representations in the occipital lobe that are known to be spatial in format—there are discrepant findings as well. It has occasionally been noted that an agnosic patient's drawings from memory are satisfactory. Recently, Behrmann, Winocur, and Moscovitch (1992) reported a severely agnosic patient who demonstrated good visual mental imagery abilities. It is difficult to reconcile this observation with the hypothesis that imagery and visual perception share representations, unless one supposes either a very peripheral perceptual abnormality that for some reason interferes more with tests of object recognition than with tests of seemingly lower level visual functions, or an impairment in the unidirectional transformation of relatively early occipital representations into higher-level object representations. In the absence of any independent support for these interpretations, they seem rather unsatisfactory.

To conclude, in most but not all cases of selective visual impairments following damage to the cortical visual system, patients manifest qualitatively similar impairments in mental imagery and perception. This provides some evidence for the hypothesis that imagery and perception share at least some modality-specific cortical representations, and that those representations are specialized for the same kinds of visual or spatial

information in both perception and imagery. Let us now turn to a different source of evidence on the relation between imagery and perception.

**BRAIN-IMAGING STUDIES IN NORMAL SUBJECTS** Starting in the mid-1980s, regional brain activity during mental imagery has been monitored in normal subjects using a variety of techniques, as summarized in table 62.1. An early study relevant to the relation of imagery and perception was reported by Roland and Friberg (1985). They examined patterns of regional blood flow using single photon emission computed tomography (SPECT) while subjects performed three different cognitive tasks, one of which was to visualize a walk through a familiar neighborhood, making alternate left and right turns. In this task, unlike the other tasks, blood flow indicated activation of the posterior regions of the brain, including visual cortices of the parietal and temporal lobes. Although most of occipital cortex was not monitored in this study, a later positron emission tomography (PET) study by the same group of researchers also failed to find significant occipital activation during the "mental walk" task (Roland et al., 1987). The most pronounced effects of imagery were seen in posterior parietal cortex, with nonsignificant increases in occipital and temporal areas. These results are therefore consistent with the hypothesis that mental imagery is a function of higher visual cortical areas, but the study failed to implicate early, occipital, areas.

Goldenberg and his colleagues have performed a series of blood-flow studies of mental imagery using SPECT. They inferred which brain areas were activated by mental imagery using very elegant experimental designs in which the imagery task was closely matched with control tasks involving many of the same processing demands, except for the mental imagery per se (e.g., Goldenberg et al., 1987; Goldenberg et al., 1989a; Goldenberg et al., 1989b; Goldenberg et al., 1991; Goldenberg et al., 1992). For example, one imagery task was the memorization of word lists using an imagery mnemonic, and its control task was memorization without imagery (Goldenberg et al., 1987). Another task involved answering questions of equal difficulty, which either required mental imagery (e.g., "What is darker green, grass or a pine tree?) or did not (e.g., "Is the Categorical Imperative an ancient grammatical form?"; Goldenberg et al., 1989a). In all of these studies, visual imagery is found to be associated

**TABLE 62.1**  
*Functional imaging studies of visual mental imagery implicating visual cortical involvement*

Authors	Method	Visual Activity	Additional Comments
Roland & Friberg (1985)	SPECT	Parietal, temporal	Most occipital activity not monitored
Roland et al. (1987)	PET	Parietal	
Goldenberg et al. (1987)	SPECT	Occipital, temporal	
Farah, Peronnet, et al. (1988)	ERP	Occipital, temporal	
Farah et al. (1989)	ERP	Occipital, temporal	Time course implicates area 18
Farah & Peronnet (1989)	ERP	Occipital	Temporal not monitored; magnitude predicted by imagery vividness
Goldenberg et al. (1989a)	SPECT	Occipital, temporal	
Goldenberg et al. (1989b)	SPECT	Occipital, temporal	
Uhl et al. (1990)	ERP	Occipital, temporal, parietal	Parietal associated with map images; occipital-temporal with face and color images
Goldenberg et al. (1991)	SPECT	Occipital	
Goldenberg et al. (1992)	SPECT	Occipital, temporal	
Charlot et al. (1992)	SPECT	Occipital, temporal	
Kosslyn et al. (1993)	PET	Occipital, temporal, parietal	Activity in area 17
Le Bihan et al. (1993)	MRI	Occipital	Activity in area 17

with occipital and temporal activation. It is possible that the greater parietal involvement observed by Roland and colleagues (Roland and Friberg, 1985; Roland et al., 1987) is related to the subjects' need to represent spatial aspects of the environment in their mental walk task (cf. the findings of Farah, Hammond, et al., 1988, on dissociable visual and spatial mental imagery).

A recent study by Chariot and colleagues (1992) used SPECT rCBF while subjects generated and scanned images in the classic cognitive psychology image-scanning paradigm developed by Kosslyn, Ball, and Reiser (1978). These authors also found activation of visual association cortex, including occipital cortex.

In general, these findings with SPECT rCBF are consistent with the previous patient work, in that they show visual cortical activity associated with mental imagery. Perhaps of greatest interest, pronounced and consistent activation of occipital cortex was observed in these studies. Thus suggests that imagery involves spatially mapped visual representations.

Our group has used event-related potentials (ERPs) to address the question of whether visual mental imagery has a visual locus in the brain. In one study, Farah, Peronnet, et al. (1988) used ERPs to map out, in space and in time, the interaction between mental imagery

and concurrent visual perception. We found that imagery affected the ERP to a visual stimulus early in stimulus processing, within the first 200 ms. This implies that imagery involves visual cortical regions that are normally activated early in visual perception. The visual ERP component that is synchronized with the effect of imagery, the N1, is believed to originate in areas 18 and 19, implying a relatively early extrastriate locus for imagery in the visual system. Interpolated maps of the scalp-recorded ERPs were also consistent with this conclusion.

In a second series of studies, Farah et al. (1989) took a very different approach to localizing imagery in the brain using ERP methods. Rather than observing the interaction between imagery and concurrent perception, we simply asked subjects to generate a mental image from memory, in response to a visually presented word. By subtracting the ERP to the same words when no imagery instructions were given from the ERP when subjects were imaging, we obtained a relatively pure measure of the brain electrical activity that is synchronized with the generation of a mental image. Again, we constructed maps of the scalp distribution of the ERP imagery effect, in order to determine whether the maxima lay over modality-specific visual perceptual areas. Despite the very different ex-

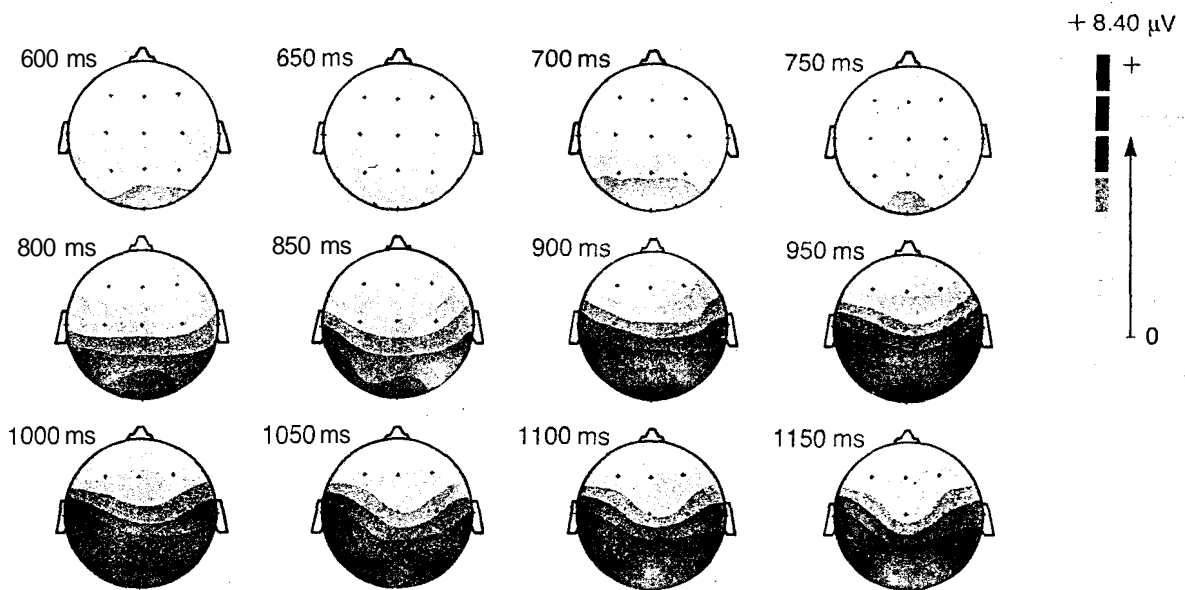


FIGURE 62.5 Scalp distribution of potentials synchronized with the generation of a mental image, in 50 ms time slices.

perimental paradigm, we found a highly similar scalp distribution to that found in the previous experiment, clearly implicating visual areas. Figure 62.5 shows the evolving scalp distribution of subjects' brain electrical activity as they generate images from memory. When the experiment was repeated using auditory word presentation, the same visual scalp topography was obtained. Control experiments showed that the imagery effects in these experiments were not due to the cognitive effort expended by subjects when imaging (as opposed to imagery *per se*), or to eye movements.

Farah and Peronnet (1989) reported two studies in which subjects who rated their imagery as relatively vivid showed a larger occipital ERP imagery effect when generating images than subjects who claimed to be relatively poor imagers. This result, which we then replicated under slightly different conditions, suggests that some people are more able to efferently activate their visual systems than others, and that such people experience especially vivid imagery.

Uhl and colleagues (1990) used scalp-recorded DC shifts to localize brain activity during imagery for colors, faces, and maps. Following transient positive deflections of the kind observed by Farah et al. (1989), a sustained negative shift was observed over occipital, parietal, and temporal regions of the scalp. Consistent with the different roles of the two cortical visual systems, the effect was maximum over parietal regions

during map imagery, and maximum over occipital and temporal regions during face and color imagery.

More recently, Kosslyn et al. (1993) brought the PET method to bear on the localization of imagery. In the first two of their experiments, subjects viewed grids in which block letters were either present or to be imagined, and judged whether an *X* occupying one cell of the grid fell on or off the letter. Comparisons between imagery and relevant baseline conditions showed activation of many brain areas, including occipital visual cortex. Figure 62.6 shows the areas of greatest significant activity when subjects generated images from memory, relative to when they performed an analogous task with perceived stimuli. In a third experiment, subjects generated either large or small images of letters of the alphabet with eyes closed, and the researchers directly compared the two imagery conditions. They found that the large images activated relatively more anterior parts of visual cortex than the small ones, consistent with the known mapping of the visual field onto area 17.

Le Bihan and colleagues (1993) used magnetic resonance imaging (MRI) to investigate the role of visual cortex in mental imagery. Like PET, MRI has excellent spatial resolution; in addition, MRI has excellent temporal resolution. Le Bihan et al. measured regional brain activity as subjects alternately viewed flashing patterns and imagined them. The results shown for one

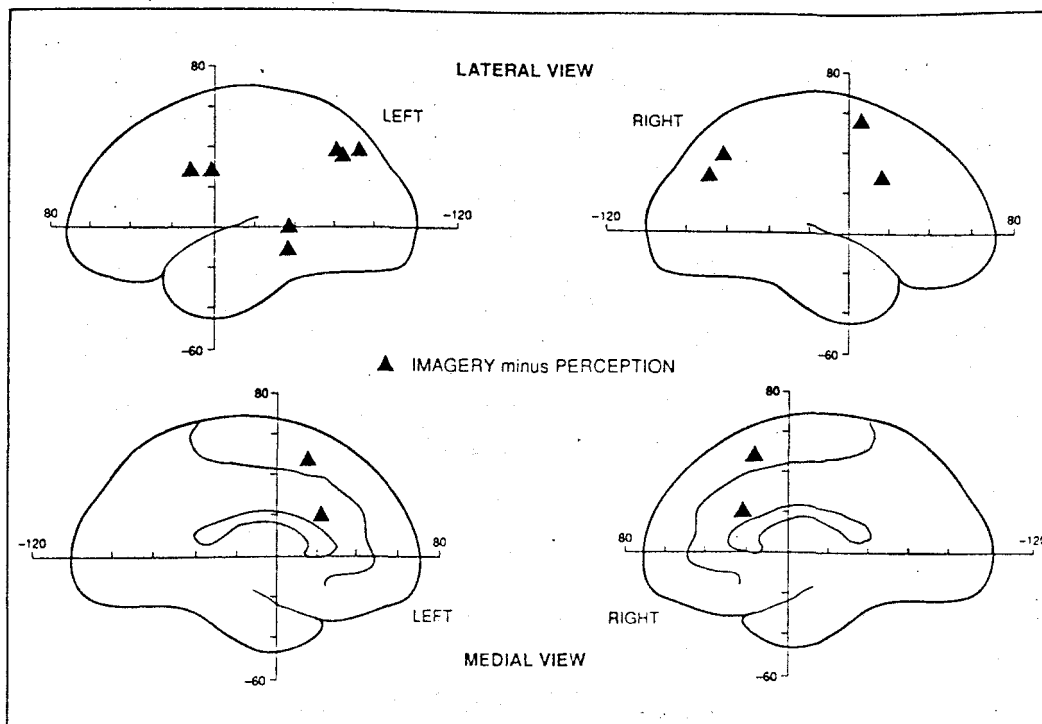


FIGURE 62.6 Areas of significant increases in activity measured by PET during the generation of images from memory, relative to an analogous perceptual task.

subject in figure 62.7 provide a striking demonstration of the involvement of area 17 in mental imagery as well as in perception.

**THE IMAGERY DEBATE REVISITED** In Anderson's (1978) discussion of the intrinsic ambiguities of behavioral data for resolving the imagery debate, he suggested that physiological data might someday provide a decisive answer. Only fifteen years later, that day appears to have arrived. Although there is much more to find out, and some of our current conclusions will doubtless need to be revised, we can point to a body of converging evidence that supports the modality-specific visual nature of mental images, and suggests that at least some of their neural substrates have a spatial representational format: Damage to visual areas representing such specialized stimulus properties as color, location, and form result in the loss of these properties in mental imagery. Spatially delimited impairments of visual attention and of visual representation are accompanied by corresponding impairments in imagery. Psychophysiological studies using blood-flow imaging methods and ERPs have operationalized imagery in a wide variety of ways, including instructions

to take a mental walk, imagery mnemonics, general knowledge questions about the appearances of familiar objects, the effect of imagery on concurrent perception, instructions to image common objects, self-reported individual differences in vividness of imagery, and judgments about imagined letters of the alphabet. Across all of these superficially different tasks, indices of regional brain activity implicate modality-specific visual cortex in mental imagery. Further, the N1 locus of the imagery-perception interaction effect suggests that specifically area 18 is involved, and the PET and MRI results suggest that area 17 may be involved as well.

#### *Image generation*

Kosslyn (e.g., 1980) made a distinction between three general components of the imagery system: the long-term visual memories, from which images are generated; the visual buffer, a spatially formatted representational medium that is activated to produce phenomenally experienced images; and an image-generation process, whereby the visual buffer is activated in accordance with memory. The two issues concerning image generation to be discussed here are

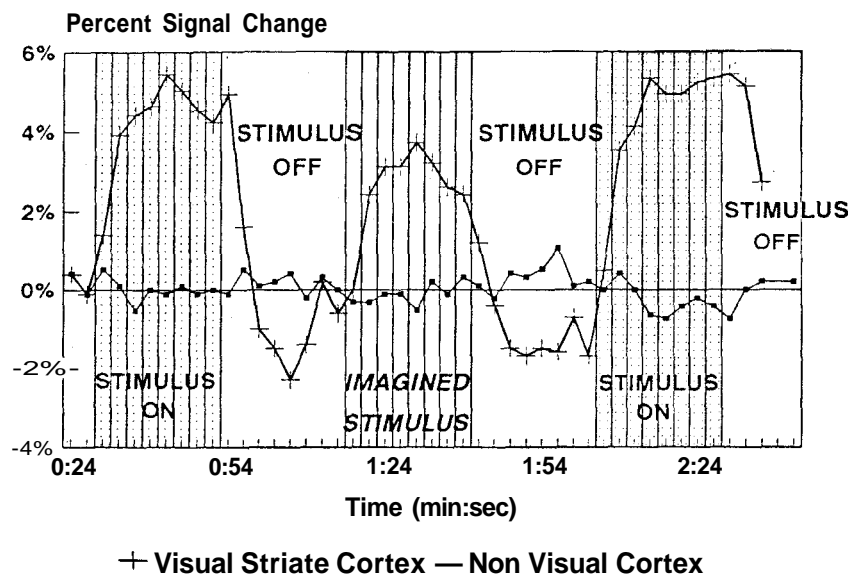
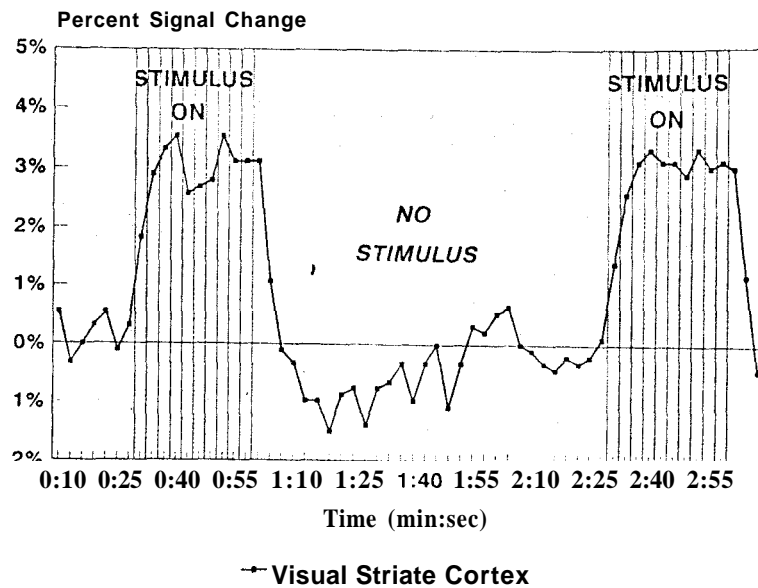


FIGURE 62.7 Plot of activity over time in striate cortex measured by MRI, as a function of the subject's activity. In upper panel, the subject was resting between two real visual

stimuli. In lower panel, the subject imagined the stimuli between actual stimulus presentations.

whether image generation is really a distinct and dissociable component from the long- and short-term representational components of imagery, and where mental image generation is localized. Readers are directed to Tippett's (1992) article for an excellent review of the neuropsychology of image generation.

From the perspective of neural network computation, the distinctions proposed by psychologists between representations and processes often appear unnecessary, and one might therefore question the need to hypothesize a separate image generation process. For example, it is sometimes assumed that visual recog-

nitition requires a kind of matching process, separate from the visual representations themselves, to compare the representations active in the visual buffer with the corresponding long-term visual memory representations (e.g., Farah, 1984). However, such a process would be superfluous in an associative network in which the representations of visual knowledge at various levels of the visual system, embodied in the connection strengths, would be sufficient to activate the appropriate high-level object representations given an active representation in the visual buffer. Even so, the generation of an image might be expected to require mechanisms beyond those needed for object recognition. It is clear that every time one thinks about an object, one's visual system does not inexorably perform pattern completion and create a mental image. The activation of early, visual buffer representations by active, high-level visual memory representations does not appear to be as automatic as the reverse direction of activation flow. This is consistent with the existence of a component of the cognitive architecture that is needed for image generation but not for visual perception and object recognition.

Farah (1984) reviewed the neurological literature on imagery impairments and identified a set of cases in which perception was grossly intact. In subsequent years, a small number of additional cases of selectively impaired imagery have been reported (e.g., Grossi, Orsini, and Modafferi, 1986; Farah, Levine, and Calvanio, 1988; Riddoch, 1990; Goldenberg, 1992). On the face of things, this seems to imply the existence of a distinct image generation component. However, this conclusion must be viewed as tentative. Many of the cases had subtle visual perceptual impairments, whose role in the imagery impairment cannot be ruled out. Another possibility is a subtle visual memory impairment, as suggested by Goldenberg and Artner (1991). In support of this hypothesis, they showed that a group of subjects selected for left posterior brain damage, who were impaired on image generation tasks, were also impaired at making subtle visual discriminations, for example between a bear with pointy ears and a bear with rounded ears. However, it is possible that when confronted with a pair of such pictures, normal people generate an image of a bear to recall whether bears have pointy or rounded ears.

The localization of mental image generation has been a controversial topic. Although mental imagery

was for many years assumed to be a function of the right hemisphere, Ehrlichman and Barrett (1983) pointed out that there was no direct evidence for this assumption. Farah (1984) noted a trend in the cases she reviewed for left posterior damage. Farah, Levine, and Calvanio (1988) suggested that the left temporo-occipital area may be critical. The recent focally damaged cases mentioned above (Grossi, Orsini, and Modafferi; Farah, Hammond, et al., 1988; Riddoch, 1991; Goldenberg, 1992) have supported this suggestion. The rarity of cases of image generation deficit suggests that this function may not be strongly lateralized in most people; however, when impairments are observed after focal unilateral damage, the left or dominant hemisphere is implicated.

Other neuropsychological methods have been brought to bear on the laterality of mental image generation and have revealed the same general trend toward left-hemisphere specialization, although exceptions exist. The ERP experiments on the generation of images described earlier showed greater effects on the left than the right, maximum over the temporo-occipital region. In addition, left temporo-occipital foci of activity have been noted by Goldenberg in several, but not all, of his rCBF studies (Goldenberg et al., 1987, 1989a, 1991, 1992). Chariot et al. (1992) also found left temporo-occipital cortex activated in their rCBF study. Kosslyn and his colleagues (1993) reported two experiments that they classified as requiring subjects to generate images from long-term visual memory. Although one of these experiments was aimed at comparing activation patterns for large and small images, and thus did not include a no-imagery baseline to allow inferences about image generation per se, the other showed greater activity in left temporal and occipital association areas associated with image generation.

Research with split-brain patients has produced variable results, although in all cases the left hemisphere has shown at least an initial or partial superiority for image generation (Farah et al., 1985; Kosslyn et al., 1985; Corballis and Sergent, 1988). Divided-field studies with normal subjects have offered less clear support. For example, Cohen (1975) and Farah (1986) found evidence consistent with a left-hemisphere locus for image generation. In contrast, Sergent (1989) reports finding opposite results in her divided-visual-field experiment. The possibility that there are different

types of mental image generation, with differing hemispheric loci, has been proposed by Kosslyn (1988) and deserves further systematic study.

### Conclusions

Research on the neural bases of mental imagery is a fairly recent development in neuropsychology, and our conclusions at present can therefore only be tentative. Nevertheless, a reasonably consistent picture seems to be emerging, across a variety of neuropsychological research methods. In this picture, mental imagery is the efferent activation of some subset of the brain's visual areas, subserving the same types of functions (what, where, color, spatial attention, and so on) in imagery and in perception. In addition, evidence from both brain-damaged patients and functional imaging of normal subjects' brains suggests that some of the visual areas shared with imagery include spatially mapped areas of the occipital lobe. This finding is particularly important for resolving the long-standing issue in cognitive psychology of the format of mental images.

The study of image generation has yielded results that are less clear and consistent, concerning both its existence as a distinct component of the cognitive architecture and its neuroanatomic localization. Although a body of evidence favors the existence of an image-generation mechanism localized to the posterior left hemisphere, discrepant data also exist, and further research will be needed to draw any firm conclusions.

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### REFERENCES

- ANDERSON, J. R., 1978. Arguments concerning representation for mental imagery. *Psychol. Rev.* 85:249-277.
- BEAUVOIS, M. F., and B. SAILLANT, 1985. Optic aphasia for colours and colour agnosia: A distinction between visual and visuo-verbal impairments in the processing of colours. *Cognitive Neuropsychol.* 2:1-48.
- BEHRMANN, M., G. WINOCUR, and M. MOSCOVITCH, 1992. Dissociation between mental imagery and object recognition in a brain-damaged patient. *Nature* 359:636-637.
- BISIACH, E., and C. LUZZATTI, 1978. Unilateral neglect of representational space. *Cortex*, 14:129-133.
- CHARLOT, V., N. TZOURIO, M. ZILBOVICIUS, B. MAZOYER, M. DENIS, 1992. Different mental imagery abilities result in different regional cerebral blood flow activation patterns during cognitive tasks. *Neuropsychologia* 30:565-580.
- COHEN, G., 1975. Hemispheric differences in the utilization of advance information. In *Attention and Performance V*, P. M. A. Rabbit and S. Domic, eds. New York: Academic Press.
- CORBALLIS, M. C., and J. SERGENT, 1988. Imagery in a commissurotomed patient. *Neuropsychologia* 26:13-26.
- DE VREESE, L. P., 1991. Two systems for colour-naming defects: verbal disconnection vs colour imagery disorder. *Neuropsychologia*, 29:1-18.
- DERENZI, E., and H. SPINLER, 1967. Impaired performance on color tasks in patients with hemispheric lesions.
- EHRlichMAN, H., and J. BARRETT, 1983. Right hemisphere specialization for mental imagery: A review of the evidence. *Brain Cogn.* 2:39-52.
- FARAH, M. J., 1984. The neurological basis of mental imagery: A componential analysis. *Cognition* 18:245-272.
- FARAH, M. J., 1986. The laterality of mental image generation: A test with normal subjects. *Neuropsychologia* 24:541-551.
- FARAH, M. J., 1988. Is visual imagery really visual? Overlooked evidence from neuropsychology. *Psychol. Rev.* 95:307-317.
- FARAH, M. J., 1989. The neural bases of mental imagery. *Trends Neurosci.* 12:395-399.
- FARAH, M. J., M. S. GAZZANIGA, J. D. HOLTZMAN, and S. M. KOSSLYN, 1985. A left hemisphere basis for visual mental imagery? *Neuropsychologia* 23:115-118.
- FARAH, M. J., K. L. HAMMOND, D. N. LEVINE, and R. CALVANO, 1988. Visual and spatial mental imagery: Dissociable systems of representation. *Cognitive Psychol.* 20:439-462.
- FARAH, M. J., D. N. LEVINE, and R. CALVANO, 1988. A case study of mental imagery deficit. *Brain Cogn.* 8:147-164.
- FARAH, M. J., and F. PERONNET, 1989. Event-related potentials in the study of mental imagery. *J. Psychophysiol.* 3:99-109.
- FARAH, M. J., F. PERONNET, M. A. GONON, and M. H. GIARD, 1988. Electrophysiological evidence for a shared representational medium for visual images and percepts. *J. Exp. Psychol. [Gen.]* 117:248-257.
- FARAH, M. J., F. PERONNET, L. L. WEISBERG, and M. A. MONHEIT, (1989). Brain activity underlying mental imagery: Event-related potentials during image generation. *J. Cognitive Neurosci.* 1:302-316.
- FARAH, M. J., M. J. Soso, and R. M. DASHEIFF, 1992. The visual angle of the mind's eye before and after unilateral occipital lobectomy. *J. Exp. Psychol. [Hum. Percept.]* 18:241-246.
- FINKE, R. A., 1980. Levels of equivalence in imagery and perception. *Psychol. Rev.* 87:113-132.
- GOLDENBERG, G., 1992. Loss of visual imagery and loss of visual knowledge: A case study. *Neuropsychologia* 30:1081-1099.

- GOLDENBERG, G., and C. ARTNER, 1991. Visual imagery and knowledge about visual appearance in patients with posterior cerebral artery lesions. *Brain Cognition* 15:160-186.
- GOLDENBERG, G., I. PODREKA, M. STEINER, and K. WILLMES, 1987. Patterns of regional cerebral blood flow related to memorizing of high and low imagery words: An emission computer tomography study. *Neuropsychologia* 25:473-486.
- GOLDENBERG, G., I. PODREKA, M. STEINER, K. WILLMES, E. SUESS, and L. DEECKE, 1989a. Regional cerebral blood flow patterns in visual imagery. *Neuropsychologia* 27:641-664.
- GOLDENBERG, G., I. PODREKA, F. UHL, M. STEINER, K. WILLMES, and L. DEECKE, 1989b. Cerebral correlates of imagining colours, faces and a map: I. Spect of regional cerebral blood flow, *Neuropsychologia* 27:1315-1328.
- GOLDENBERG, G., I. PODREKA, M. STEINER, P. FRANZEN, and L. DEECKE, 1991. Contributions of occipital and temporal brain regions to visual and acoustic imagery: A spect study. *Neuropsychologia* 29:695-702.
- GOLDENBERG, G., M. STEINER, I. PODREKA, L. DEECKE, 1992. Regional cerebral blood flow patterns related to verification of low- and high-imagery sentences. *Neuropsychologia* 30:581-586.
- GROSSI, D., A. ORSINI, and A. MODAFFERI, 1986. Visuoimaginal constructional apraxia: On a case of selective deficit of imagery. *Brain Cogn.* 5:255-267.
- INTONS-PETERSON, M. J., 1983. Imagery paradigms: How vulnerable are they to experimenters' expectations? *J. Exp. Psychol. [Hum. Percept.]* 9:394-412.
- KOSSLYN, S. M., 1978. Measuring the visual angle of the mind's eye. *Cognitive Psychol.* 10:356-389.
- KOSSLYN, S. M., 1980. *Image and Mind*. Cambridge, Mass.: Harvard University Press.
- KOSSLYN, S. M., 1988. Aspects of a cognitive neuroscience of mental imagery. *Science* 240:1621-1626.
- KOSSLYN, S. M., N. M. ALPERT, W. L. THOMPSON, V. MALJKOVIC, S. WEISE, C. F. CHABRIS, S. E. HAMILTON, S. L. RAUCH, and F. S. BUONANNO, 1993. Visual mental imagery activates topographically organized visual cortex: PET investigations. *J. Cognitive Neurosci.* 5:263-287.
- KOSSLYN, S. M., T. M. BALL, and B. J. REISER, 1978. Visual images preserve metric spatial information: Evidence from studies of image scanning. *J. Exp. Psychol. [Hum. Percept.]* 4:47-60.
- KOSSLYN, S. M., J. D. HOLTZMAN, M. J. FARAH, and M. S. GAZZANIGA, 1985. A computational analysis of mental image generation: Evidence from functional dissociations in split-brain patients. *J. Exp. Psychol. [Gen.]* 114:311-341.
- LE BIHAN, D., R. TURNER, T. A. ZEFFIRO, C. A. CUENOD, P. JEZZARD, and V. BONNEROT, in press. Activation of human primary visual cortex during visual recall: A magnetic resonance imaging study. *Proc. Nat. Acad. Sci. U.S.A.*
- LEVINE, D. N., J. WARACH, and M. J. FARAH, 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.
- MAUNSELL, J. H. R., and W. T. NEWSOME, 1987. Visual processing in monkey extrastriate cortex. *Annu. Rev. Neurosci.* 10:363-401.
- PAIVIO, A., 1971. *Imagery and Verbal Processes*. New York: Holt, Rinehart, and Winston.
- PYLYSHYN, Z. W., 1973. What the mind's eye tells the mind's brain: A critique of mental imagery. *Psychol. Bull.* 80:1-24.
- PYLYSHYN, Z. W., 1981. The imagery debate: Analogue media versus tacit knowledge. *Psychol. Rev.* 88:16-45.
- RIDDICH, M. J., 1990. Loss of visual imagery: A generation deficit. *Cognitive Neuropsychol.* 7:249-273.
- ROLAND, P. E., L. ERIKSSON, A. STONE-ELANDER, and L. WIDEN, 1987. Does mental activity change the oxidative metabolism of the brain? *J. Neurosci.* 7:2373-2389.
- ROLAND, P. E., and L. FRIBERG, 1985. Localization of cortical areas activated by thinking. *J. Neurophysiol.* 53:1219-1243.
- SERGENT, J., 1989. Image generation and processing of generated images in the cerebral hemispheres. *J. Exp. Psychol. [Hum. Percept.]* 15:170-178.
- SHEPARD, R. N., 1978. The mental image. *Am. Psychol.* 33:125-137.
- TIPPETT, L. J., 1992. The generation of visual images: A review of neuropsychological research and theory. *Psychol. Bull.* 112:415-432.
- UHL, F., G. GOLDENBERG, W. LANG, G. LINDINGER, M. STEINER, and L. DEECKE, 1990. Cerebral correlates of imagining colours, faces and a map: II. Negative cortical DC potentials. *Neuropsychologia* 28:81-93.
- UNGERLEIDER, L. G., and M. MISHKIN, 1982. Two cortical visual systems. In *Analysis of Visual Behavior*, D. J. Ingle, M. A. Goodale, and R. J. W. Mansfield, eds. Cambridge, Mass.: MIT Press.

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