Ψ Psychology Press
Taylor & Francis Group

Mental images and the brain

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One theory of visual mental imagery posits that early visual cortex is also used to support representations during imagery. This claim is important because it bears on the "imagery debate": Early visual cortex supports depictive representations during perception, not descriptive ones. Thus, if such cortex also plays a functional role in imagery, this is strong evidence that imagery does not rely exclusively on the same sorts of representations that underlie language. The present article first outlines the nature of a processing system in which such a dual use of visual cortex (in perception and in imagery) makes sense. Following this, literature bearing on the claim that early visual cortex is used in visual mental imagery is reviewed, and key issues are discussed.

During the late 1970s and early 1980s there was vigorous debate about the nature of visual mental imagery. One position (championed primarily by Pylyshyn, 1973, 1981) held that representations that underlie the experience of mental imagery are the same type as those used in language; the other position (which my colleagues and I supported, e.g., Kosslyn, 1980, 1994) held that these representations serve to depict, not describe, objects. The debate evolved over time (for a summary, see Chapter 1 of Kosslyn, 1994), but always centred on the nature of the internal representations that underlie the experience of visualisation (e.g., Tye, 1991). The initial debate focused on conceptual issues and behavioural results, such as the finding that people require more time to scan farther distances in their visual mental images (Kosslyn, 1973; Kosslyn et al., 1978) and require more time to rotate objects in mental images by greater amounts (e.g., Shepard & Cooper, 1982). Interest in imagery waned by the mid-1980s, probably for several reasons (including the facts that definitive data had not been produced and other topics became fashionable). Nevertheless, research has continued on the topic, much of it in Europe (e.g., see Behrmann, Kosslyn, & Jeannerod, 1996), and progress has been made.

The debate moved into a new phase when neuroimaging began to be used to study the activation of early visual cortex during visual mental imagery (e.g., for review, see Kosslyn, Ganis, & Thompson, 2001a). Some studies found such activation, but others did not—and thus it was not clear how to interpret the full set of findings (for review, see Kosslyn & Thompson, 2003). At the same time, Pylyshyn (2002, 2003) rejected the very idea that neural evidence could bear on the imagery debate, and repeatedly claimed that

there is no viable theory of mental imagery. Pylyshyn's general concept of a theory (never spelled out in any detail) appears to require something analogous to a theory of linguistic competence, and does not fully address the empirical results that have driven the field.

In this brief article I provide an overview of one attempt to develop a theory that captures the regularities underlying the empirical results, and show how it can help us to formulate testable predictions about brain function. The theory is not complete and may not even be accurate as far as it goes, but it is definitely a "theory of mental imagery." I focus here in particular on one aspect of the theory, namely the dual role of early visual cortex in perception and imagery. This is crucial for the debate because these brain areas are topographically organised, and hence patterns of activation in these areas serve specifically to depict objects.

We must begin by distinguishing between *visual mental imagery* and *visual perception*: Visual perception occurs while a stimulus is being viewed, and includes functions such as visual recognition (i.e., registering that a stimulus is familiar) and identification (i.e., recalling the name, context, or other information associated with the object). Two types of mechanisms are used in visual perception: "bottom-up" mechanisms are driven by the input from the eyes; in contrast, "top-down" mechanisms make use of stored information (such as knowledge, belief, expectations, and goals). Visual mental imagery is a set of representations that gives rise to the experience of viewing a stimulus in the absence of appropriate sensory input. In this case, information in memory underlies the internal events that produce the experience. Unlike afterimages, mental images are relatively prolonged.

The approach offered here is unabashedly reductionistic: In my view, "the mind is what the brain does." We will consider imagery in light of neural mechanisms that give rise to the internal phenomena that underlie both the experience of visualisation and the behaviour that accompanies such experiences (for reviews of such behaviour, see Finke, 1989; Kosslyn, 1980, 1994; Shepard & Cooper, 1982).

A BRAIN SYSTEM

In order to discuss the role of early visual cortex (i.e., Areas 17 and 18) in visual mental imagery, we first must put it in context. Imagery is not simply a pattern of activation in these areas, but arises when such activation is embedded in a larger system.

Visual imagery and visual perception

All of the mental functions that we label with a single word, such as perception, memory, reasoning, and imagery, are accomplished by systems of processes in the brain. Numerous distinct processes are used to accomplish such functions (see Kosslyn & Koenig, 1992/1995, for a characterisation of the concept of "process" in this context). We gain enormous leverage in understanding the system of processes used in visual mental imagery because numerous researchers have shown that many of the same processes are also used in visual perception, and much is known about perception (e.g., see Farah, 1988; Finke, 1989; Kosslyn, 1994). Two types of evidence support this inference.

First, patients with brain damage often show deficits in imagery that parallel their deficits in perception (see Farah, 1988; Kosslyn, 1994; Kosslyn & Koenig, 1992/1995). For example, patients with damage to the parietal lobes sometimes exhibit "unilateral visual neglect"—they ignore objects to one side of space. These patients often ignore objects at the same side of space in both perception and mental imagery (e.g., Bisiach & Luzzatti, 1978; Bisiach, Luzzatti, & Perani, 1979). However, Behrmann, Winocur, and Moscovitch (1992) and Jankowiak, Kinsbourne, Shalev, and Bachman (1992) have described patients who have disrupted perception but retain relatively intact imagery, which underscores the fact that the two systems are not identical: In particular, imagery is based on previously stored information, and thus it can operate effectively even if the processes that organise visual input are awry.

Second, researchers have used neuroimaging techniques, primarily positron emission tomography (PET) and functional magnetic imaging (fMRI), to assess brain activity while participants perform visual mental imagery tasks (for reviews,

see Kosslyn et al., 2001a; Kosslyn & Thompson, 2003; Mellet, Petit, Mazoyer, Denis, & Tzourio, 1998). These studies have often reported activation in brain areas used in visual perception (e.g., Farah, Peronnet, Gonon, & Girard, 1988; Goldenberg, Podreka, Steiner, Willmes, Suess, & Deecke, 1989). Kosslyn, Thompson, and Alpert (1997) found that two thirds of all brain areas activated during either visual imagery or visual perception were activated in common; a more recent fMRI study from my lab, Ganis et al. (in press), demonstrated an even greater overlap in activation when the imagery and perception tasks were designed to be maximally similar. In this study, when the same task was performed in perception (with the stimuli visible) and during imagery (with eyes closed), approximately 90% of the same voxels were activated.

Perceptual processes used in visual imagery

Given the extant literature, I take it as a working assumption that imagery shares mechanisms with like-modality perception. In this section I provide a very brief overview of the major features of my current theory of visual mental imagery. The theory posits six major "components," as schematised in Figure 1. Each of these "components" is a coarsely described system of processes in its own right; each accepts input and transforms it in specific ways to produce output. Each component is also assumed to store information (in fact, the stored information plays crucial roles in producing the transformations). In my 1994 book I referred to the theory diagramed in Figure 1 as a "protomodel" because it is simply the bare bones of a theory. In that book I attempted to refine each of these major components, typically by dividing it into more specialised subcomponents, but I will not summarise that level of detail here. The motivation for positing each component rests largely on findings about the neurophysiology and neuroanatomy of visual perception. (The following summary has been adapted from that of Kosslyn, Alpert, Thompson, Chabris, Rauch, & Anderson, 1994.)

Visual buffer

Introspectively, visual mental images appear to embody the spatial layout of shapes. For example, consider what seems to occur when you try to
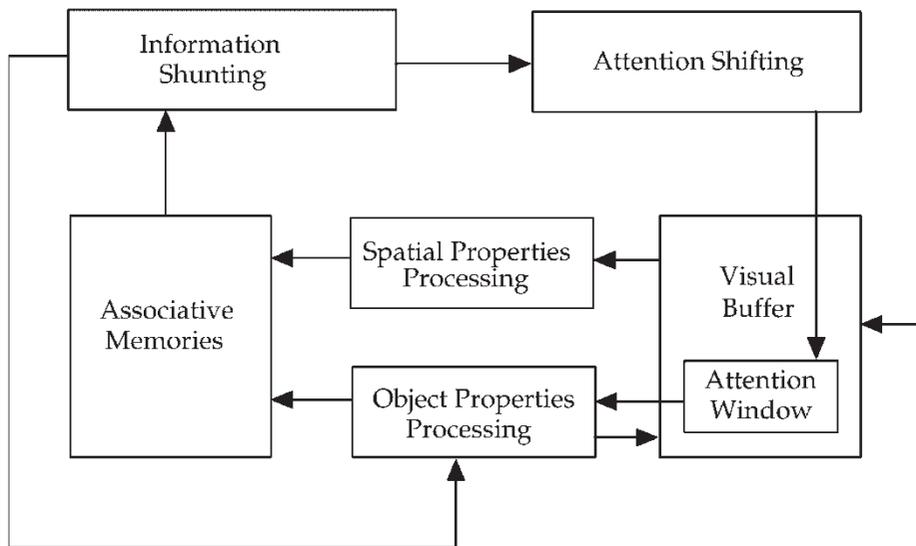

Figure 1. *The major processing systems posited to be used in visual imagery and the later phases of visual perception.*

answer questions such as, "Which is longer, a donkey's ears or an ear of corn?" "How many windows are in your living room?" "Which is wider, a light bulb or a tennis ball?" Most people report that they visualise the objects, and "see" the necessary properties. This sort of introspection suggests that visual mental images reconstruct the spatial geometry of objects. In fact, numerous areas of cerebral cortex are topographically organised; patterns of activity within these areas make explicit and accessible the spatial organisation of the planar projection of a stimulus. In these areas, the cortex is folded so that the fovea typically projects to the posterior part, with increasingly parafoveal regions projecting to increasingly anterior parts. The areas typically represent only the contralateral field, or even only a quadrant of the field. Neuroanatomical studies of nonhuman primates have revealed that about half of the cortical areas involved in vision are topographically organised, including Areas 17 and 18 (see Felleman & Van Essen, 1991; Heeger, 1999; Sengpiel & Huebener, 1999; Sereno et al., 1995; Tootell, Silverman, Switkes, & DeValois, 1982; Van Essen, 1985). Fox, Mintun, Raichle, Miezen, Allman, and Van Essen (1986) used PET to demonstrate that the largest such area, Area 17 (also known as primary visual cortex, striate cortex, area OC, and area V1), is topographically organised in humans (see also Heeger, 1999).

I group the topographically organised visual areas of cortex into a single functional structure, which I call the "visual buffer." A strong claim of the theory is that the brain areas that implement the visual buffer are also crucial during visual mental imagery (as will be discussed below). This is important because the visual buffer depicts shape. By "depict" I mean that each part of the representation corresponds to a part of the object such that the distances among the parts on the object are reflected (albeit not perfectly) by the distances among the representations of the parts (see Kosslyn, 1980).

Rather than thinking of the visual buffer as a simple "blackboard," a better analogy might be to a pegboard. As suggested by Tye (1991), at each location in the topographically organised buffer

are a set of "symbolic" codes that indicate information such as the colour and luminance at that specific point. Thus, in addition to this "picture-like" depictive aspect of the representation, the visual buffer specifies information that is interpreted as nonspatial properties associated with each location. Finally, the visual buffer is not a passive screen, but rather serves to organise input in various ways, such as delineating figure from ground.

Attention window

There is far more information in the visual buffer than can be processed in detail. Thus, an "attention window" operates within this structure, which selects a region of the buffer and sends the pattern of activation in it to other areas for further processing (cf. Brefczynski & DeYoe, 1999; Moran & Desimone, 1985; Treisman & Gelade, 1980). The attention window can be covertly shifted, and allows one to scan over entire images in the visual buffer without moving one's eyes.

Processing object properties versus spatial properties

The information in the visual buffer would be useless if it could not be processed. In fact, such information is processed along two pathways. One runs from the occipital lobe ventrally to the inferior temporal lobe, while the other runs dorsally to the posterior parietal lobe. Many findings have shown that the ventral pathway acts as an object-properties processing subsystem whereas the dorsal pathway acts as a spatial-properties processing subsystem (e.g., Anderson, Essick, & Seigel, 1985; Hyvarinen, 1982; Maunsell & Newsome, 1987; Mountcastle et al., 1975; Ungerleider & Mishkin, 1982). By "object properties" I mean shape, colour, and texture; by "spatial properties" I mean relative positions in space of two or more objects or parts. The distinction between the two kinds of properties is not quite as straightforward as it may appear. For example, if you look closely at a TV screen, you will notice that the shapes are made up of individual pixels in specific locations—and thus

location information gives rise to shape information. However, we can distinguish between the two types of properties in the following way: Spatial relations always include one point that has a privileged role; it is the "origin" from which the locations of other points are compared. Shapes, in contrast, emerge from the relations among all possible points—no one point has a privileged role. Instead, the local spatial relations give rise to higher-order patterns, such as contours, and it is these patterns (not the individual locations of constituent points) that define a shape.

Neuroimaging studies suggest that the middle temporal gyrus, inferior temporal gyrus, and fusiform gyrus may be the locus of visual memories in the human brain (see Haxby et al., 1991; Kosslyn et al., 1994; Sergent, Ohta, & MacDonald, 1992). These areas are selectively activated when one must recognise a stimulus. In addition, findings of Tanaka and colleagues (e.g., Fujita, Tanaka, Ito, & Cheng, 1992; Tanaka, Saito, Fukada, & Moriya, 1991) suggest that information is stored in the object-properties- processing system using a "population code" that, essentially, compresses the information. Shapes are stored by coding the presence or absence of each of a large set of attributes (which are not themselves interpretable in simple ways), and are not depicted in these areas.

According to our theory, images (i.e., topographically organised representations) are not stored in long-term memory. Rather, images in the visual buffer must be created by activating the stored memories in such a way that the implicit shape information is "unpacked" (for a detailed theory of how this may occur, see Kosslyn, 1994). Indeed, at least in the monkey brain, neural connections exist between the areas that store visual memory (nontopographically) and early visual cortex (which is topographically organised): Virtually every area involved in vision that has an afferent (forward) connection to another area also receives an efferent (backwards) connection from that area, and the forward and backward projections are of comparable size (e.g., Van Essen, 1985). These features of the anatomy imply that a great deal of information flows backwards in the visual system, from "higher-level" areas to the "lower-level," topographically organised areas. In fact, Douglas and Rockland (1992) have found direct connections from area TE (in the anterior inferior temporal lobe) to Area 17 in the macaque (see also Rockland, Saleem, & Tanaka, 1992). Such direct cortico–cortico connections from the higher-level areas to the lower-level areas are consistent with the hypothesis that visual mental images are formed by using stored information to reconstruct spatial patterns in topographically organised cortical areas. Similar ideas have long been popular (e.g., cf. Damasio, Damasio, Tranel, & Brandt, 1990; Hebb, 1968; James, 1890).

On the other hand, according to our theory, spatial representations in the dorsal system are often (but not always) used in the service of guiding movements (cf. Milner & Goodale, 1995). To this end, the spatial representation includes a "map," where the locations of parts and objects are represented by distinct points.

Associative memory

One of the advances of research on memory is the finding that different types of memories are often stored in different regions of the brain (e.g., Schacter, 1996; Squire, 1987). We can infer that there must be a long-term memory (LTM) representation that associates object properties with spatial properties; the mere fact that people can recall where furniture is located in their homes indicates that the two sorts of information must have been cross-indexed in memory. This memory representation is multimodal, associating not only visual object properties and spatial properties, but also auditory, tactile, and other sorts of information. Moreover, because many complex objects are encoded over the course of numerous eye movements, parts may be encoded separately as distinct shape representations in the object-properties-processing system, and a representation of the structure of the object is built up in associative memory as one's eyes move. Long-term associative memory appears to rely on cortex in the region of the angular gyrus and part of Area 19 (Kosslyn, Thompson, & Alpert, 1995a).

Information shunting

During perception, one sometimes cannot identify an object at first glance; the information encoded in a single eye fixation is not sufficient to match a stored representation (cf. Neisser, 1967). However, the input provides some indication of what is being viewed, and the partial match to stored representations may serve as a hypothesis. In this case, additional information is needed to identify the input. Frontal lobe processes apparently access information in long-term associative memory, and shunt this information to processes that guide further encodings, allowing one to seek a particularly diagnostic part or characteristic of an object. Many researchers have found that damage to the frontal lobe disrupts systematic search (e.g., Luria, 1980), and others have found that the frontal lobes are in fact active when one must access information in memory (see Berthoz, 1996; Nyberg, Cabeza, & Tulving, 1996).

Attention shifting and top-down priming

Finally, an attention-shifting system actually shifts attention to the location of a possibly distinctive part during perception, which allows one to encode it. And here is a crucial idea for the theory of imagery: At the same time that attention is shifted to the location of an expected part or characteristic, the representation of that part or characteristic in the object-properties processing system is primed. Such priming allows one to encode the sought part or property more easily (for evidence of such priming, see Kosslyn, 1994, pp. 287–289; McAuliffe & Knowlton, 2000; McDermott & Roediger, 1994).

According to the theory, in order to create an image representation in the visual buffer on the basis of stored information, frontal lobe processes access the stored representation of the structure of an object in associative memory, and send a signal to the object-processing system in the inferior temporal lobes to activate a representation of visual properties of the object. This activation process is identical to the priming that occurs during top-down hypothesis testing in perception, only now the priming is so strong that the activation propagates backwards and a depictive representation is formed in the visual buffer.

When visualising detailed objects or scenes, representations in associative memory of spatial relations among parts or characteristics (or objects, in scenes) lead one to shift attention to the appropriate location on the imaged object, and to visualise each part or characteristic at the correct relative locations, so that a composite image is built up sequentially over time (for further details, see Kosslyn, 1994). Kosslyn, Cave, Provost, and Von Gierke (1988) provide evidence that images are generated by building them up part-by-part over time. Indeed, the segments of letters are placed in the image in the same order that they typically are drawn when block letters are printed.

This theory has generated many predictions, some of which have been tested (e.g., Kosslyn et al., 1994, 1995a, 1997). In the context of the present article, all that is important is that after such tests the theory remains viable. It is indeed plausible that early visual cortex—the neural underpinnings of the visual buffer—is used in both imagery and perception, as hypothesised in the theory. Let us now focus on these topographically organised representations.

THE ROLE OF TOPOGRAPHICALLY ORGANISED VISUAL AREAS IN IMAGERY

All of the functions incorporated in the theory rely on areas that operate during both perception and imagery. However, the representation in the visual buffer plays a special role in this theory. These representations give rise to the depictive aspects of the experience of "seeing with the mind's eye." (Note: it is unlikely that consciousness arises directly out of activity in the earliest visual area, but rather from projections from that area to other parts of the brain; see Crick & Koch, 1994; Kosslyn, 1999.) Thus, a strong prediction of the theory is that the topographically organised areas in early visual cortex should be used in both imagery and perception. If so, they should be activated during imagery, and disrupting activity in these areas should disrupt imagery.

Activation of topographically organised visual areas

The first PET and fMRI neuroimaging studies of visual mental imagery were reported by Kosslyn et al. (1993) and LeBihan, Turner, Zeffiro, Cunod, Jezzard, and Bonnerot (1993), respectively. Although the two studies used very different tasks, both reported finding activation of Area 17 during imagery. The Kosslyn et al. task involved visualising letters in a grid and deciding whether the letter would cover an X in the grid, and the LeBihan et al. task involved simply visualising sets of stripes. Shortly thereafter, Damasio et al. (1993), using PET, and Menon et al. (1993) and Sabbah et al. (1995), using fMRI, also reported that Area 17 is activated during visual mental imagery.

My colleagues and I conducted numerous additional experiments to investigate whether Area 17 per se is activated during visual mental imagery. In the first follow-up study, Kosslyn et al. (1993, Experiment 3) adapted the logic of Fox et al. (1986) to an imagery experiment. Fox et al. showed that different-sized stimuli activated different portions of Area 17, as predicted from previous studies of which parts of the visual field were disrupted following damage to specific parts of this structure. Rather than varying the visual angle subtended by a perceived object, we varied the "visual angle" subtended by imagined patterns. If imagery activates topographically organised visual cortex, then we would expect different portions of it to be more strongly activated when objects are visualised at different sizes. In this experiment the participants closed their eyes and listened to names of letters of the alphabet along with cue words. Each cue specified one of four judgments (e.g., "all straight" was a cue to decide whether the upper-case letter has only straight lines or any curved lines). The participants visualised the letters at the smallest possible "visible" size in one condition and at the largest possible "nonoverflowing" size in another condition. In both cases, the letters were to be centred in front of them and maintained at the appropriate size until a probe was presented.

We were determined to find an appropriate baseline condition for this task. We decided that, given the question we wanted to answer, an ideal control task was another version of the task itself: If the participants form images of tiny letters directly in front of them, much spatial variation would occur in a small, foveal region of a topographically organised area. In contrast, if the participants formed images of large letters, this foveal region would contain little spatial variation (only part of one segment of a larger letter, at most). Hence we expected greater metabolic activity (and corresponding blood flow) within the foveal region for small images than for large ones. In contrast, large images should extend into more peripheral regions. Hence we expected greater metabolic activity farther from the foveal representation when large images were formed. This reasoning led us to subtract the blood flow in the large image condition from blood flow in the small image condition, which revealed regions that were more activated by small images. Similarly, we subtracted the blood flow in the small image condition from blood flow in the large image condition, which revealed regions that were more activated by large images.

The results were encouraging. First, when we examined selective activation when large images were formed (i.e., the pattern of blood flow for small images was subtracted from the pattern of blood flow for large images), we found greater blood flow in a region of Area 17 (as identified by the Talairach & Tournoux, 1988, atlas) that was about 69 mm posterior to the anterior commissure (AC, the origin of the coordinate space defined by the Talairach & Tournoux atlas). In contrast, when we examined selective blood flow when small images were formed (i.e., the pattern of blood flow from large images was subtracted from the pattern of blood flow from small images), we found greater activity in a region of Area 17 that was 89 mm posterior to the AC. Both areas of activation were to the right of the midline, which is consistent with Sergent's (1989) finding that participants perform this sort of task faster when the cues are presented to the left visual field. The activation we found in the large/small experiment is about where one would expect if Area 17 were in fact activated (based on the previous findings reported by Fox et al., 1986).

At this juncture, a new phase of the imagery debate began. Some researchers were not convinced by the results of the experiments just described. For example, some argued (informally, so far), that the large images and the small images actually activated different areas. Moreover, the fact that the two conditions were compared to each other only indicated relative amounts of activation during imagery; it did not allow one to localise activation due to imagery per se. And there appeared to be a more serious problem: Roland and Gulyas (1994) reported that when they performed similar experiments, they found no evidence of activation of topographically organised areas, and Mazoyer and his colleagues (e.g., Charlot, Tzourio, Zilbovicius, Mazoyer, & Denis, 1992; Mellet, Tzourio, Denis, & Mazoyer, 1995) also failed to find such activation.

We were greatly puzzled over the fact that our results were not replicated, and thus looked very carefully at what had actually been done. Kosslyn and Ochsner (1994) suggested a number of reasons why some researchers had failed to obtain the results we did, and Kosslyn, Thompson, Kim, and Alpert (1995b) tested one account that we found particularly plausible. We had noticed that Roland and his colleagues and Mazoyer and his colleagues always compared blood flow in imagery conditions to blood flow in a resting baseline condition. Indeed, Roland and colleagues asked participants to close their eyes in darkness and to "visualize blackness," and then subtracted cerebral blood flow in this condition from that in the imagery condition. We reasoned that Area 17 might be activated in this baseline condition, and thus subtracting activation in it from that in the imagery condition would remove evidence of activation during imagery.

To test this idea, we asked participants to take part in five conditions. There were two baseline conditions. One was the same resting baseline used by Roland and colleagues. The other required them to listen to stimuli of the following form, "anchor… right-higher" and to press a response pedal as soon as they heard the comparison terms; the participants received this baseline before having any idea about the nature of the experimental conditions. After participating in the listening baseline, the participants memorised a set of line drawings of common objects, and then received three imagery conditions. The imagery conditions had trials of the following form: The participants first heard the name of one of the drawings and visualised it (with their eyes closed), and then heard a comparison term, at which point they decided whether it characterised the drawing (e.g., whether the right side of the drawing was higher than the left?). Before each of the three imagery conditions the participants studied a different-sized square, which subtended either 0.25, 4, or 16 degrees of visual angle. They were told to form images, and hold them, at the size of that square during all the trials in that condition. Counterbalancing ensured that the same auditory stimuli occurred equally often in the listening baseline and in each of the imagery conditions, and also ensured that images at each size were formed equally often in each of the serial orders.

The most important results were as follows: First, when Kosslyn et al. (1995b) compared the imagery trials to the listening baseline, we found additional blood flow during imagery in Area 17. But more than that, the small images activated the portion of this area that registers central stimuli that subtend small visual angles during visual perception, the medium images activated cortex that registers medium-sized objects, and the large images activated cortex that registers objects that subtend large visual angles. Second, when we compared the imagery trials to the resting baseline, we found just what Roland and colleagues found: No additional blood flow during imagery in Area 17 (but instead evidence for parieto-occipital activation, in an area very close to the one reported by Roland & Friberg, 1985). Third, as expected, when we simply compared the two baseline conditions, we found that Area 17 was more activated during the resting baseline than during the listening baseline. Thus, our original conjecture was correct.

More than one kind of imagery

However, after we reported the research just described, it became clear that our story was far

from complete. We initially thought that the difference in baselines was sufficient to explain why some researchers did not find activation of Area 17 during imagery. But this was not the case. For example, Mellet et al. (1996) report that they failed to find activation in Area 17 during imagery even when a listening baseline was used. Their task required participants to visualise rectangular blocks pointed in specific directions, building up a multi-armed 3-D figure (and later, after scanning, to recognise the figure). This task differs from the ones we have used in two important ways.

First, it is spatial; it requires keeping track of a set of directions. Such tasks may not activate the areas that underlie the object-properties-processing system or the visual buffer. Instead, such images require only spatial information and thus may be formed in parietal structures. Indeed, Levine, Warach, and Farah (1985) reported that a patient with damage to the parietal lobes could visualise objects (including faces) but not directions, and vice versa for a patient with damage to the temporal lobes. Thus, it is possible that the spatial nature of the task explains why Mellet et al. (1996) failed to obtain activation of medial occipital cortex (as they themselves hypothesise).

Second, this task required only very coarse resolution; the directions were very distinct, and the participants were not told that they would be tested after the scan. It is possible that Area 17 is activated during imagery only when patterns must be visualised with high resolution to perform the task. When less resolution is necessary to perform the task, areas with larger receptive fields, and hence presumably poorer resolution, may be adequate. D'Esposito et al. (1997) present the limiting case of this situation, where no task at all was required and participants were not allowed enough time to form images; in this case, images may be so vague that only temporal lobe activation is present (as was found, without medial occipital activation).

Kosslyn and Thompson (2003) reviewed the neuroimaging literature on visual mental imagery (over 50 studies have now been reported), and used a novel type of meta-analysis to analyse the conditions in which Areas 17 or 18 (both of which are topographically organised) are activated during visual imagery. We found that whether or not a study documented activation in Areas 17 or 18 can be accounted for by three variables: If the task requires high resolution images of the details of shape, Areas 17 or 18 will tend to be activated; if the task requires using spatial images, these areas will tend *not* to be activated; and if more sensitive techniques (such as 4-T fMRI) are used, activation will tend to be documented. Thus, the finding that topographically organised cortex is activated during visual mental imagery is not likely to be an artifact or an accident. More likely is the possibility that there is more than one way to form images, and that different mechanisms may be called into play in different circumstances (for similar views, see Mazard, Tzourio-Mazoyer, Crivello, Mazoyer, & Mellet, 2004; Mellet et al., 1998).

Indeed, a parallel issue has arisen in a related area of mental imagery, namely mental rotation. This issue concerns the role of primary motor cortex (Area M1). Some researchers have found activation in this area (especially when participants are to mentally rotate body parts) whereas others have not (e.g., for reviews, see Kosslyn, Thompson, Wraga, & Albert, 2001b; Wraga, Thompson, Albert, & Kosslyn, 2003). The resolution of this issue is now emerging: There is more than one way to mentally rotate objects. For example, participants can be told in advance to imagine that they mentally rotate by physically twisting the stimulus with their hands or can be told to imagine that they mentally rotate by observing an electric motor turn the stimulus (Kosslyn et al., 2001b). Although the behavioural data in both cases indicate that the participants mentally rotated the objects, only when the former strategy was used (when participants imagined that they were physically moving the stimuli) was primary motor cortex activated.

Epiphenomenal activation?

But what evidence do we have that imagery in fact relies on (as opposed to merely causes incidentally) activation in topographically organised brain areas that we identify with the visual buffer? We have

three sorts. First, Farah, Soso, and Dasheiff (1992) used the Kosslyn (1978) technique to study the visual angle subtended by images in a patient before and after she had one occipital lobe removed (for medical reasons). The visual angle subtended by mental images shrank by about a half following the operation. In contrast, the vertical extent was preserved after surgery. This was as expected because the vertical extent is represented redundantly in topographically organised areas in the two hemispheres, whereas horizontal extent in each half field is represented preferentially in the areas in the contralateral hemisphere. We (unpublished data) have extended these results with a series of patients, and provided converging evidence that damage to Area 17 per se disrupts the ability to form sharp images in the affected visual field.

Second, Kosslyn et al. (1999) used repetitive transcranial magnetic stimulation (rTMS) to disrupt Area 17 in normal volunteers prior to an imagery task; this technique involves pulsing a strong magnetic field on a specific place on the scalp, directed inwards to disrupt a relatively small set of neurons. These tasks involved visualising or seeing sets of stripes and making judgments among them (such as which set had more stripes, longer stripes, etc.). A prior PET study had demonstrated that the task activated Area 17. We found that immediately after rTMS was used to disrupt activity in this area, the participants had deficits in both a visual imagery and a corresponding visual perception task. Moreover, these deficits were of comparable magnitude in imagery and perception—which is consistent with the claim that early visual cortex is used in both tasks.

Third, Kosslyn, Thompson, Kim, Rauch, and Alpert (1996) reasoned that if activation of Area 17 gives rise to imagery representations used in information processing, then characteristics of the neural activity ought to be reflected in performance. Thus, we re-examined the data from the 16 participants tested by Kosslyn et al. (1993, Experiment 3) in the original size-variation experiment. We now pooled the data over size, and normalised each person's brain to the same mean blood flow value. We then examined the relative amount of blood flow in Area 17 for each person (compared to the global mean), and correlated this measure with the mean time the participants required to evaluate the images (which was recorded while the participants were being scanned). We found that the slowest participants were in fact those who had the least amount of blood flow in Area 17 ($r = -.65$). Moreover, this effect persisted when we factored out the contributions of two other regions of interest that were correlated with response times. Klein, Paradis, Poline, Kosslyn, and Le Bihan (2000) performed a similar analysis, and also found a negative correlation between response times and activation in Area 17.

CONCLUSIONS

The rapid expansion of behavioural studies of mental imagery (from roughly 1965–1993) and then neuroimaging studies (1993–present) has vastly increased our understanding of the phenomena. Not only have the data become far richer, but also more constrained. The hypotheses being considered are more subtle than those previously offered, and the methods of testing those hypotheses are becoming increasingly refined. However, there are still many unresolved issues, surrounding questions about when depictive images are used, exactly how they are created, and their roles in cognition more generally. The existence of such open issues should not be discouraging; rather, the fact that the issues often are couched within a common conceptual framework seems to me to be evidence of genuine progress.

At this juncture, it is clear that the bulk of the evidence supports the claim that visual mental imagery not only draws on many of the same mechanisms used in visual perception, but also that topographically organised early visual areas play a functional role in some types of imagery. Many additional questions are sure to arise—but as long as these questions are empirically tractable I have confidence that we will continue to learn more about the nature of visual imagery and how it arises in the brain.

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