How the Brain Creates Imagery: Projection to Primary Visual Cortex

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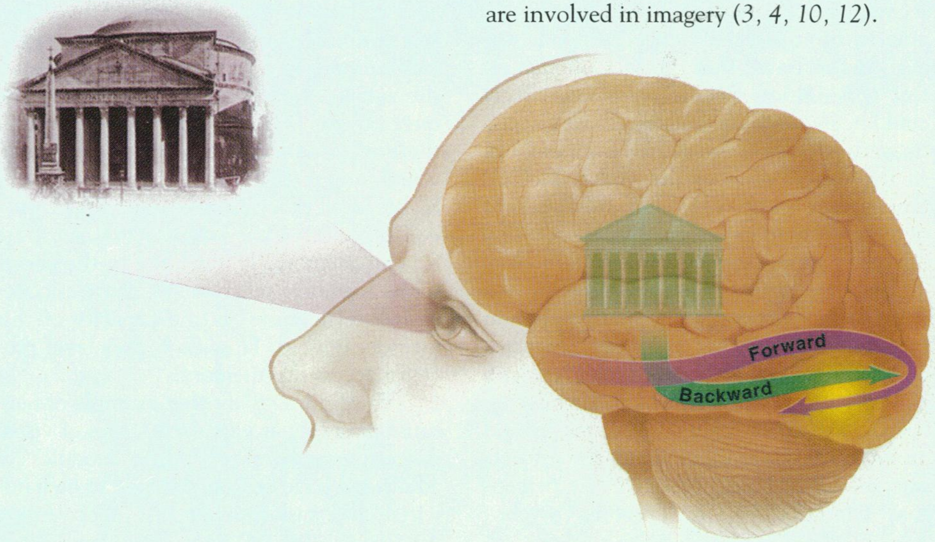
Create an image of the Pantheon in your mind. Can you count the columns that support its pediment (1)? Our ability to create mental imagery—to "see with the mind's eye"—has been of interest to philosophers and scientists for a long time. At the moment, we define visual imagery as the recreation of a perceptual experience in the absence of visual input. How our brain creates an imagery experience may appear extremely difficult to elucidate with empirical methods. There are, however, many approaches (neuroimaging, electrophysiology, psychophysics, and neuropsychology) that test where and how in the brain the images of the things we see are generated, stored, and maintained (2). There is general agreement that at least some higher order brain areas in the temporal and parietal lobes, which are used for cognitive information processing during various mental activities, participate in imagery experiences. A longstanding controversy, however, concerns the extent to which the processes of visual perception and imagery share a common neural substrate and whether visual imagery is based on contributions of the early visual areas (2–4).

A report in this week's issue of *Science* (5) provides particularly clear evidence that speaks to this problem. In certain tests of visual perception, the ability to see a target can be enhanced by other stimuli around it (called mask stimuli). Ishai and Sagi (5) used one of these psychophysical tests to show that detection of the visual target can be enhanced when the mask stimuli were absent, but the subjects imagined that they were there. To their surprise, the imagery-induced facilitation had many of the same characteristics as the perception-induced facilitation—monocularity and specificity of orientation and retinal location. These properties are hallmarks of the first cortical area in visual processing, providing support for the hypothesis that visual imagery activates the primary visual cortex.

The visual system in the primate consists of a mosaic of more than 30 visual areas, which are functionally heterogeneous and hierarchically organized, starting from the primary visual cortex (V1 or striate cortex) (6). A visual stimulus on the retina is analyzed in terms of its elementary features—orientation, color, texture, and depth—by low-level visual processing in the striate cortex and the prestriate areas, most of which are organized retinotopically. The analyzed features are integrated by high-level visual processing in the temporal and parietal cortex into a unique configuration that functions as the internal representation of an object and its spatial properties. The connections among the visual areas are notably reciprocal, projecting both forward and backward (6). Visual perception relies mainly on the forward, bottom-up flow of information. Imagery, in contrast, likely uses the backward projections as the anatomical substrate of top-down mental operations (see the figure). Some theories have predicted that, if an imagery task requires reconstruction of the detailed local geometry of the image (as counting the columns of the Pantheon), backward signals from higher order representations would reach topographically organized visual areas (2, 4, 7). This prediction seems to be borne out by the new results from Ishai and Sagi (5).

Although there has been debate as to whether depictive (quasi-pictorial) or propositional representation lies in the deepest structure for image generation (2, 8), the processes that produce and utilize visual images most likely rely on high-level visual mechanisms. For example, when subjects imagine that they started at their front door and then walked alternately to the left or the right each time they reached a corner (9), or when subjects imagine a letter in a grid and decide whether the letter would have covered a mark presented in the grid (10), positron emission tomography (PET) analysis consistently reveals activation of the dorsal (area 19) and ventral (fusiform gyrus) visual association areas, superior and inferior parietal cortex, as well as other nonvisual cortices such as the dorsolateral prefrontal cortex and angular gyrus. Single-unit recording from the monkey inferior temporal cortex, a candidate for the homolog of the human fusiform gyrus, revealed picture-specific neural discharges when the monkey retrieved from its long-term memory store the image (paired associate) that was instructed by a previous cue stimulus (11). Contrary to this agreement on activation of high-level visual mechanisms, evidence from neuroimaging and physiology appears both to support and contradict the hypothesis that early visual areas are involved in imagery (3, 4, 10, 12).



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Visual perception relies mainly on the forward, bottom-up flow of information. In contrast, imagery experience requires a top-down mental operation, which activates backward projections. If an imagery task requires reconstruction of the detailed local geometry of the image (as counting the columns of the Pantheon), backward signals from higher order representations would reach topographically organized visual areas.

Psychophysical studies have also addressed this problem on the basis of neuronal response characteristics in the primary visual cortex (V1), which are specific to the stimulated eye as well as to orientation and retinal location of the stimulus (see the table). For example, subjects decided whether two line segments were perfectly aligned (a vernier acuity task); when the subjects did not form mental images, ac-

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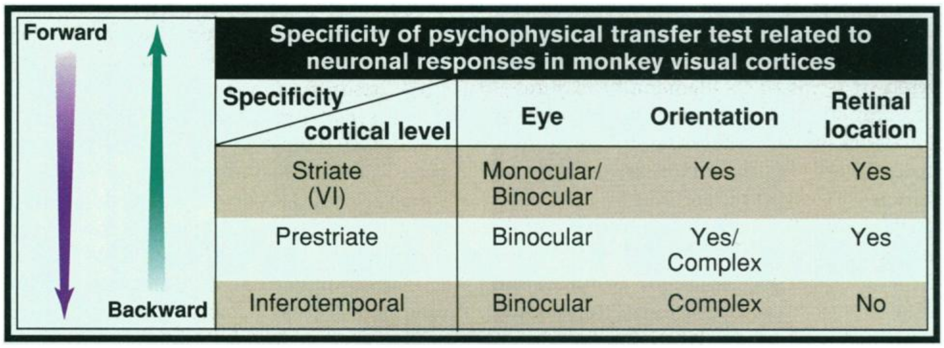
curacy was 80%, but when they formed images, accuracy was only 65% (13). Moving the image away from the target almost eliminated the effect (location specificity); however, effects observed when the subjects formed images of vertical lines were comparable to those observed when the subjects formed images of horizontal lines (no orientation specificity). Farah (14) showed that forming an image of a shape (a letter) enhanced detection of that shape, only for the same letter, and only if the image was in the location in which the shape appeared. This location specificity, however, may have originated from increased expectation. It was also demonstrated that the McCullough effect (orientation-specific color aftereffect) could be induced via imagery. However, the imagery effect was transferred from one eye to the other, whereas the actual McCullough effect is not (15). Thus, involvement of early visual areas, especially V1, in visual imagery has not been clearly ascertained.

Ishai and Sagi (5) have now investigated the effect of imagery on visual perception by comparing subjects' abilities to detect a computer-generated "Gabor target" under a perceptual condition, in which the target is flanked by two peripheral Gabor masks, and an imagery condition, in which the subjects imagined the absent masks. In the perceptual condition, as in previous psychophysical experiments, there was a facilitatory interaction between spatial channels, which was specific to the stimulated eye, orientation, spatial frequency, and retinal location of the stimulus (16). Each of these same facilitatory characteristics was found in the imagery condition. Such parallels indicate that the mental images can be interfaced with perceptual representations at early stages of visual information processing.

At the same time, the results obtained by Ishai and Sagi (5) point to the existence of a new class of visual memory that has an "iconic" nature but is maintained for as long as 5 minutes. From the fact that the imagery facilitation lasted for about 5 minutes after the subject looked at the masks with the targeted eye, the authors conclude that there is an iconic memory of the masks in visual areas that can be reactivated by higher level processing (imagining) for several minutes. What is the neural substrate for this memory? Is it related to the short-term memory mechanism that encodes high-level features? Is the capacity of this memory limited? How do higher level processes access this memory?

This finding is another example of neuronal plasticity at very early stages of visual processing, where processing modules in adulthood have been considered to be hard-wired and task-independent. Converging evidence from studies on the psychophysics of visual texture segmentation learning (17) and electrophysiological topography mapping after tactile or tonal discrimination training (18) has demonstrated the involvement of primary sensory cells in a certain type of perceptual learning that develops slowly but is retained for years. As we search for localizations and neural mechanisms of memory of various time courses, we must not ignore the possible participation of and modulation by low-level modules. This holds true to an even greater extent for the mechanisms of imagery.



Specificity of psychophysical transfer test related to neuronal responses in monkey visual cortices

Specificity / cortical level	Eye	Orientation	Retinal location
Striate (VI)	Monocular/ Binocular	Yes	Yes
Prestriate	Binocular	Yes/ Complex	Yes
Inferotemporal	Binocular	Complex	No

Which brain areas are used in imagery? The transfer test is based on neuronal response specificity in various visual areas. If the imagery experience is specific to the stimulated eye, as well as to orientation and retinal location of the stimulus, it strongly suggests involvement of the striate cortex.

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