

In search of occipital activation during visual mental imagery

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Visual mental imagery seems destined to remain a controversial topic. Unlike memory, language and motor control, imagery has no easily observable sequelae; it is a quintessential private event, and notoriously difficult to study. The study of imagery over the past 15 years has focused on the nature of the internal representations that produce the experience of 'seeing with the mind's eye'¹⁻⁶ rather than on its relation to perception (although that topic has also been debated; for example, see Ref. 7). Some researchers have proposed that at least some of the underlying representations depict information (that is, they embody spatial extent), while others have proposed that the depictive properties of imagery that are evident to introspection are entirely epiphenomenal (like the heat from a light bulb while one is reading, which plays no role in the reading process); these theorists claimed that the functional representations that underlie imagery are entirely propositional, no different in kind from the representations that underlie language (for example, see Ref. 4).

Traditionally, researchers investigated imagery by collecting introspective reports or studying the behavioral consequences of using imagery in specific ways, either in normal or brain-damaged people^{2,3,8,9}. Such research has clear limitations, and it has proven extremely difficult, if not impossible, to infer the nature of the underlying representations using these traditional techniques (for example, see Ref. 1). However, advances in brain-scanning techniques, coupled with discoveries about the neurophysiology and neuroanatomy of visual perception in nonhuman primates, offer a new approach to this issue. It has long been known that some visual areas (roughly half of those in the macaque) are organized topographically. If these areas could be shown to be activated during imagery, this would provide evidence that image representations depict information. Furthermore, if it could be shown that spatial properties of the imaged pattern directly influence the pattern of neural activity in these areas, that would be even stronger evidence that imagery relies, at least in part, on depictive representations (perhaps in addition to propositional representations).

Kosslyn and colleagues reported one such study¹⁰ in which subjects closed their eyes and visualized an uppercase letter at a large or small size, held this image, and determined whether it has a specific property (for example, any curved lines). They found that there was greater activation towards the posterior portion of the medial occipital lobes for small images (compared with large images), whereas there was greater activation towards the anterior portion of this region for large images (compared with small images). Given that area 17 is mapped topographically with foveal regions represented at the posterior portion, it makes sense that a depictive representation of a small object would activate more posterior portions, whereas a depictive represen-

tation of a large object would activate more anterior portions of this region. Moreover, the coordinates of the activated regions were consistent with the possibility that area 17 had been activated, given previous results reported by Fox and colleagues¹¹.

Using positron emission tomography (PET), Damasio and colleagues¹² reported activation in area 17 when subjects form visual mental images. Moreover, as noted by Roland and Gulyás¹³, results using functional magnetic resonance imaging (fMRI) have since corroborated the PET findings. In addition to the findings that they note^{14,15}, we, in collaboration with Belliveau (unpublished observations), have found activation in area 17 when subjects form images with their eyes closed. Indeed, in several subjects we have found clear differences in such activation when they form images of large letters versus small letters.

It could still be argued that such activation is epiphenomenal, perhaps a spill over of synchronized activity in other visual association areas (see Ref. 13). Farah and colleagues¹⁶ used the task developed by Kosslyn¹⁷ to measure the 'visual angle of the mind's eye' of a patient before and after resection of the occipital lobe in one hemisphere. They found that the maximum angle subtended by the patient's images was reduced by approximately half following removal of one occipital lobe, demonstrating that the representations in visual cortex are not simply epiphenomenal.

So, what can account for the inconsistent results from Roland's laboratory? We have identified three possible causes for the discrepant results:

(1) Selection of baseline tasks

As Roland and Gulyás suggest, one key to the discrepant results might lie in differences among the paradigms and methods used by different researchers. In all of the studies that Roland and Gulyás cite that did not find activation in occipital cortex¹⁸⁻²³, activation in test conditions was compared with activation in a baseline condition in which subjects performed no task, and lay motionless with eyes closed (and in some cases covered). In not one of the studies was it reported that subjects were debriefed following the experiment to determine whether they daydreamed or engaged spontaneously in visual imagery while resting. Indeed, in one case subjects were told to imagine 'having it black in front of the mind's eye'²³; this might have induced subjects to form an image of blackness. If subjects did visualize during the baseline condition, then subtracting blood flow during this condition from that in a test condition would indicate erroneously that visual cortex was not active during the test task. Thus, tasks that seem to require visual imagery, such as imaging walking along a familiar route^{21,22} and visualizing the letters of the alphabet and words of the Hungarian national anthem¹⁹, might not reveal visual cortical activity when compared with a resting baseline.

Although the PET studies performed at the Massachusetts General Hospital rely on comparisons between conditions also, the choice of baseline and test tasks is often motivated by a logic of inference different from that used by Roland, Gulyás and colleagues. This approach is rooted in the 'additive factors' method²⁴, and requires preserving the nature of the test task for the baseline condition, manipulating only a single variable for the two conditions; the variable to be manipulated is chosen because it alters the amount of activity of a specific process. The experiment in which image size was manipulated¹⁰ is an example of this approach: using the same task for both conditions, different foci of activity were revealed when imaging large versus small objects. This approach eliminates the potential problems of comparing two different tasks³.

(2) Task validation

We have found activation in medial occipital cortex¹⁰ even when the additive factors method was not used. Another important factor concerning the selection of paradigms is that one must ensure that imagery is used in the task. To verify that subjects used imagery to perform the tasks, Kosslyn and colleagues¹⁰ always obtained behavioral 'signatures' of imagery online (that is, specific effects of using imagery). Indeed, when the response-time data from the large–small experiment were analysed, three subjects (of 16) were found who did not show the usual increase in the time taken to evaluate objects visualized at small sizes. When their PET data were excluded, the significance level for the large–small difference in occipital activation increased. If subjects are not performing the task using imagery, the occipital lobe should not be activated.

It is important, therefore, to note that in some of the tasks Roland and Gulyás cite, subjects need not have used imagery. For example, Roland and Gulyás asked subjects to recall and visualize a series of 10 complex patterns that had been learned previously during a training session of 70 min²². Although the authors note that they have no empirical data to verify use of imagery by subjects, they contend that EEG indicating augmentation of the β rhythm, and subjects' introspective reports, suggest that some visualization did occur. Nevertheless, imagery need not have been used to perform this recall task. In fact, over the course of the training session of 70 min, information about the increasingly familiar patterns might have been coded verbally. Thus, asking subjects to visualize or answer questions about these overlearned attributes might require access only to semantic knowledge of the attributes in question, and little or no use of imagery.

Similarly, the delayed-pointing task^{18,20} need not require the use of imagery. In this task, subjects were given 5 s to memorize the locations of seven different-sized circles presented simultaneously on a computer screen. Subjects then closed their eyes, and after a brief delay were cued to point to a blank screen, indicating the previous locations of the circles in order of increasing size. Because the same

task was used on each trial, the subjects knew that they would always have to report the sequence. Thus, they could perform the task by encoding motor commands for pointing, or by labeling each size, for example, with a number, and associating each number with a location. Neither of these strategies requires imagery.

In addition to verifying that imagery is used in a particular task, the types of imagery that are required must be determined precisely. Imagery is not a unitary ability^{3,25} but consists, instead, of a host of specialized abilities. Not all imagery tasks need to recruit topographically mapped areas to the same degree. It has been shown that both hemispheres of a split-brain patient could perform tasks that require only low-resolution images (for example, deciding whether an object is higher than it is wide), but only the left hemisphere could also perform tasks that require high-resolution images (for example, deciding whether an animal's ears protrude above the top of its skull)²⁶. It is possible that area 17 is activated only by tasks that require high-resolution images, and other areas (some topographically organized, some not) are adequate for performing other types of imagery tasks³.

(3) Individual differences

It has become clear from single-subject fMRI studies (Tank, D. W., pers. commun.) that not all subjects show activation in area 17 during visual mental imagery. Indeed, it has been reported that subjects who rated their images as more vivid had greater blood flow in the inferior occipital lobe²⁷. It is possible that differences in how subjects are selected might contribute to the discrepant results.

In summary, the fact that many laboratories have found occipital activation during imagery cannot be ignored; at least some of the time, imagery relies on depictive representations in the occipital lobe. Nevertheless, it is of great interest that such results are not obtained in all tasks, and such negative findings must be explained. It might well be that if a task does not require reconstructing the detailed local geometry of a shape, then imagery need not necessarily invoke a pattern of activation in topographically mapped areas of cortex.

Note: a full description of the methods used in Ref. 20 was not available to us at the time this article was submitted. Ref. 19 is an abstract for research presented at the Eur. Neurosci. Assoc. conference, and as such provides few details on the paradigms. Our interpretation of the tasks used by these researchers is based upon the figure legend (1F and 1G) of Roland and Gulyás, Ref. 13. In addition, Roland and Friberg²² do report occipital activation in their route-finding task, albeit in the superior occipital cortex.

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Do PETS have long or short ears? Mental imagery and neuroimaging

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The question addressed by Roland and Gulyás is whether visual perception and mental imagery are mediated by a common neural substrate¹. There is general agreement that at least some higher-order visual areas in temporal and parietal lobes participate in both perception and imagery. The focus of the dispute, then, concerns the involvement in imagery of early, retinotopically organized areas of visual cortex, namely areas 17 and 18 which correspond, in part, to areas V1–V4 and VP (ventralis posterior) in the monkey (the topographic-area hypothesis). Based primarily on data from their own positron emission tomography (PET) activation studies, Roland and Gulyás argue that areas 17 and 18 are involved in perception only and not in visual imagery of complex forms.

In examining the evidence, we propose that PET studies in normal people can only provide information about activation of early visual areas during imagery but do not demonstrate conclusively whether this activation is necessary for imagery. To determine whether this activation is needed for imagery, evidence from studies of brain-damaged patients is required. We will summarize this evidence briefly and consider its implication for neuropsychological theories concerned with the overlap between perception and imagery.

Are areas 17 and 18 involved in mental imagery?: evidence from neuroimaging

Roland and Gulyás contrast two sets of PET studies on visual imagery: those from their own laboratory, which did not find activation in areas 17 and 18, and those from other laboratories that did (topographic view)^{2–5}. They suggest that the 'conflict is due to differences in method and stimulus paradigms' but they provide no indication of what those differences are. For their argument to be convincing at an empirical level, Roland and Gulyás must establish that (1) their own tasks have a strong

imagery component, and (2) the activation of areas 17 and 18 in these other studies is unrelated to imaging.

(1) Roland and Gulyás do not provide any independent validation that their experimental tasks involve visual imagery, and that their baseline tasks are identical to the experimental ones except for the imaging component (at least as described in their opening article¹). This makes their tasks suspect.

(2) Even taken at face value, Roland and Gulyás' evidence does not discredit other studies that reported activation in areas 17 and 18 during imagery. In at least two of those studies^{2,4}, the tasks used were ones that satisfied imagery criteria in tests of normal and brain-damaged people. Consequently, based on PET studies, the only rational alternative is to concede that some, but perhaps not all, tests involving visual imagery activate areas 17 and 18.

Is activation of areas 17 and 18 necessary for visual imagery?

According to Kosslyn and his colleagues^{2,6}, because imagery involves analogue visual representations, activation of topographically organized areas is needed to construct the geometry of shape during imagery. Roland and Gulyás, however, argue that if the 'brain already possesses a computed representation' in the form of an image 'why do the job over again' by re-activating retinotopically organized areas whose function is to deliver the raw material for those computations? This debate cannot be settled by PET activation studies of normal people because all these can reveal is which areas are activated during imagery and not whether those areas are critical for imagery. To answer this question, patients with brain damage need to be studied. Only two types of patients are crucial for the debate: patients with damage to the occipital cortex and patients with intact imagery but impaired