

# Chapter 2

## Visual Mental Imagery

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**Abstract** Visual mental imagery is an important aspect of our mental life. Without it, we would be unable to reactivate and transform visual representations of objects and events that are not unfolding in front of us. Until recently, the investigation of visual mental imagery relied on subjective and behavioral paradigms. These paradigms typically only enabled us to examine the end product of visual mental imagery processes, making it impossible to resolve empirical questions such as which representations are shared by visual perception and imagery. This chapter illustrates how the conceptual and methodological frameworks introduced by cognitive neuroscience in the last three decades have enabled researchers to address these kinds of questions by leveraging our knowledge about the neuroscience of the primate visual system.

**Keywords** Cognitive neuroscience • Visual mental imagery • Visual perception • Top-down • Bottom-up • Striate cortex • Extrastriate cortex • Prefrontal cortex

### 2.1 Background

During most of our waking life, our visual systems extract information from the visual world to ensure smooth interactions with the environment. This is possible because, during perception, our brains construct and maintain internal representations of objects and events unfolding in the visual world. However, these internal

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representations can also be reactivated during visual mental imagery without the aid of any external visual stimuli, such as when we find ourselves visualizing people's faces from last weekend's party to figure out if a certain acquaintance was present or not. Mental imagery can take place in all modalities (visual, auditory, olfactory, and so on), but here the focus will be on visual mental imagery of shapes, probably the most well-studied modality and type of mental imagery.

To answer questions about the visual appearance of an object that is not in front of our eyes, such as "What shape is a pelican's beak?", one typically visualizes a pelican and then "zooms in" on parts of the image containing the animal's beak to assess its shape. Reactivating and inspecting internal representations in the absence of a corresponding external stimulus is one of the core aspects of mental imagery. Using the language of cognitive science, visual mental imagery involves reactivating visual representations in long-term memory and using them to construct representations in working memory; these representation can then undergo further processing, for example, by reinterpreting or transforming them (Kosslyn et al. 2001, 2006).

Although we have talked about reactivating internal representations, visual mental imagery entails more than the simple reactivation of visual representations of previously experienced events: People not only construct images using fragmentary information stored in long-term memory, but in many cases, they also can use visual mental imagery to extract new information (i.e., information that had not been encoded explicitly) by parsing and reassembling visual images in new ways (Finke et al. 1989). This constructive and combinatorial aspect of visual mental imagery is why it plays a key role in numerous domains, such as engineering and mathematics, and is important for numerous cognitive skills, such as reasoning (e.g., Blajenkova et al. 2006).

## 2.2 Visual Mental Imagery and Cognitive Neuroscience

Two general classes of theories have been put forward to account for the details of the internal organization of visual mental images. Depictive theories embrace the view that visual mental images are distinct types of mental representations and function to depict visual objects and scenes (Kosslyn 1980; Shepard and Cooper 1982). Under this view, visual images make explicit shape and spatial relations by virtue of their internal structure: Distances among parts in the image correspond to distances among parts of the stimulus they represent. In contrast, non-depictive theories support the view that visual mental image representations are not different from the type of "propositional" representations used for general-purpose thought (Pylyshyn 1981). According to this view, the pictorial aspects of imagery available to introspection are epiphenomenal and play no role in information processing. During the "imagery debate" of the late 1970s and early 1980s, behavioral evidence was found both in favor and against both theories. As the debate unfolded, it became more and more clear that these questions about internal representations could not be answered conclusively, even with the novel empirical methods of cognitive psychology. A clever theoretical paper (Anderson 1978) demonstrated formally that behavioral results from a class of visual imagery paradigms could be interpreted both

within a depictive and a propositional account of visual imagery simply by modifying the processing assumptions. Anderson showed that, for any theory defined by a set of assumptions about depictive representations and processes operating on them, it was possible to generate a second theory defined by an alternative set of assumptions about propositional representations and processes that could mimic the first theory. This finding illustrated that behavioral results alone were not strong enough to support conclusive inferences about specific representation–process pairs: Such inferences could only be made by using additional findings, such as those provided by neuroscientific research. This is one of the main reasons why evidence from neuroscience is crucial to constraining and understanding the details of how visual mental imagery works.

Behavioral studies showing parallels between visual mental imagery and perception provided an obvious starting point for using neuroscientific data (Kosslyn 1980). The logic here is that if visual mental imagery recruits the same processes engaged by visual perception, then the neural structures that support vision should also support visual mental imagery (Kosslyn 1994). Using this logic, one could leverage the large body of preexisting neuroscientific knowledge about the visual system of nonhuman animals to understand visual mental imagery. Until recently, information about the neurophysiological organization of the human visual system was mostly indirect and came from studies in nonhuman primates, under the assumption of homology among different species. Recent advances in noninvasive neuroimaging and brain stimulation techniques and paradigms have made it possible to test this assumption directly by enabling cognitive neuroscientists to study the neural basis of vision in humans. Cognitive neuroscience techniques such as positron emission tomography (PET), functional magnetic resonance imaging (fMRI), and transcranial magnetic stimulation (TMS) have provided evidence complementary to more traditional observations in brain-damaged patients and confirmed that the organization of the visual system in human and nonhuman primates, especially that of early visual areas, is quite similar (e.g., Sereno and Tootell 2005). These same techniques have also enabled the study of visual mental imagery noninvasively in humans.

In the following sections, we will review and discuss some of the classic and recent empirical literature on the cognitive neuroscience of visual mental imagery, focusing on the topic of the extent to which visual mental imagery and visual perception recruit similar neural resources.

## **2.3 Shared Neural Systems in Visual Mental Imagery and Perception**

Do visual mental imagery and perception recruit similar brain regions and neural processes, as many cognitive studies have suggested? The handful of neuroimaging studies that have quantified the similarity between visual mental imagery and perception across the entire brain have found that there is substantial overlap (more than 90%) between brain regions recruited by visual perception and visual mental imagery

(e.g., Ganis et al. 2004). The vast majority of the neuroimaging literature, however, has focused on the qualitative question of whether, and under what circumstances, visual mental imagery recruits visual areas also recruited during visual perception. Next, we will review and discuss the results of some of these studies.

## 2.4 The Role of Early Visual Cortex in Visual Mental Imagery

Numerous studies have focused on the specific issue of whether visual mental imagery recruits early visual cortical areas engaged during visual perception. To understand why this question is key, it is necessary to review some basic principles of the organization of the primate visual system and to consider how these principles may relate to depictive theories of visual mental imagery.

The primate visual system is organized as a loose hierarchy of parallel processing streams (Felleman and Van Essen 1991), with early visual areas (areas V1 and V2, also known as areas 17 and 18, respectively) at the lowest level in the hierarchy. Area V1, in particular, is the first cortical region that receives visual information from subcortical nuclei (mostly from the lateral geniculate nucleus), which in turn receive input from the retina. V1 and V2 feed information to two parallel streams in the hierarchy, the ventral stream, which encompasses ventrolateral areas in the occipital and temporal lobes, and the dorsal stream, which encompasses dorsal areas in the occipital and parietal lobes (Desimone and Ungerleider 1989). These two streams have been implicated in two different sets of functions: The ventral stream subserves predominantly object vision (Desimone and Ungerleider 1989; Haxby et al. 1991; Mishkin et al. 1983; Ungerleider and Mishkin 1982), whereas the dorsal stream subserves primarily spatial vision and action (Goodale et al. 2004; Ungerleider and Mishkin 1982).

A defining attribute of early visual cortical areas is that they have a topographic organization in which nearby points in the visual space (which is projected onto the retina) are mapped onto nearby points on the cortical mantle. Thus, topographically organized areas employ distance on the cortex to represent distance in the visual space. This retinotopic representation of the visual space is defined by two dimensions in polar coordinates, eccentricity and polar angle. The eccentricity of a point is its distance from the fovea (the central, high-resolution, region of the visual field), whereas the polar angle is the angle between a line connecting the point to the center of the visual field and a horizontal line. Polar angle and eccentricity are represented in V1 along roughly orthogonal directions. As one ascends the visual hierarchy, this retinotopic organization becomes less and less precise (Felleman and Van Essen 1991; Fox et al. 1986; Heeger 1999; Sereno et al. 1995; Tootell et al. 1998). The receptive fields, that is, the region of the visual field “seen” by a neuron, are very small in area V1 and become larger and larger as one moves toward inferotemporal cortex. At the same time, the visual attributes to which neurons are selective become more and more complex in later visual areas. Neurons in area V1 are maximally driven by small bars at very specific spatial locations, but neurons in inferotemporal

cortex are maximally driven by specific combinations of shape, texture, and color appearing almost anywhere in the visual field (Fujita et al. 1992; Lehky et al. 2011; Miyashita and Chang 1988; Tanaka 1996; Tanaka et al. 1991). Because of this organization, the topographic code used in area V1 makes explicit the spatial layout of a stimulus, whereas the distributed code used in inferotemporal cortex makes explicit similarities between complex features of object classes (Lehky et al. 2011; Tanaka 1996).

Another key feature of the organization of the primate visual system is that visual areas that are connected via feedforward fibers in the hierarchy are usually also connected via corresponding feedback fibers, although with different distributional properties (Barone et al. 2000; Budd 1998; Felleman and Van Essen 1991; Rockland and Pandya 1979; Salin and Bullier 1995). These feedback connections provide a mechanism by which later visual areas, such as those in the inferotemporal cortex, can potentially modulate activity in neurons in early visual areas.

These organizational aspects of the primate visual system, and others not covered here, have guided neurally inspired depictive theories of visual mental imagery (cf. Kosslyn 1994). The key idea is that the precise spatial layout of objects is stored only implicitly in a distributed code in the inferotemporal cortex and that this layout can only be made explicit during visual mental imagery by recreating the corresponding pattern of retinotopic activation in early visual areas via feedback connections (Kosslyn 1994). Since neurally grounded depictive theories posit a key role for retinotopically organized visual areas in visual mental imagery, evidence that such brain areas are used during visual mental imagery would provide strong support for these theories.

## 2.5 The Functional Role Played by the Retinotopic Organization of Early Visual Cortex

Before discussing specific studies, it is important to counter two arguments often made against neurally inspired depictive theories of visual mental imagery. The first argument is that the retinotopic organization of early visual cortex is epiphenomenal and serves no functional role for visual imagery, and possibly even for visual perception. According to this argument, the relationship between retinotopic organization and visual mental imagery is accidental (Pylyshyn 2002) and akin to that between hard drive access processes on a computer and the LED that signals such access: Although the state of the LED correlates perfectly with hard drive access, it has no functional role in the working of the computer, and the computer would keep working properly without the LED. This criticism is refuted by evidence that the topographic organization in early visual cortex has a functional role in visual processing. First, damage to discrete portions of early visual areas produce visual scotomas (i.e., blind spots) in corresponding parts of the visual field, and the extent of the damage is systematically related to the size of the scotoma (e.g., Chiang et al. 2004). Second, TMS stimulation of discrete portions of early visual cortex can produce

faint visual sensations known as phosphenes in the corresponding parts of the visual field (Elkin-Frankston et al. 2011; Siniatchkin et al. 2011). Asking people to draw the perceived phosphenes during TMS stimulation enables researchers to determine the relationship between phosphene properties (e.g., their location, shape, and color) and stimulation parameters (e.g., TMS location and intensity). For instance, Kammer and collaborators were able to induce predictable shifts in the perceived location of phosphenes by shifting the TMS coil systematically over the occipital lobe in neurologically normal subjects (e.g., Kammer et al. 2005b). At higher TMS intensities, they were also able to produce scotomas (identified by asking people to detect small squares at various locations in the visual field and by determining at what locations detection rates were reduced) within the same regions of the visual field (e.g., Kammer et al. 2005a, b).

The second argument is that this retinotopic organization is not a geometrically accurate representation of the visual field, and so it cannot possibly provide useful depictive information about the visual world. For example, the same visual stimulus has a much larger cortical representation when it falls on the fovea than on more peripheral parts of the visual field because of the cortical magnification distortion (Sereno et al. 1995). Furthermore, in addition to deformations due to eccentricity, there are discontinuities in the visual maps, for instance, along the representation of the horizontal meridian in V2 and later areas (Felleman and Van Essen 1991). This is not a critical problem for neurally based depictive theories of visual mental imagery because early visual cortical areas are only one node in a large network (Felleman and Van Essen 1991) and the information they represent is decoded by other brain areas.

## 2.6 Visual Mental Imagery and Early Visual Cortex: Brain Imaging Findings

Two original studies using PET revealed that area V1 is recruited during visual mental imagery and that the pattern of activation is as predicted by the known retinotopic organization of this area. The first study (Kosslyn et al. 1993), leveraged the systematic representation of eccentricity in area V1. Blood flow was monitored with PET, while participants visualized capital letters at either a very small size (as small as they could visualize them) or at a very large size (as large as they could, while still being able to visualize the entire letter). The participants were asked to maintain the image for four seconds and then to make a judgment about the geometric properties of the letter (e.g., whether it had any straight lines). The rationale was that, if visual mental imagery uses topographical representations in area V1, then large visual images should engage parts of area V1 that are involved in representing more eccentric regions of the visual field located in increasingly anterior regions along the calcarine sulcus. Consistent with this prediction and with the retinotopic organization of area V1, results showed stronger activation in anterior parts of area V1 when participants visualized large letters and in more posterior parts when they visualized small letters. The second study used a similar logic but with different experimental stimuli (Kosslyn et al. 1995). During the PET session, participants

visualized line drawings of objects they had studied in advance within boxes of different sizes: small, medium, and large. To make sure participants were actually carrying out visual mental imagery, the task involved performing various visual judgments on the images (e.g., whether the left side of the pictures they had studied was higher than the right side). The results, again, nicely confirmed the predictions based on the representation of eccentricity in V1.

These initial findings have been replicated and extended in fMRI studies conducted in the last decade, overcoming the low spatial resolution of PET. An event-related fMRI study investigated whether visual mental imagery elicits activation consistent with the topographic representation of polar angle in early visual cortex (Klein et al. 2004). In this study, six participants either looked at bow-tie stimuli (perception) or visualized them (visual mental imagery) in independent blocks of trials. The stimuli were either vertical or horizontal, and each orientation was associated with a different auditory tone to indicate which stimulus to visualize during visual mental imagery. During the perception condition, participants pressed a key to report the orientation of the bow-tie stimuli, whereas during the visual mental imagery condition, they pressed a key as soon as they had formed a vivid image of the bow-tie stimulus indicated by the auditory tone at the beginning of each trial. Results revealed significant activation in area V1 in five out of six participants when visual imagery (eyes closed) was contrasted with a baseline defined by BOLD activation during the periods between trials. However, this comparison revealed no topographic differences between visual mental imagery of horizontal versus vertical bow-tie stimuli. This absence of retinotopic effects was hypothesized to be due to a large, nonspecific activation in early visual cortex in the task, possibly due to visual attention. A follow-up analysis tested this hypothesis and eliminated such nonspecific activation by contrasting activation between the horizontal and vertical bow-tie stimuli directly. And in fact, this direct comparison showed the expected retinotopic differences in V1 and V2. The effects found in the study, however, were rather weak (the significance threshold for the contrast was set at 0.01, uncorrected, with four voxel clusters), with only four out of six participants showing a significant overlap between voxels active during visual imagery and perception in the corresponding conditions. The individual variability of the results is consistent with other findings about individual differences in brain activation during visual mental imagery (e.g., Ganis et al. 2005; Kosslyn et al. 1996).

Another study employed standard retinotopic mapping methods (Serenio et al. 1995) to determine whether visual mental imagery elicits activation consistent with the representation of polar angle in visual cortex (Slotnick et al. 2005). The stimuli were rotating checkerboard “bow-tie” shapes. During the visual perception condition, six participants fixated the center of the display and pressed a key every time a small red square was flashed inside the revolving bow tie. During the visual mental imagery condition, the stimulus was made up of two thin arcs, outlining the outer edges of the bow tie. The task was to visualize the rest of the pattern and, again, to press a key when a small red square was flashed inside the region that the bow tie (now only visualized) would occupy. There was also a control attention condition (within participant), during which all parameters were identical to the imagery condition with the difference that participants were not instructed to create visual



mental images, but only to wait for the red square and to press a key depending on whether it was presented to the left or to the right of fixation. Results for the imagery condition showed small activation foci in V1 that were not observed in the control attention conditions in three out of six participants. Activation in extrastriate regions was observed in four out of six participants. Although there was—for some participants—topographically organized activation that was not found in the control attention condition described earlier, the majority of the imagery-induced activation overlapped with activation induced by visual attention, which could indicate that spatial attention may function as a scaffolding for visual imagery.

A more recent study (Thirion et al. 2006) used machine learning methods and an “inverse retinotopy” approach to extract information from single fMRI trials during visual perception and visual mental imagery. This approach inverts the mapping between visual space and visual cortex to estimate the actual visual stimulus that would be most likely to have generated a given pattern of activation in early visual cortex. During the perception condition, nine participants looked at patterns of rotating Gabor patches (there were a total of six possible patterns), whereas during the visual mental imagery condition, they chose one of the six patterns and visualized it to the left or right of a fixation point, depending on the direction of a probe arrow that was presented on each trial. The results showed an average of over 80% classification rates for the perception conditions (chance was 1/6, 16.7%, given that there were six possible patterns). All hemispheres examined showed robust classification performance (between 70 and 96%, using a leave-one-out classification method). Most of the voxels that contributed to successful classification were located in area V1 (50–60%), followed by area V2 (20%), which is not surprising, given the topographic characteristics of these areas discussed earlier. The results were much weaker for the visual mental imagery condition: With averaged data, the imagined pattern could be correctly predicted only using data from 5 hemispheres out of 16, and even these cases were rather marginal. Low generalization to imagery was also found for trial-specific analyses, (min 38%, max 67%, using a leave-one-out classification scheme and a Bonferroni correction for multiple comparisons). Additional studies on this issue will be reviewed in Chap. 15.

Thus, these results provide evidence in favor of the claim that mental images of shapes sometimes activate topographically organized areas in early visual cortex. However, the signals observed are much weaker than for visual perception, and usually they are difficult to detect in individual participants.

## **2.7 V1 Recruitment During Visual Mental Imagery: Potential Inconsistencies in the Neuroimaging Literature**

Although numerous studies have shown early visual cortex engagement during visual mental imagery, some studies have failed to observe such engagement (Kosslyn and Thompson 2003). Since many paradigms and methods were used in different studies, one way to try to figure out which factors may be reliably associated with activation in early visual cortex during visual mental imagery is by carrying



out a meta-analysis of the literature. In one meta-analysis of this type (Kosslyn and Thompson 2003), three theories were described that could account for the observed activation in early visual cortex (areas V1 or V2) during visual mental imagery. The first theory, referred to as “perceptual anticipation theory,” was the depictive theory of visual mental imagery described earlier (Kosslyn et al. 2006). The second theory, “propositional theory,” was the type of non-depictive theory put forward by Pylyshyn (1981), which predicts no activation in early visual cortex during visual mental imagery, and it postulates that activation in this area, if observed, is purely artifactual. The third theory, referred to as “methodological factors theory,” postulates that activation in early visual cortex is always present during visual mental imagery, but is not detected in some studies because of methodological issues.

The meta-analysis classified the visual mental imagery tasks used in 59 neuroimaging studies of visual mental imagery according to six variables: use of high-resolution details, use of shape judgments (vs. spatial judgments), use of exemplars (vs. prototypes), number of participants, neuroimaging technique, and use of a resting baseline (vs. a more controlled baseline in which participants perform a well-defined task not involving visual mental imagery, rather than an uncontrolled resting task). Perceptual anticipation theory predicts early visual cortex activation when using high-resolution details and shape judgments of specific exemplars. In contrast, propositional theory predicts that visual mental imagery never engages early visual cortex. According to this theory, any activation observed in early visual cortex during visual mental imagery is artifactual and caused by factors such as small numbers of participants, less powerful techniques, and a resting baseline (all factors that increase the chance of false positives). The methodological factors theory predicts the opposite, namely, that activation in early visual cortex is present regardless of the type of visual mental imagery. This theory also predicts that the only factors that determine whether this activation will be detected or not are methodological. For instance, (real) activation in early visual cortex would be more likely to be detected by using larger numbers of participants. Although these factors also apply to perceptual anticipation theory, methodological factors theory postulates these are the *only* factors that would make a difference.

A theory-driven regression analysis revealed that early visual cortex activation was predicted by four variables, two associated with perceptual anticipation theory (use of high-resolution details and shape judgments) and two with methodological factors theory (use of more powerful brain imaging technique and non-resting baseline). The non-resting baseline finding is consistent with findings that resting baselines (e.g., simple fixation) can cause activation increases in early visual cortex, thereby canceling out the small increases that may occur during visual mental imagery (Kosslyn et al. 1995).

An exploratory analysis was also conducted (Kosslyn and Thompson 2003) in which the presence or absence of early visual cortex activation across studies was correlated with 15 additional variables (for a total of 21). Results showed that 9 out of these 21 variables were correlated with early visual cortex activation across studies. Since some of these variables were correlated with each other, a forward stepwise logistic regression on these results showed that the use of high-resolution details and shape judgments in the task, and the neuroimaging technique employed reliably

predicted activation in early visual cortex, consistent with the results of the theory-driven regression analysis.

The finding that high-resolution details are key for recruiting early visual areas makes sense because of the high-resolution topographic organization of these areas. Later areas, such as V4, have much coarser retinotopic organization than V1 and V2, and so they may not be able to support tasks requiring the visualization of fine details. Furthermore, the importance of using shape judgments (as opposed to spatial ones) can be understood by remembering that visual memories about shapes are stored in inferotemporal cortex by means of a distributed code (Tanaka 1996; Lehky, et al. 2011) that does not make spatial layout explicit; this spatial layout can be made explicit by reconstructing the image in early visual cortex. In contrast, spatial judgments may be stored already in a suitable code in retinotopically organized areas in the parietal cortex (Saygin and Sereno 2008; Sereno et al. 2001), and so they may not require early visual cortex.

In sum, these findings indicate that the apparent inconsistencies in the neuroimaging literature about early visual cortex activation during visual mental imagery may not be due to random factors, but to systematic variables that can be manipulated.

## 2.8 Visual Mental Imagery and Early Visual Cortex: Findings in Neurological Patients

If early visual cortex is indeed required for carrying out at least some forms of visual mental imagery (those involving high-resolution images of shapes, as just discussed), then patients with damage to this part of the cortex should be impaired at these types of visual mental imagery. Neuroimaging measures activation in a brain region during a given task, but it leaves open the possibility that such activation is only *correlated* with the performance of the task, but plays no functional role.

As mentioned earlier, unilateral focal damage to V1 produces scotomas in small parts of the visual field that are represented by the damaged cortical tissue. If the damaged region is large and encompasses both hemispheres (for instance, because of posterior cerebral artery infarct), then the result is cortical blindness. If early visual cortex is necessary for visual mental imagery, then such damage should impair some forms of mental imagery.

Although this logic seems straightforward, there are important limitations in the type of inferences that can be made from data from neurological patients. First, one cannot be sure that brain tissue that looks normal is functionally normal because some abnormalities may not be detectable with the technique employed (e.g., these abnormalities may be at a scale that is smaller than the voxel size used). Second, brain damage is not a variable that can be manipulated experimentally because we cannot control the location or size of the lesion and large lesions can affect nearby regions that nonetheless carry out different functions, potentially leading to the incorrect inference that these functions are related. Third, the brain is not a static organ, and damage can trigger compensatory mechanisms

(e.g., Barbay et al. 2006; Dancause et al. 2005) such as when other areas attempt to compensate for lost functions, further complicating the interpretation of the findings. Fourth, in most published patient studies, performance on visual mental imagery tasks has not been assessed rigorously. For example, the time patients take to respond is rarely measured. Finally, the literature consists largely of single-case studies that cannot be replicated in principle because patients may not be available to other groups or because the specific impairment may be short lived. This is clearly a major methodological issue that can only be resolved by pooling resources and increased sharing of patients among interested groups.

Despite these limitations, cases have been described in which visual mental imagery is impaired as a result of damage to the occipital cortex. Patients with hemianopia (i.e., blindness in one-half of the visual field, following damage to one cerebral hemisphere) are particularly relevant because it is possible to administer a visual mental imagery task in the functioning hemifield and compare the results with the same task in the impaired hemifield within the same individual. In an elegant study using this logic, eight hemianopic participants were tested on a mental scanning task, an objective test of visual mental imagery, which is rare in the assessment of visual mental imagery in patients (Butter et al. 1997). Participants were shown a pattern of four dots, and subsequently, after the pattern had disappeared, they were asked to decide whether an arrow pointed at a location previously occupied by one of the dots. Compared to healthy controls, patients showed the expected pattern: lower accuracy when the arrow pointed at a dot in the hemifield that was affected compared to when it pointed at a dot in the intact hemifield. Several control conditions ruled out potential confounds such as that the patients were unable to see the dot pattern or the arrow to begin with. A limitation of this study is that only computed tomography scans were performed, and only on a subset of the patients, which makes it impossible to know the extent to which the brain damage affected early visual cortex. Other limitations are discussed in Chap. 13, which also reports recent evidence at odds with the findings by Butter and collaborators, a clear indication that more systematic research on this issue is needed. The findings from the study by Butter and collaborators dovetailed with those obtained in an earlier study by Farah and collaborators in a single patient after removal of the occipital lobe in one hemisphere (Farah et al. 1992): In this patient, the horizontal extent of visual images was reduced in half after the surgery, whereas the vertical extent was normal and consistent with the fact that the representation of half of the horizontal meridian was lost.

There are also cases in the literature that may seem to contradict neurally inspired depictive theories. In some of these cases, widespread damage to early visual cortex, including V1, results in cortical blindness but does not seem to impair visual mental imagery. One of the most striking cases is that of a young woman who became cortically blind after a stroke that damaged her primary visual cortex bilaterally (Chatterjee and Southwood 1995). Despite her blindness, apparently she could carry out many visual mental imagery tasks including some that involved judging the shape of capital letters or common animals or drawing common objects from memory. She also reported using visual mental imagery during her high school studies (which she completed after becoming cortically blind). There have been other cases of cortical blindness and apparent sparing of visual mental imagery abilities

(Goldenberg et al. 1995), but the tests used to assess visual mental imagery often have been rather crude (Bartolomeo 2002).

Cases such as these, however, do not constitute strong evidence against the hypothesis that V1 is needed to perform at least certain types of visual mental imagery for reasons that go beyond the methodological issues summarized earlier (see also Chap. 13). First of all, especially with the low-resolution brain scans used in the past, it is difficult to rule out that spared parts of early visual cortex were still functioning normally in these patients. This is an important point because brain imaging studies of visual mental imagery usually show activation in only small portions of V1 (e.g., Slotnick, et al. 2005) relative to visual perception conditions. Second, many of the tasks used to test visual imagery may have not been sufficiently sensitive or may have not recruited V1 to begin with. For example, imagery questions such as whether the body of a snake has curved parts may be answered by using information stored in semantic memory and may not require high-resolution imagery. In addition, imagery tasks involving stimuli with an overlearned motor component, such as drawing letters or drawing simple objects, may be carried out using information stored in the motor system (e.g., James and Gauthier 2006). Third, many visual mental imagery tasks may be carried out by using late visual areas or even areas that are not involved in vision per se. For example, as discussed earlier, if a particular task does not require discriminating high-resolution details in the visual image, then V1 may not be necessary and later areas may be able to support adequate performance on the task. In such a task, damage to V1 should not disrupt the ability to perform imagery tasks.

Finally, how can we explain that some patients who are cortically blind, such as the patient described by Chatterjee and Southwood, claim to have vivid mental imagery? Critically, these types of introspective reports do not prove that these patients can actually use visual mental images in memory and reasoning any more than the introspective feeling one has of being able to perceive all details of a visual scene proves that we actually perceive them; in fact, there is evidence that we perceive only few details of the visual world at any time (Rensink 2002). This is because the subjective experience of having a vivid mental image may reflect only in part activation in visual cortex and is probably the product of processes taking place in many other brain areas.

## 2.9 Visual Mental Imagery and Early Visual Cortex: Virtual Lesion Findings

One of the few techniques for testing the functional role of a brain region (in a particular task) is TMS. With this technique, a coil is used to deliver magnetic pulses to a targeted brain region, creating slight disruptions of neural activity for a short period (from milliseconds with single-pulse TMS to a few minutes with repetitive TMS). The advantages of TMS are that the stimulation can be controlled precisely, the disruption is reversible, the impairment is too short lived to allow compensatory

phenomena to take place, and one can easily conduct studies on large groups of people instead of having to rely on single cases. More details about using this technique to study mental imagery are provided in Chap. 15. Perhaps the most convincing TMS study showing that early visual cortex is necessary for both visual perception and high-resolution visual mental imagery (Kosslyn et al. 1999) used low-frequency repetitive TMS, which is known to decrease cortical excitability for several minutes after stimulation (Muellbacher et al. 2000; Siebner et al. 2000). In the perception condition, five participants were asked to compare attributes of four sets of black-and-white stripes, arranged into four quadrants. The stripes varied in length, width, spacing, and orientation. In the imagery condition, the task was identical (e.g., the participants compared the relative lengths of stripes in two specific quadrants), but the same participants had to visualize the visual pattern array. A parallel PET study had shown that visual mental imagery of these same stimuli elicited activation in early visual areas. Stimulation was delivered either to these early visual areas by targeting the occipital pole (real-TMS condition) or directing the coil away from the brain (sham-TMS control condition). Results showed that real TMS (compared to sham TMS) slowed down responses in both the perception and imagery conditions, supporting the idea that early visual cortex is necessary to perform visual mental imagery.

## **2.10 Visual Mental Imagery and Late Visual Areas in the Ventral Stream**

Early visual areas provide input to visual areas in the ventral stream (which processes object properties such as shape, texture, and color). Studies in neuroimaging and neurological patients have shown that there is spatial segregation in the representation of at least some object classes (Downing et al. 2006; Kanwisher and Yovel 2006) but also that visual objects are represented in a spatially distributed manner in these cortical areas (Haxby et al. 2001). For example, some patches of cortex in the lateral fusiform gyrus are selective for images of faces, relative to other object categories (Kanwisher and Yovel 2006), and, similarly, patches of cortex in the medial fusiform and parahippocampal gyri respond more strongly to pictures of buildings than to images of other objects (Downing et al. 2006). Next, we will review briefly the empirical evidence that this organization also characterizes the system used during visual mental imagery of objects.

## **2.11 Late Visual Areas and Visual Mental Imagery: Brain Imaging Findings**

Although the causes and function of the spatial segregation in the ventral stream (Hasson et al. 2003; Levy et al. 2004) are still under debate, this organization can be exploited to further address the issue of the similarity between the processes and

representations recruited during vision and visual mental imagery. Accordingly, several studies have used this logic by comparing the spatial pattern of brain activation in ventrotemporal cortex during visual identification of objects and visual mental imagery of these same objects (Ishai et al. 2002; 2000; Mechelli et al. 2004; O'Craven and Kanwisher 2000). In the first of such studies, eight participants recognized pictures of familiar faces and buildings or they visualized them (O'Craven and Kanwisher 2000). During the perception blocks, a contrast between stimulus category conditions revealed a clear segregation in ventrotemporal cortex between activation elicited by faces and buildings. This pattern was paralleled by the results in the imagery condition, but activation was much weaker than that observed during perception (50% weaker, on average) and encompassed much smaller regions (17% for faces and 39% for buildings, relative to the number of voxels active in the corresponding perception conditions). Furthermore, almost all the voxels that were active during visual mental imagery were included in the regions that were active during the corresponding perception condition (84% for faces and 92% for buildings). Finally, in the visual mental imagery condition, there was considerable individual variability. For instance, only four participants out of eight showed face-specific activation during imagery. This is consistent with the individual variability observed in many of the V1 activation studies of visual mental imagery described earlier (e.g., Thirion et al. 2006). In a similar study (Ishai et al. 2000), nine participants were tested in visual perception and imagery conditions. During the main perception condition, participants passively viewed pictures of faces, houses, and chairs in independent blocks. During the main visual mental imagery condition, they visualized familiar faces, houses, or chairs while looking at a gray background. Perception and imagery baseline conditions involved passive viewing of scrambled versions of the pictures used in the perception condition and the same gray background used in the imagery condition, respectively. After removing the respective baselines and comparing the three stimulus types, researchers found several regions in the ventral stream that showed differential responses to pictures of faces, houses, and chairs. Critically, about 15% of voxels in these regions showed a similar pattern during visual mental imagery. This confirms the finding by O'Craven and Kanwisher (2000) that only relatively small subsets of voxels in regions that respond differentially during visual perception show the same pattern during imagery. Interestingly, activation during visual mental imagery (compared to the control condition) was also found in parietal and frontal regions, but no corresponding activation was observed during the perception condition, probably reflecting the stronger engagement of top-down processes during visual mental imagery than perception.

A follow-up fMRI study contrasted visual perception and imagery of famous faces (Ishai et al. 2002). In the perception condition, nine participants were shown pictures of famous faces, whereas in the baseline perception condition, participants saw scrambled pictures of faces. In the visual mental imagery conditions, participants visualized famous faces against a blank screen, following a written probe name. Participants were trained on half the faces immediately prior to the study,

whereas they relied on their preexisting long-term memories for the other half. Furthermore, for half the blocks (attention condition), they made a judgment on a feature of each face (e.g., whether it had a large nose), whereas no task was used for the other half. During the baseline imagery condition, participants saw letter strings and passively viewed a blank screen.

Results confirmed previous findings by showing activation in the lateral fusiform gyrus during face imagery in a subset of voxels (about 25%) active during face perception. This activation was stronger for faces that had been studied just before the scan. Attention modulated activation in regions outside the ventral stream: the intraparietal sulcus and the inferior frontal gyrus. A more recent study reanalyzed a subset of these data, trying to understand differences in the connectivity of category-specific late visual areas within a large-scale network during visual perception and imagery (Mechelli et al. 2004). Results showed that functional connectivity to late visual areas was strongest from early visual areas during perception, but strongest from frontal and parietal regions during visual mental imagery. This indicates that the functional role of the same late visual areas changes depending on whether the task is visual perception or imagery. Additional studies on this topic are described in Chap. 15.

One potential explanation for the weaker and less reliable signals and smaller foci of activation during imagery than perception is that the feedback signals generated during visual mental imagery are less strong than the feedforward signals generated during visual perception. This idea is consistent with the generally more diffuse organization of feedback projections (Budd 1998), which may suggest that fewer neurons are driven by such signals. After all, introspectively, visual mental images are much “fainter” than percepts, which is probably one way that the visual system can distinguish percepts from visual images. Another possible explanation, not mutually exclusive with the first, is that some of the regions activated in ventral cortex only during the perception conditions may reflect various perceptual processes—such as feature analysis and high-level grouping of visual features—that are not fully engaged during imagery.

An important question is whether these similarities between visual perception and imagery in late visual cortex hold at the single-neuron level. The only technique that enables us to address this question involves recording the intracranial electroencephalogram. Patients with epilepsy resistant to pharmacological treatment may decide to undergo surgical resection of the affected areas, and in some cases, chronic electrodes are implanted in their brain to measure brain activity during seizures, allowing the surgeon to determine the location of affected areas. Between seizures, researchers can collect data from these patients in experimental paradigms. One such study compared visual perception and imagery, recording activity from 276 single neurons (from a total of nine patients) in the medial temporal lobe, including the parahippocampal cortex (Kreiman et al. 2000). Results showed that a small subset of neurons responded to both visual stimuli and visual mental imagery of the same stimuli. Furthermore, the pattern of selectivity was very similar in the two cases, indicating that the similarities seen at the macroscopic level in these regions are also present at the single-neuron level.



## 2.12 Late Visual Areas: Findings in Neurological Patients

The neuroimaging data just discussed are generally consistent with data from patients with damage to late visual areas in the ventral stream (Ganis et al. 2003). Given the relative spatial segregation in the ventral stream of visual object representations, one could predict that some neurological patients should exhibit problems visualizing certain classes of visual stimuli but not others, depending on the site of the damage. In addition, because of the similar spatial segregation for visual mental imagery and visual perception, patients should show parallels in the patterns of impairment during visual perception and visual mental imagery. As expected, patients have been described with domain-specific deficits in visual perception and with parallel deficits in visual imagery. For example, some patients are impaired at identifying faces (prosopagnosia) but not other objects—and they are also impaired at tasks involving visual imagery of faces (Shuttleworth et al. 1982; Young et al. 1994). A single-case study reported a patient who exhibited a selective deficit in identifying animals and showed a parallel deficit when asked to describe animals or to draw them from memory (Sartori and Job 1988). An early review of the patient literature (Farah 1984) described 28 cases of object agnosia and reported that in 14 cases, there was a parallel visual imagery impairment. The remaining cases were either not tested for imagery or the imagery tests were not sufficiently rigorous.

At least some of these parallel deficit cases can be explained by assuming damage in brain regions that support long-term visual memories for objects and faces stored in later visual areas; such areas would be used during both visual perception and visual imagery. Given that the clusters of activation in late visual areas elicited by visual perception are much larger than those elicited by imagery (and usually encompass them), dissociations should result from damage to the unshared portions of these areas. Indeed, some patients with visual agnosia have also been observed with relatively normal visual mental imagery (Bartolomeo et al. 1998; Behrmann et al. 1994; Servos and Goodale 1995). Although some dissociation cases can be attributed to crude visual mental imagery testing (as seen in our discussion on early visual areas), some patients could carry out rather challenging visual mental imagery tasks (Servos and Goodale 1995). Another possible explanation is that these patients sustained damage to other ventral regions that are necessary for visual perception but not for visual mental imagery. These regions may be important for grouping and other perceptual processes that are needed for identifying objects but not for visual mental imagery (Behrmann et al. 1994). Finally, there is sparse data on a few cases with normal visual perception but impaired visual mental imagery (Farah 1984; Goldenberg 1993). Damage to inferior frontal and intraparietal regions that modulate activation in the ventral stream during visual mental imagery (Mechelli et al. 2004) may explain some of these cases, but more research needs to be done to draw meaningful conclusions from these dissociations.

## 2.13 Conclusions

The development of cognitive science and neuroscience has resulted in substantial and ongoing progress in the investigation of visual mental imagery. Cognitive science and neuroscience tools and paradigms have enabled researchers to study visual mental imagery more objectively than was possible by using purely introspective methods. Furthermore, the huge and rapidly expanding knowledge based on the organization and working of the primate visual system (human, in particular) has been providing key information for generating more detailed theories of visual mental imagery. However, this progress has also revealed important holes in our grasp and conceptualization of visual mental imagery processes. First, we still know very little about the commonalities and differences between neural processes supporting visual mental imagery and other cognitive processes such as selective or spatial attention and working memory. Second, the neural causes of individual differences in visual mental imagery observed in many studies are still poorly understood. Third, despite numerous single-case studies, systematic investigations of visual mental imagery using rigorous tests in groups of neurological patients are still lacking (see Chap. 13 for evidence of progress in this direction). Fourth, there has been only very limited effort toward developing computational neuroscience theories of visual mental imagery; such theories are necessary to generate predictions to test theories of visual mental imagery and its neural implementation.

Progress in filling these and related research gaps will require continued interdisciplinary collaborations involving psychologists, neuroscientists, and computer scientists of the type we have been witnessing in cognitive science over the last three decades.

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