



chapter 13

The Occipital Lobes

P. M., a colonel in the British army who fought in North Africa during the Second World War, was struck by a bullet that went through the back of his brain. Miraculously, P. M. survived, but his vision was severely affected. He completely lost sight in the right visual field but the central part of his left visual field survived. He reported that he could see “normally” in a region of the left visual world that was about the diameter of your fist held at arm’s length directly in front of your face.

P. M.’s symptoms reveal a topographical map of the visual world in the occipital cortex and the possibility of seeing through only a small part of it. But what did P. M. experience in the rest of the visual world? Shortly after his injury, he reported that the lost world appeared black, as though the lights were out. Occasionally, however, he was aware that the lost regions were different, “almost gray,” although he could never express specifically what exactly was different other than the grayness.

P. M. also experienced a phenomenon that many patients with extensive visual-field defects experience: if asked to guess whether a spot of light had blinked in his blind field, he could “guess” at above-chance levels. He was not consciously aware that the light had appeared and seemed bemused that he could guess, sometimes quite accurately, about the presence or absence of the light.

In spite of his residual central vision, P. M. had two particular (and, for him, aggravating) problems: he found it very difficult to read and he had difficulty recognizing faces. Curiously, however, P. M. could recognize other objects more easily, even though he could not see any more of them than he could the faces.

Cases such as P. M.’s are especially interesting because our brains are organized around vision. Our perception of the world is predominantly visual, our movements are guided by visual information, our social and sexual behavior is highly visual, our entertainment is largely visual, and our nights

are enriched by visual dreams. In this chapter, we first consider the anatomical organization of the occipital lobes and then examine the extent of the visual system within the brain. Next, we examine disorders of the visual pathways and of the visual system. We shall see why faces present a special problem for the visual system and why the ability to visualize presents humans a unique opportunity.

Anatomy of the Occipital Lobes

The occipital lobes form the posterior pole of the cerebral hemispheres, lying under the occipital bone at the back of the skull. On the medial surface of the hemisphere, the occipital lobe is distinguished from the parietal lobe by the parieto-occipital sulcus, as illustrated in Figure 13.1. No clear landmarks separate the occipital cortex from the temporal or parietal cortex on the lateral surface of the hemisphere, however, because the occipital tissue merges with the other regions. The lack of clear landmarks makes it difficult to define the extent of the occipital areas precisely and has led to much confusion about the exact boundaries.

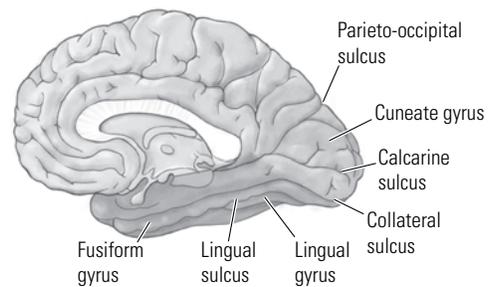
Within the visual cortex, however, are three clear landmarks. The most prominent is the calcarine sulcus, which contains much of the primary cortex (see Figure 13.1). The calcarine fissure divides the upper and lower halves of the visual world. On the ventral surface of the hemisphere are two gyri (lingual and fusiform). The lingual gyrus includes part of visual cortical regions V2 and VP, whereas V4 is in the fusiform gyrus.

Subdivisions of the Occipital Cortex

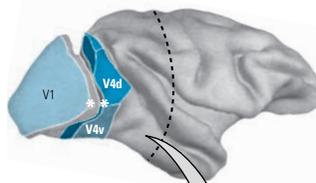
The monkey cortex was first divided by Brodmann into three regions (areas 17, 18, and 19, see Figure 10.7), but studies using imaging, physiological, and newer anatomical techniques have produced much finer subdivisions. Although the map is still not complete, the consensus is that the occipital cortex contains at least nine different visual areas, as illustrated in Figure 13.2: V1, V2, V3, VP, V3a, V4d, V4v, DP, and MT (also known as V5).

Figure 13.2 shows the locations of some of these areas on the lateral surface of the monkey brain as well as their locations on a two-dimensional flattened map that includes both the lateral areas and those

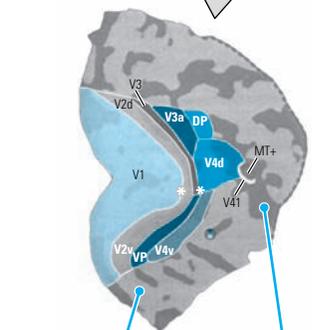
Figure 13.1 Medial view of the occipital lobe, illustrating the major landmarks.



(A) Monkey right hemisphere



(B) Flattened cortex

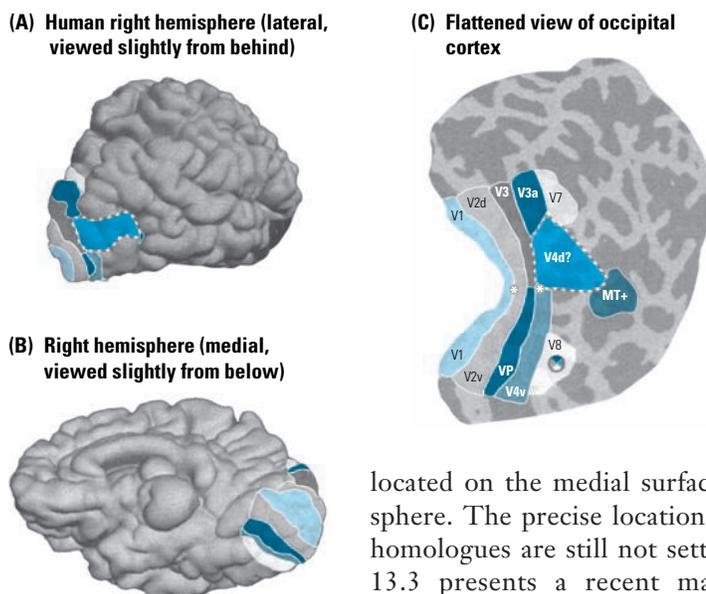


Light shading represents gyrus "hills"...

...and dark shading represents sulcus "valleys."

Figure 13.2 Topography of the visual cortex of the macaque monkey. (A) A nearly normal rendition of the lateral surface of the brain in which the sulci are opened slightly. (B) A flattened cortical surface showing both the lateral and the medial regions. The shaded areas represent regions that are normally curved up (gyri) or down (sulci). The asterisks refer to the foveal representation in areas B1 and V4. (After Tootell and Hadjikhani, 2001, with permission.)

Figure 13.3 Topography of the human visual cortex. (A) A nearly normal rendition of the lateral surface of the brain in which the sulci are opened slightly. (B) The medial surface in which the sulci are opened slightly. (C) A flattened cortical surface showing both the lateral and medial regions. The shaded areas represent regions that are normally curved up (gyri) or down (sulci). The asterisks refer to the foveal representation in areas V1 and V4. (After Tootell and Hadjikhani, 2001, with permission.)



located on the medial surface of the hemisphere. The precise locations of the human homologues are still not settled, but Figure 13.3 presents a recent map constructed by Tootell and Hadjikhani that includes all of the monkey areas as well as an additional color-sensitive area (V8).

Some of the areas contain a complete visual field, whereas others have only an upper or lower visual field. This distinction is curious, and Previc has suggested that the upper and lower fields may have different functions, with the upper more specialized for visual search and recognition and the lower more specialized for visuomotor guidance.

A remarkable feature of area V1 is its complex laminar organization, which, as illustrated in Figure 13.4, is probably the most distinct of all cortical areas. Although we usually say that the cortex has six layers, it is possible to see many more in area V1, partly because layer IV alone features four distinct layers. Another surprising feature of area V1 is that, although it appears to be anatomically homogenous, it can be shown to actually be heterogeneous by staining it for the enzyme cytochrome oxidase, which is crucial in making energy available to cells. Regions of cytochrome-rich areas, known as blobs, are separated by interblob regions of little cytochrome activity (see Figure 10.10). It turns out that cells in the blobs take part in color perception and the interblobs have a role in form and motion perception.

The discovery that area V1 is functionally heterogeneous—that a given cortical area may have more than one distinct function—was unexpected. It

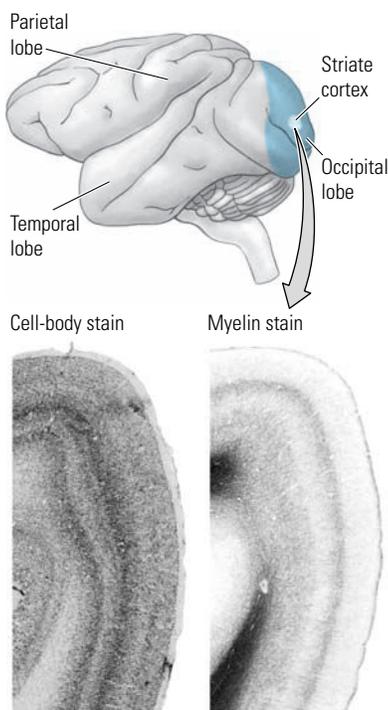


Figure 13.4 The visual cortex is highly laminated, as can be seen in a cell body stain (left) or a myelin stain (right) in these sections from a monkey brain. Because of the distinct stripes, the visual cortex is sometimes called the striate cortex.

Because of the distinct stripes the visual cortex is sometimes called the striate cortex.

turns out that area V2 also is heterogeneous when stained with cytochrome oxidase, but, instead of blobs, stripes are revealed (see Figure 10.10). One type, the “thin stripe,” takes part in color perception. Two other types, known as thick stripes and pale stripes, have roles in form and motion perception, respectively. Thus, we see that the heterogeneity of function observed in area V1—representing color, form, and motion—is preserved in area V2, although it is organized in a different way.

The distribution of color function across much of the occipital cortex and beyond (i.e., areas V1, V2, V4, V8) is important because, until recently, the perception of form or movement was believed to be colorblind. It has now become clear that color vision is integral to the analysis of position, depth, motion, and structure of objects (see a review by Tanaka et al., 2001).

A key point here is that, although the relative amount of color processing certainly varies across occipital regions, with area V4 having color processing as its major function, the processing of color-related information does more than simply allow us to tell red from green. The appreciation of color also enriches our capacity to detect motion, depth, and position. In the absence of significant color analysis, dogs and cats thus not only see an essentially black-and-white world, but have reduced visual capacities more generally as well.

An example of the advantage of color vision can be seen in the type of photoreceptors in primates. Sumner and Mollon found that the color system of primates is optimized for differentiating edible fruits from a background of leaves. This ability to differentiate is an important advantage when having to select edible fruits from a complex scene and is especially important when the fruits are partly occluded by leaves, which is fairly common. In fact, color provides important information for object recognition in such cases. A partly occluded yellow banana is quickly seen, whereas a gray banana would be difficult to detect in a black-and-white scene.

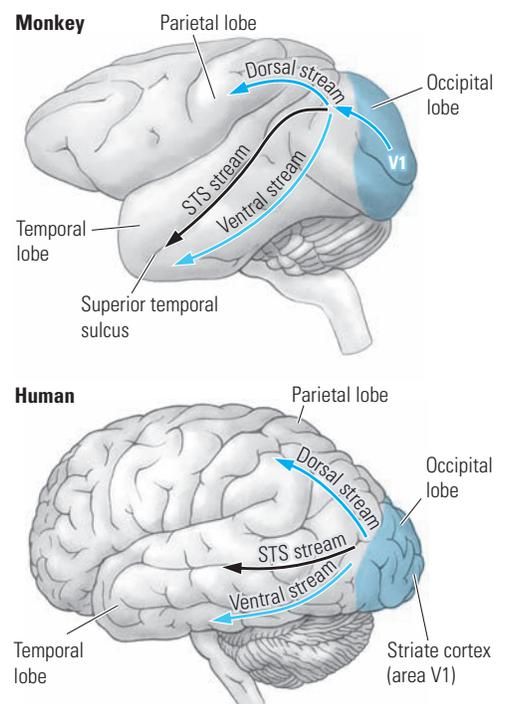
Connections of the Visual Cortex

By the late 1960s, the consensus was that the visual cortex is hierarchically organized, with visual information proceeding from area 17 to area 18 to area 19. Each visual area was thought to provide some sort of elaboration on the processing of the preceding area. This strictly hierarchical view is now considered too simple, and has been replaced by the notion of a distributed hierarchical process with multiple parallel and interconnecting pathways at each level, much as illustrated in Figure 10.16.

There is still a hierarchy for vision, but with separate functions. As indicated in Chapter 10, the details of all the connections between the occipital areas and from them to the parietal, temporal, and frontal regions are bewildering, but it is possible to extract a few simple principles (Figure 13.5):

1. V1 (the striate cortex) is the primary vision area: it receives the largest input from the lateral geniculate nucleus of the thalamus and it projects to all other occipital regions. V1 is the first processing level in the hierarchy.

Figure 13.5 Streams of visual processing. The occipitoparietal (dorsal) stream takes part in visual action and flows from area V1 to the posterior parietal visual areas. The occipitotemporal (ventral) stream takes part in object recognition and flows from area V1 to the temporal visual areas. The superior temporal sulcus (STS) stream, where information to and from the dorsal and ventral streams converges, flows from area V1 into the superior temporal sulcus.



2. V2 also projects to all other occipital regions. V2 is the second level.
3. After V2, three distinct parallel pathways emerge en route to the parietal cortex, superior temporal sulcus, and inferior temporal cortex, for further processing.

As we shall see in more detail shortly, the parietal pathway, or **dorsal stream**, has a role in the visual guidance of movement, and the inferior temporal pathway, or **ventral stream**, is concerned with object perception (including color). The middle pathway along the superior temporal sulcus is probably important in visuospatial functions.

A Theory of Occipital-Lobe Function

We have seen that areas V1 and V2 are functionally heterogeneous and that both segregate processing for color, form, and motion. The heterogeneous functions of areas V1 and V2 contrast with the functions of the areas that follow in the hierarchy. In a sense, areas V1 and V2 appear to serve as little mailboxes into which different types of information are assembled before being sent on to the more specialized visual areas.

From areas V1 and V2 flow three parallel pathways that convey different attributes of vision. The information derived from the blob areas of area V1 goes to area V4, considered to be a color area. Cells in area V4 are not solely responsive to color, however; some cells respond to both form and color.

Other information from area V1 (the magnocellular input discussed in Chapter 8) also goes to area V2 and then to area V5, which is specialized to detect motion. Finally, an input from areas V1 and V2 to area V3 is concerned with what Zeki calls “dynamic form”—that is, the shape of objects in motion. Thus, we see that vision begins in the primary cortex (V1), which has multiple functions, and then continues in more specialized zones.

It is not surprising to discover that selective lesions up the hierarchy in areas V3, V4, and V5 produce specific deficits in visual processing. People who suffer damage to area V4 are able to see only in shades of gray. Curiously, patients not only fail to perceive colors but also fail to recall colors from before their injuries or even to imagine colors. In a real sense, the loss of area V4 results in the loss of color cognition, or the ability to think about color. Similarly, a lesion in area V5 produces an inability to perceive objects in motion. Objects at rest are perceived but, when the objects begin to move, they vanish. In principle, a lesion in area V3 will affect form perception but, because area V4 also processes form, a rather large lesion of both V3 and V4 would be required to eliminate form perception.

An important constraint on the functions of areas V3, V4, and V5 is that all these areas receive major input from area V1. People like Colonel P. M., with lesions in area V1, act as though they are blind, but visual input can still get through to higher levels—partly through small projections of the lateral geniculate nucleus to area V2 and partly through projections from the colliculus to the thalamus (the pulvinar) to the cortex. (This system is the tectopulvinar pathway described in Chapter 8.)

People with V1 lesions seem not to be aware of visual input and can be shown to have some aspects of vision only by special testing. Thus, when asked what they see, patients with V1 damage often reply that they see nothing. Nonetheless, they can act on visual information, indicating that they do indeed “see.”

Area V1 thus appears to be primary for vision in yet another sense: V1 must function for the brain to make sense out of what the more specialized visual areas are processing. We must note, however, reports of people with significant V1 damage who are capable of some awareness of visual information, such as motion. Barbur and colleagues suggested that the integrity of area V3 may allow this conscious awareness, but this suggestion remains a hypothesis.

Visual Functions Beyond the Occipital Lobe

Neuroscientists have known since the early 1900s that the occipital lobes house vision, but only in the past two decades have they begun to understand the extent of visual processing that takes place beyond the occipital lobes. In fact, it is now clear that more cortex is concerned with vision than with any other function in the primate brain.

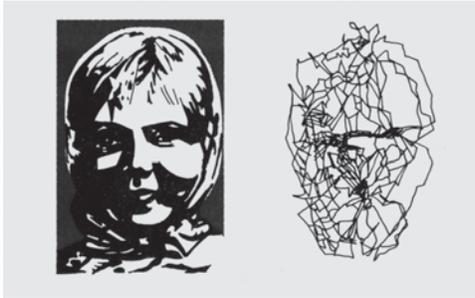
Felleman and van Essen’s flattened cortical map in Figure 10.17 illustrates that, of the 32 cortical areas (of a total of about 70 in their scheme) that have visual functions in the monkey brain, only 9 are actually in the occipital lobe. The total surface area of the vision-related regions is about 55% of the whole cortical surface, which compares with 11% and 3% for the somatosensory and auditory regions, respectively. (It is interesting that so little of the monkey cortex represents audition, which is certainly evidence of a major difference between the brains of humans and those of monkeys; we humans have a much larger auditory representation, which is no doubt responsible for our preoccupation with both language and music.)

Visual processing in humans therefore does not culminate in secondary visual areas such as areas V3, V4, and V5 but continues within multiple visual regions in the parietal, temporal, and frontal lobes (see Figure 10.17). Functions have not been assigned to all these additional visual regions, but it is possible to speculate on what their functions must be. To do so, we can divide visual phenomena into five general categories: vision for action, action for vision, visual recognition, visual space, and visual attention.

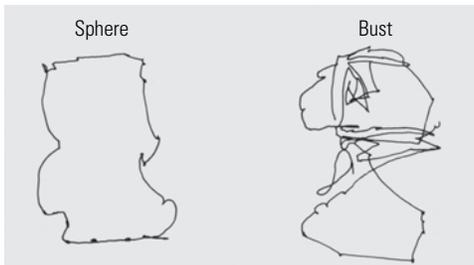
Vision for Action

This category is visual processing required to direct specific movements. For example, when reaching for a particular object such as a cup, the fingers form a specific pattern that allows grasping of the cup. This movement is obviously guided by vision, because people do not need to shape their hands consciously as they reach.

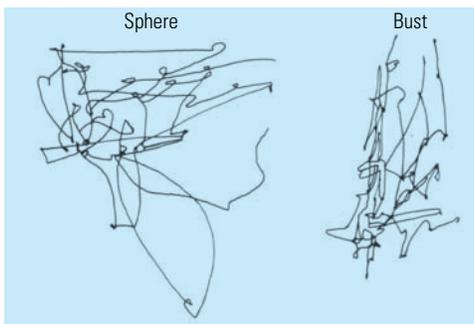
In addition to that for grasping, there must be visual areas that guide all kinds of specific movements, including those of the eyes, head, and whole body. A single system could not easily guide all movements, because the requirements are so different. Reaching to pick up a jellybean requires a very different kind of motor control than that required to duck from a snowball, but both are visually guided.

(A) Normal subject

Eye movements of a normal subject concentrate on facial features and are directed more to the left side of the photograph.

(B) Normal subject

Eye movements of a normal subject concentrate on the shapes of the objects examined,...

(C) Agnosic subject

...but those of an agnosic subject are random.

Figure 13.6 Eye movements during the examination of a visual stimulus. (A) The concentration of eye movements (by a normal subject) to distinctive features of the face (eyes, nose, mouth); these movements are directed more to the left side of the photograph. (B) The eye movements of a normal subject examining a sphere (left) and a bust (right). (C) The eye movements of an agnosic subject examining the same shapes. Note the random movements of the agnosic subject. (From A. R. Luria, *The Working Brain*, © 1973, The Copyright Agency of the USSR. Reprinted with permission.)

Finally, vision for action must be sensitive to movement of the target. Catching a moving ball requires specific information about the location, trajectory, speed, and shape of the object. Vision for action is thought to be a function of the parietal visual areas.

Action for Vision

In a more “top down” process, the viewer actively searches for only part of the target object and attends selectively to it (Figure 13.6). When we look at a visual stimulus, we do not simply stare at it; rather, we scan the stimulus with numerous eye movements. These movements are not random but tend to focus on important or distinct features of the stimulus.

When we scan a face, we make a lot of eye movements directed toward the eyes and mouth. Curiously, we also make more eye scans directed to the left visual field (the right side of the person’s face) than to the right visual field. This scanning bias may be important in the way that we process faces, because it is not found in the scanning of other stimuli. People with deficits in action for vision are likely to have significant deficits in visual perception, although such deficits have not been studied systematically.

An interesting aspect of action for vision consists of the eye movements that we often make when we visualize information. For example, when people are asked to rotate objects mentally in order to answer simple questions about the objects’ appearance, they usually make many eye movements, especially to the left. When people are doing things in the dark, such as winding photographic film onto spools for processing, they also make many eye movements. Curiously, if the eyes are closed, these movements stop. Indeed, it appears that it is easier to do many tasks in the dark if the eyes are closed. Because things are done by touch in the dark, the visual system may interfere until the eyes are closed.

Visual Recognition

We enjoy the ability both to recognize objects and to respond to visual information. For example, we can both recognize specific faces and discriminate and interpret different expressions in those faces. Similarly, we can recognize letters or symbols and assign meaning to them.

We can recognize different foods, tools, or body parts, but it is not reasonable to expect that we have different visual regions for each category or object. We may have at least some specialized areas for biologically significant information, such as faces, however. Cells in the temporal cortex appear to be highly specific in their preference for particular faces or hands. These visual areas in the temporal lobe are specialized for visual recognition.

Visual Space

Visual information comes from specific locations in space. This information allows us to direct our movements to objects in space and to assign meaning to objects. But spatial location is not a unitary characteristic. Objects have location both relative to an individual (**egocentric space**) and relative to one another (**allocentric space**).

Egocentric visual space is central to the control of your actions toward objects. It therefore seems likely that visual space is coded in neural systems related to vision for action. In contrast, allocentric properties of objects are necessary for you to construct a memory of spatial location.

A key feature of allocentric spatial coding is that it depends on the identity of particular features of the world. Thus, it is likely to be associated with the regions of visual recognition. In summary, different aspects of spatial processing probably take place in both the parietal and the temporal visual regions, and respective functions are integrated in areas that interact and exchange information.

Visual Attention

We cannot possibly process all the visual information available. This page has shape, color, texture, location, and so on, but the only really important characteristic is that it has words. Thus, when we read the page, we select a specific aspect of visual input and attend to it selectively.

In fact, neurons in the cortex show various attentional mechanisms. For example, neurons may respond selectively to stimuli in particular places or at particular times or if a particular movement is to be executed. Independent mechanisms of attention are probably required both for the guidance of movements (in the parietal lobe) and for object recognition (in the temporal lobe).

Visual Pathways Beyond the Occipital Lobe

Vision evolved first for motion, not for recognition. Simple organisms can detect light and move to or from the light. For example, the single-cell organism *Euglena* alters its swimming pattern as a function of the ambient light levels in different parts of the pond in which it lives. Because sunlight helps manufacture food in this aquatic environment, it is an advantage for *Euglena* to move toward the light.

Notice that *Euglena* need not “perceive” the light or make an internal map of the outside world. Rather, it is only necessary that some type of link exist between the amount of ambient light and locomotion. For *Euglena*, “vision” acts to guide movement—the most primitive form of vision for action.

However, our vision is far more complicated than that of *Euglena*. But even much of human vision can be understood without reference to recognition. Consider, for example, a major-league baseball batter who swings at a ball before it is possible for him to perceive what the object actually is. The visual guidance of his movement is independent of his recognition of the ball.

Nonetheless, as primitive animals interacted with their environment, they are adapted to learn more about their environment. Thus distinct visual systems evolved to recognize objects in the environment. The system of knowing what an object is includes the flow of visual information from area V1 to

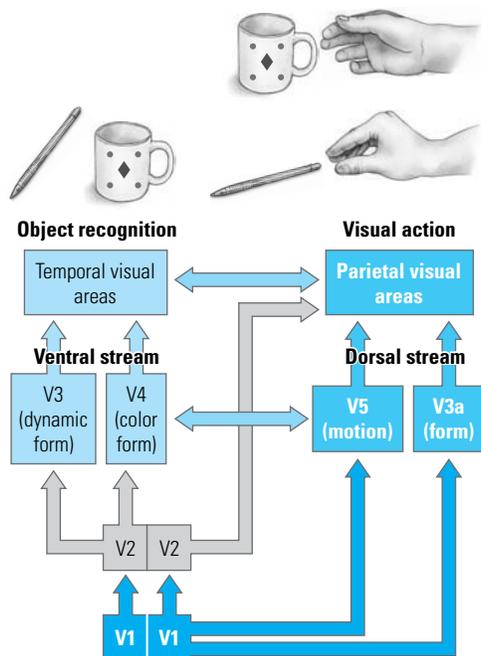
the temporal lobe, called the ventral stream (see Figure 13.5). The system controlling the visual guidance of movements includes the flow of information from area V1 to the parietal lobe, known as the dorsal stream.

The distinction between the ventral and the dorsal streams can be seen clearly in a series of patients studied by Milner and Goodale. They first described D. F., a patient who was blind but who nevertheless shaped her hand appropriately when asked to reach for objects. Her dorsal stream was intact, as revealed by the fact that she could “unconsciously” see location, size, and shape. On the other hand, Milner and Goodale noted that patients with dorsal-stream damage consciously reported seeing objects but could not reach accurately or shape the hand appropriately when reaching.

Milner and Goodale proposed that the dorsal stream should be thought of as a set of systems for the on-line visual control of action. Their argument is based on three main lines of evidence:

1. The predominant characteristic of the neurons in posterior parietal regions is that they are active during a combination of visual stimulation and associated behavior. For example, cells may be active only when a monkey reaches out to a particular object. Looking at an object in the absence of movement does not activate the neurons. Thus, these “visual” neurons are unique in that they are active only when the brain acts on visual information.
2. These posterior parietal neurons can therefore be characterized as an interface between analysis of the visual world and motor action taken on it. The demands of action have important implications for what type of information must be sent to the parietal cortex—information such as object shape, movement, and location. Each of these visual features is likely to be coded separately, and at least three distinct pathways within the dorsal stream run from area V1 to the parietal cortex. As illustrated on the right in Figure 13.7, one pathway goes from area V1 directly to area V5 to parietal cortex, a second goes from area V1 to areas V5 and V3a and then to parietal regions, and a third goes from area V1 to area V2 to the parietal cortex. These three pathways must certainly be functionally dissociable.
3. Most of the visual impairments associated with lesions to the parietal cortex can be characterized as visuomotor or orientational. (We return to this subject in Chapter 14.)

Figure 13.7 A summary of the visual processing hierarchy. The dorsal stream, which takes part in visual action, guides movements such as the hand postures for grasping a mug or pen, as illustrated. The ventral stream, which takes part in object recognition, identifies objects such as mugs and pens in our visual world. The dorsal and ventral streams exchange information through polysensory neurons in the superior temporal sulcus stream, as shown by double-headed arrows. (After Goodale, 1993.)



The Milner-Goodale model is an important theoretical advance in understanding how our visual brain is organized. As detailed in Figure 13.7, two distinct visual streams have evolved to use visual information in two fundamentally different ways: the dorsal stream for guiding movements and the ventral for identifying objects. This model can likely be applied to the organization of the auditory and somatosensory systems as well—both systems also function to guide movements and identify stimuli. An important point here is that we are conscious of only a small amount of what the brain actually does; even with effort, we cannot gain awareness of much of our sensory processing.

One wrinkle must be added to the Milner-Goodale model—the third stream of visual processing, which originates from

structures associated with both the parietal and the temporal pathways and flows to a region of the temporal lobe that is buried in the superior temporal sulcus (see Figure 13.5). The superior temporal sulcus is characterized by **poly-sensory neurons**—neurons that are responsive to both visual and auditory or both visual and somatosensory input. The interaction of the parietal and temporal streams in the superior temporal sulcus is probably due to interaction between the dorsal and the ventral—the “action” and “recognition”—streams.

Imaging Studies of Dorsal and Ventral Streams

Brain regions associated with specific visual pathways can be identified by measuring regional blood flow as people perform visual tasks. Ungerleider and Haxby reviewed such PET studies, as summarized in Figure 13.8.

In studies by Haxby and colleagues, subjects were given two tasks. In the first, the subjects indicated which of two faces was identical with a sample face. In the second, the subjects were asked to identify which of two stimuli had a dot (or square) in the same location as in a sample. The results showed activation of the temporal regions for the facial stimuli and activation of the posterior parietal region for the location task (see Figure 13.8A). Note, in addition, the activation of frontal areas for the spatial task, supporting the idea that the frontal lobe plays a role in certain aspects of visual processing.

One difficulty with interpretation of the spatial-task PET images is that subjects have to make eye movements, which activate regions in the dorsal stream; so whether the spatial or the movement components activate the parietal region is not clear. The important point, however, is that different regions take part in the two tasks.

A similar dissociation was identified among the processes that detect motion, color, and shape (see Figure 13.8B). Detection of motion activates regions in the

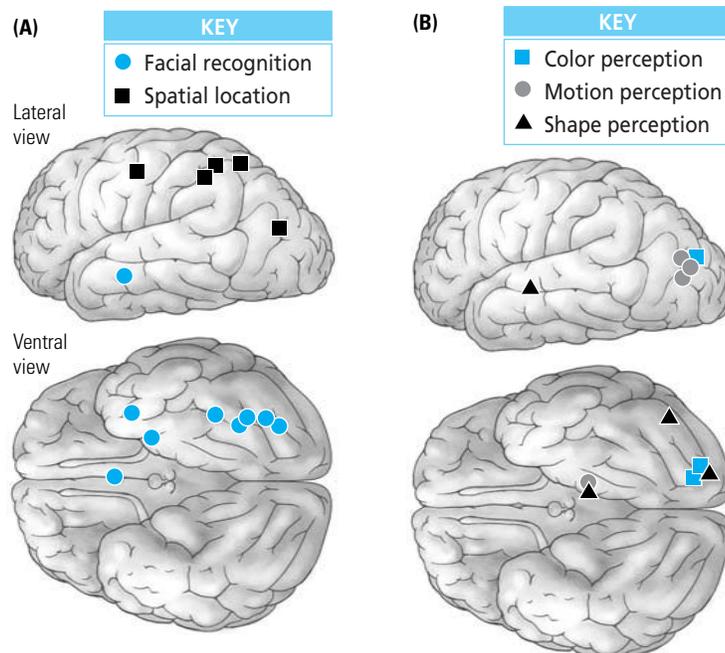
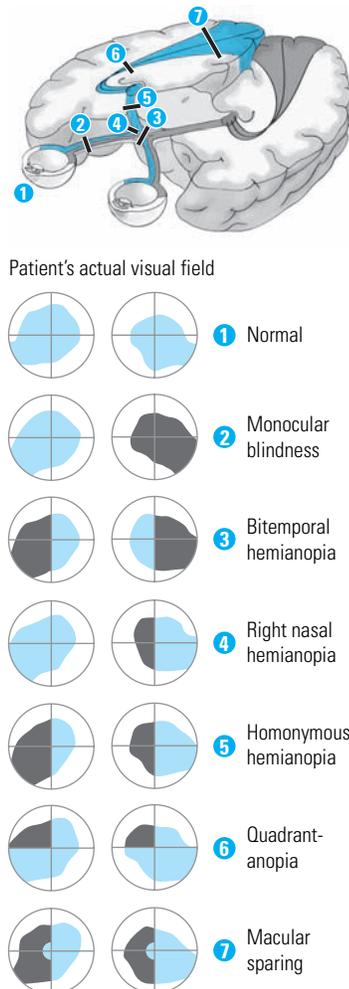


Figure 13.8 Summary of results of PET studies illustrating selective activation of (A) cortical regions by tasks of facial recognition (circles) versus spatial location (squares) and (B) areas associated with perception of color (squares), motion (circles), and shape (triangles). (After Ungerleider and Haxby, 1994.)

vicinity of area V5, whereas detection of shape activates regions along the superior temporal sulcus and the ventral region of the temporal lobe. The perception of color is associated with activation of the region of the lingual gyrus, which is the location of area V4. One study also found activation of a lateral occipital region, which is difficult to interpret in the light of lesion studies. This study made special visual attention demands of its participants, potentially an important factor in interpreting the observed activation.

In summary, studies of regional blood flow in normal subjects show results consistent with the general notion of two separate visual streams, one to the parietal lobe and the other to the temporal lobe. In addition, it is clear that separate visual functions reside in different temporo-occipital regions.

Figure 13.9 Visual defects subsequent to damage at different levels of the visual system, keyed by number. A darkened region in the visual field denotes a blind area. (After Curtis, 1972.)



Disorders of Visual Pathways

Before we consider the deficits associated with damage to the visual pathways, we must revisit two key elements in the way in which the brain organizes the visual fields:

1. The left half of each retina sends its projections to the right side of the brain, whereas the right half of each retina sends its projections to the left side of the brain (see Figure 11.5). Thus, the representation of each side of the visual world seen by each eye is sent to the same place in area V1. As a result, damage to area V1 affects vision in both eyes. Conversely, if a visual disturbance is restricted to just one eye, then the damage must be outside the brain, either in the retina or in the optic nerve.
2. Different parts of the visual field are topographically represented in different parts of area V1 (Figure 13.9). Thus, injury to a specific region of area V1 produces a loss of vision in a specific part of the visual world.

Now let us consider what happens when there is damage to different places in the visual pathways, as keyed on Figure 13.9.

Destruction of the retina or optic nerve of one eye produces monocular blindness—the loss of sight in that eye. A lesion of the medial region of the optic chiasm severs the crossing fibers, producing **bitemporal hemianopia**—loss of vision of both temporal fields. This symptom can arise when a tumor develops in the pituitary gland, which sits medially, next to the chiasm. As the tumor grows, it can put pressure on the medial part of the chiasm and produce the loss, or disturbance, of lateral vision.

A lesion of the lateral chiasm results in a loss of vision of one nasal field, or **nasal hemianopia**. Complete cuts of the optic tract, lateral geniculate body, or area V1 result in **homonymous hemianopia**—blindness of one entire visual field (see Figures 13.9 and 13.10A). Note that, because the disturbance affects information coming from both eyes, the visual defect is present in both eyes.

Indeed, the effects of such injuries enable investigators to determine whether a lesion is in the eye or optic tract versus the optic nerve or brain. The former injuries produce visual disturbance in one eye, whereas the latter injuries produce visual disturbance in the visual field and thus in both eyes. Should this lesion be partial, as is often the case, only a part (quadrant) of the visual field is destroyed (see Figures 13.9 and 13.10).

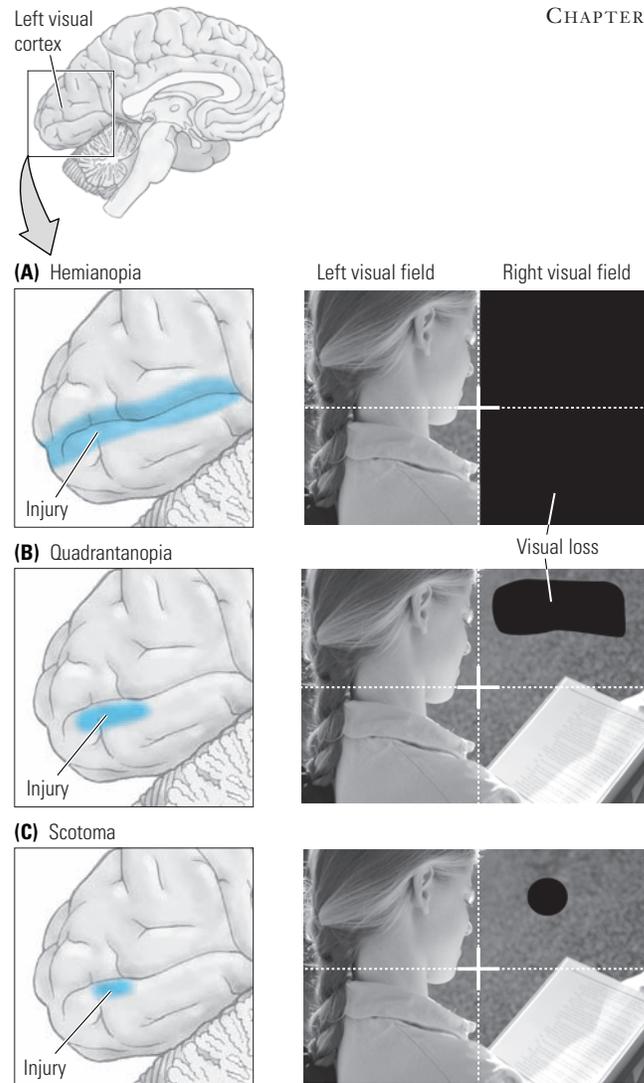


Figure 13.10 Consequences of lesions in area V1. The blue areas indicate the regions of visual loss. (A) The effect of a complete lesion of area V1 in the left hemisphere is hemianopia affecting the right visual field. (B) A large lesion of the lower lip of the calcarine fissure produces a quadrantanopia that affects most of the upper-right visual quadrant. (C) A smaller lesion of the lower lip of the calcarine fissure results in a smaller injury, a scotoma. (Jim Pickerell/Stock Connection/PictureQuest.)

Lesions of the occipital lobe often spare the central, or macular, region of the visual field, although the reason is uncertain. The most reasonable explanations are that (1) the macular region receives a double vascular supply, from both the middle and the posterior cerebral arteries, making it more resilient to large hemispheric lesions, or (2) the foveal region of the retina projects to both hemispheres, and so, even if one occipital lobe is destroyed, the other receives projections from the fovea. The first explanation is more likely.

Macular sparing of the central visual field helps to differentiate lesions of the optic tract or thalamus from cortical lesions, because macular sparing occurs only after lesions (usually large) to the visual cortex. Macular sparing does not always occur, however, and many people with visual-cortex lesions have a complete loss of vision in one-quarter (quadrantanopia) or one-half (hemianopia) of the fovea (see Figures 13.9 and 13.10B). A curious aspect of both hemianopia and quadrantanopia is that the border between the impaired visual area and the adjacent, intact visual field, or quadrant, is sharp, much as if a pair of scissors were used to cut away part of the visual field (see Figure 13.9). This sharp demarcation of intact and impaired visual regions is due to the anatomical segregation between the left and the right and the upper and the lower visual fields.

Small lesions of the occipital lobe often produce **scotomas**, small blind spots in the visual field (Figure 13.10C). A curious aspect of scotomas is that people are often totally unaware of them because of *nystagmus* (constant, tiny, involuntary eye movements) and “spontaneous filling in” by the visual system. The eyes are usually in constant motion; so the scotoma moves about the visual field, allowing the brain to perceive all the information in the field. If the eyes are held still, the visual system actually completes objects, faces, and so on, resulting in a normal percept of the stimulus.

The visual system may cover up the scotoma so successfully that its presence can be demonstrated to the patient only by “tricking” the visual system. Such tricking can be achieved by placing objects entirely within the scotoma region of the patient’s visual field and, without allowing the patient to shift gaze, asking what the object is. If no object is reported, the examiner moves the object out of the scotoma so that it suddenly “appears” in the intact region of the patient’s visual field, thus demonstrating the existence of a blind region.

A similar phenomenon can be demonstrated in your own “blind spot.” Stand beside a table, close or cover one eye, stare at a spot on the table, and move a pencil along the table laterally, from directly below your nose to between 20 and 30 cm toward the periphery. Part of the pencil will vanish when you reach the blind spot. You can move the pencil through the blind spot slowly, and it will suddenly reappear on the other side. Notice that, like a scotoma, the normal blind spot is not noticeable, even when you look around the world with just one eye. Even the normal brain “fills in” missing bits of the visual world.

Disorders of Cortical Function

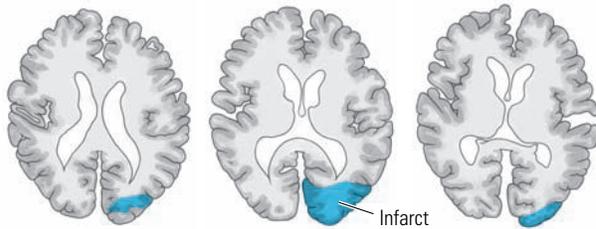
Research into selective disturbances of human visual functions is limited mainly to case studies, such as case P. M., whom you met at the beginning of this chapter, and these natural lesions seldom respect the boundaries of specific visual areas. Several case histories, each with distinctly different symptoms and pathology, will give you a feeling for the specific symptoms of injury to the visual cortex. We begin with damage to area V1 and proceed along the hierarchy to higher areas and more-complicated visual disturbances.

Case B. K.: V1 Damage and a Scotoma

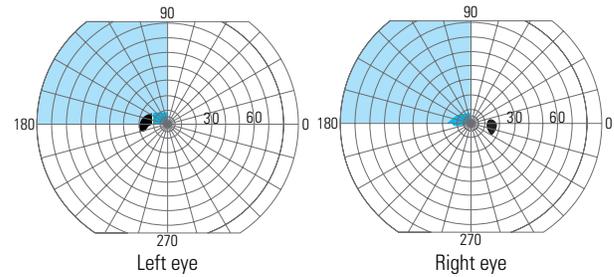
One morning B. K. awoke to discover that he was hemianopic in the left visual field. Given a history of classic migraine, in which the aura was nearly always in the left visual field, it is likely that he had a migraine stroke. Within a few hours, the left lower field began to return, but the left upper quadrant was slow to show any change.

A CT scan (Figure 13.11A) showed a clear infarct (dead tissue) in the right occipital area. The size of a visual-field defect is routinely measured with perimetry, a standardized method in which the subject fixates on a black dot in the center of a large white hemisphere. A small light is moved around the field, and the task is to indicate when it can be seen. The brightness and size of the light can be varied, thus manipulating the difficulty of the task.

(A) Three planes of section through B.K.'s brain



(B) The visual fields of the left and right eyes



Performance is mapped by indicating the area of “blindness” on a schematic map of the visual fields (Figure 13.11B). Size in the visual field is measured by visual angle, in degrees. (A degree is roughly the size of your thumb viewed at arm’s length.) Thus, for B. K., the area of complete inability to perceive even a very large bright light is measured from the center, 6° upward along the vertical midline and about 15° laterally along the horizontal midline. The area beyond this zone in the left upper quadrant does not have normal vision, however, because B. K. is still unable to perceive less-bright lights in this area.

The nature of B. K.’s visual defects can be illustrated best in the context of their poststroke evolution. For the first 2 to 3 days, his visual field appeared dark, much as though a piece of smoked glass were blocking his view of the world beyond. On the fourth day, this darkness had disappeared and was replaced by “visual noise” (a scintillating scotoma) throughout much of the field, especially in the area of the scotoma. Visual noise is best described as being like colored “snow” on a television screen. At about the same time, B. K. first perceived movement in the field as a traveling “wave,” much like ripples on a pond. There was no perception of form or pattern.

A curious phenomenon was first observed during perimetry testing 4 days after the stroke. If the stimulus light was moved into the blind field, it was not perceived until it moved into another quadrant. Curiously, however, B. K. immediately became aware (in hindsight) that the light had been present in the blind field and could accurately state where it entered the blind field. In other words, B. K. perceived location without being able to perceive content. Recall that Colonel P. M. also experienced this phenomenon, known as **blindsight**.

In the ensuing 4 to 6 months, the area of blindness decreased somewhat and acuity in the periphery improved significantly for B. K. Nonetheless, roughly 15 years later, form vision remains poor in the left upper quadrant, outside the scotoma. The scintillating colored snow is still present, showing little change from the first few days after the stroke.

The visual phenomena observed by B. K. indicate that area V1 (and perhaps area V2) probably has an area of total cell death (the dense scotoma). The presence of poor form vision in the rest of the quadrant may be due to a loss of some but not all neurons in area V1, possibly only those neurons that are especially sensitive to a period of reduced blood flow, known as ischemia. The poor form vision might also be attributed to the fact that other visual areas, especially area V2, remain intact.

B. K.’s symptoms show that other occipital areas are functional, because he perceives color and motion even though there is no form perception. Thus, B. K. can accurately perceive the color or motion of objects that he cannot

Figure 13.11 Scan and map of B. K.’s brain. (A) Schematic representation of B. K.’s CT scan, showing the infarct in the right occipital area in different views. (B) Map of B. K.’s visual fields 6 months after the stroke. Subnormal vision persists in the upper-left quadrant.

identify. Those who are myopic (nearsighted) experience a similar phenomenon: the colors of objects or lights can be perceived, whereas the form is not recognizable. B. K.'s stroke thus indicates the presence of at least four independent visual functions: form (which is absent), as well as color, movement, and location (which are spared).

The loss of one-quarter of the fovea leads B. K. to make a variety of visual errors. Immediately after the stroke, he was able to read only with great difficulty. When we look at a word, the fixation point is in the center of the word; so, for B. K., half of the word is absent. Indeed, he had difficulty finding the edge of the page because it was in the blind field. Normal reading returned as B. K. learned to direct his gaze slightly to the left and upward (probably about 2° in each direction), which allowed words to fall in the normal visual field.

This "recovery" took about 6 weeks. Returning to playing squash and tennis was equally challenging because, when a ball entered the scotoma, it was lost. Similarly, facial recognition was slower than it had been before the stroke, because the information in the left visual field appears to be particularly important for face recognition.

Case D. B.: V1 Damage and Blindsight

D. B. is one of the most extensively studied people with visual disturbance from an occipital lesion (see the detailed monograph by Weiskrantz). D. B.'s right calcarine fissure was removed surgically to excise an angioma, which is a collection of abnormal blood vessels. D. B. therefore has a hemianopia based on standard perimetry but nevertheless has surprising visual capacities.

When questioned about his vision in the left field, D. B. usually reports that he sees nothing, as did P. M. and B. K. Occasionally, D. B. indicates that he had a "feeling" that a stimulus was "approaching" or was "smooth" or "jagged." But, according to Weiskrantz, D. B. always stresses that he "saw" nothing, that typically he is guessing, and that he is at a loss for words to describe any conscious perception.

In contrast, when D. B. was asked to point to locations in the impaired field in which spots of light were turned on briefly, he was surprisingly accurate. His blindsight contrasts with his subjective impression that he saw nothing at all. Furthermore, he appears to be able to discriminate the orientation of lines, which he could not report "seeing." Thus, he can discriminate a 10° difference in orientation between two successively presented gratings in his impaired field.

Finally, D. B. can detect some forms of movement. When a vigorously moving stimulus was used, he reported "seeing" something. In this case, he did not report actually seeing a visual stimulus but rather spoke of complex patterns of lines and grids. These patterns may have been something like B. K.'s moving lines. In summary, D. B. has "cortical blindness," or blindsight, in which he reports no conscious awareness of "seeing" but still is able to report the movement and location of objects that he cannot recognize.

Case J. I.: V4 Damage and Color

Oliver Sacks and Robert Wasserman report the touching story of J. I., an artist who suddenly became color-blind. In 1986, the man was in a car accident in which he sustained a concussion. His principal symptoms after

the injury were an inability to distinguish any colors whatsoever, but his visual acuity had actually improved. “Within days . . . my vision was that of an eagle—I can see a worm wiggling a block away. The sharpness of focus is incredible.”

The effect of the loss of color vision was far greater than one would have expected. J. I. could barely stand the pain of living in a world that appeared in shades of gray. He found the changed appearance of people unbearable, because their flesh was an abhorrent gray (“rat-colored”) to him. He found foods disgusting in their grayish, dead appearance, and he had to close his eyes to eat. He could not even imagine colors any longer. The mental image of a tomato looked as black as its actual appearance. Even his dreams, which had once been in vivid colors, were now in black and gray.

Detailed visual testing by Sacks and Wasserman, and later by Zeki, revealed that J. I. was color-blind by the usual definitions, but this color blindness was attributed to specific damage to the occipital cortex. In addition, it did appear that his acuity had improved, especially at twilight or at night. Two years after his injury, J. I.’s despair had declined, and he appeared to no longer be able to remember color well. This failure to remember color is curious, because people who become blind through injury to the eyes or optic nerves do not lose their imagery or memory of color. There is little doubt from J. I.’s case that imagery and memory rely on the operation of at least some cortical structures necessary for the original perception.

Case P. B.: Conscious Color Perception in a Blind Patient

Zeki and his colleagues described the case of a man who was electrocuted, resulting in cardiac and respiratory arrest. P. B. was resuscitated but had suffered brain ischemia that produced a large area of posterior cortical damage. P. B. was left virtually blind, although he can detect the presence or absence of light. The remarkable visual feature, however, is that P. B.’s capacity to identify and name colors remains intact, as does his ability to name the typical color of imagined objects.

P. B.’s vision is in many ways opposite that of J. I.; the results of fMRI studies show that P. B. has activation in areas V1 and V2 in response to colored stimuli. As we reflect on the visual capacity of P. B., it is hard to imagine a world that is filled with color but no form, almost like an out-of-focus kaleidoscope that changes as we gaze around the world.

Case L. M.: V5 Damage and the Perception of Movement

Zihl and his colleagues reported the case of a 43-year-old woman who had a bilateral posterior injury resulting from a vascular abnormality. Her primary chronic complaint was a loss of movement vision. For example, she had difficulty pouring tea into a cup because the fluid appeared to be frozen. And she could not stop pouring, because she could not see the fluid level rise.

L. M. found being in a room with other people disturbing because she could not see them moving; they suddenly appeared “here or there,” but she did not see them move in between. The results of other tests of visual function appeared essentially normal. She could discriminate colors, recognize objects, and read and write.

Her condition is especially intriguing because we would not believe intuitively that such a syndrome is likely. Loss of color or form vision fits with our everyday experience that people can be color-blind or myopic; loss of the ability to see moving objects is counterintuitive indeed. Case L. M. is important because she shows that the brain must analyze movement of form separately from the form itself.

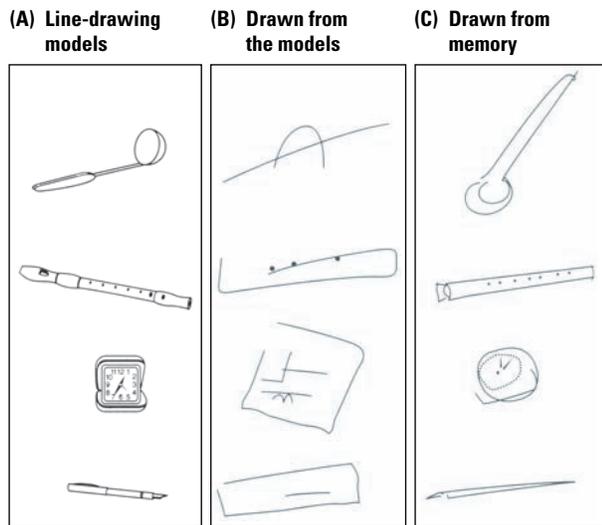
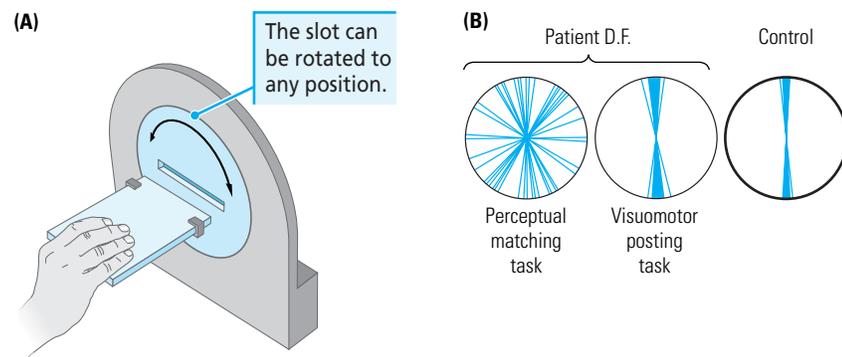


Figure 13.12 Samples of D. F.'s drawings. (A) Examples of the original line drawings presented to D. F. (B) Examples of D. F.'s drawings of the models. (C) D. F.'s drawings based on memory of the models. Note that the drawings from memory are superior to the copies of the line drawings of the models.

Figure 13.13 Testing visuomotor guidance. (A) The apparatus that was used to test sensitivity to orientation in patient D. F. The slot could be placed in any orientation around the clock. The task is to “post” the card into the slot as shown. (B) Plots of the orientation of the card in a perceptual matching task and in the visuomotor posting task. For illustration, the correct orientation has been rotated to vertical. D. F. was unable to match the orientation of the card to that of the slot unless she made a movement to post it. (Adapted with permission from Goodale, 2000.)



Case D. F.: Occipital Damage and Visual Agnosia

Visual agnosia is the term coined by Sigmund Freud for an inability to combine individual visual impressions into complete patterns—thus, the inability to recognize objects or their pictorial representations or the inability to draw or copy them. Goodale and Milner and their colleagues have extensively studied a 35-year-old visual agnostic who suffered carbon monoxide poisoning that resulted in bilateral damage to the lateral occipital region (mainly areas 18 and 19) and in the tissue at the junction of the parietal and occipital cortex.

D. F., whom we met earlier in the chapter in considering Goodale and Milner’s distinction between the dorsal and the ventral streams, has essentially

normal color vision and can see well enough to get around in the world. Her principal deficit is *visual-form agnosia*, a severe inability to recognize line drawings of objects. Thus, although D. F. can recognize many actual objects, she is unable to recognize drawings of them. Furthermore, as illustrated in Figure 13.12, although she can draw objects from memory, she has real difficulty in drawing objects from life and even more difficulty in copying line drawings. Thus, D. F. appears to have a serious defect in form perception.

Recall that the remarkable thing about D. F. is her apparently nearly intact ability to guide hand and finger movements toward objects that she cannot recognize. For example, although D. F. had a gross deficit in judging lines as horizontal or vertical, she could reach out and “post” a hand-held card into a slot rotated to different orientations, as illustrated in Figure 13.13. Indeed, analysis of video records of D. F.’s reaching revealed that, like normal control subjects, she began to orient the card correctly even as her hand was being raised

from the start position of the task. In other words, D. F. could use visual information to guide movements to objects (the dorsal stream), but she could not use visual information to recognize the same objects (the ventral stream).

Case V. K.: Parietal Damage and Visuomotor Guidance

Damage to the posterior parietal lobe produces a disorder known as **optic ataxia**, a deficit in visually guided hand movements, such as reaching, that cannot be ascribed to motor, somatosensory, or visual-field or -acuity deficits. V. K. is a woman with bilateral hemorrhages in the occipitoparietal regions, as described by Jakobson and colleagues. Although V. K. initially appeared virtually blind, her symptoms dissipated in a month, and she was left with disordered control of her gaze, impairment in visual attention, and optic ataxia. (Collectively, these symptoms are known as Balint's syndrome; see Chapter 14.)

V. K. had good form and color vision and could recognize and name objects; however, her ability to reach for objects was grossly impaired. Thus, in contrast with D. F., who was able to reach and orient her hand posture toward different objects that she could not perceive, V. K. was unable to coordinate reaching and grasping for objects that she could perceive.

This difficulty was not merely one of being unable to direct movements in space, because V. K. could point to objects. What she could not do was to form the appropriate hand postures needed to grasp objects of different shapes, as illustrated in Figure 13.14. Taken together, cases D. F. and V. K. suggest that the mechanisms underlying the conscious perception of object form are dissociable from the mechanisms controlling visually guided movements to the same objects.

Cases D. and T.: Higher-Level Visual Processes

Two cases described by Campbell and colleagues illustrate an intriguing dissociation of visual functions. Case D. has a right occipitotemporal lesion associated with a left upper quadrantanopia that extends into the lower quadrant. As would be expected from B. K.'s case, D. had some initial difficulties in reading, but her language abilities were intact. Curiously, she was completely unable to recognize people by their faces and had difficulty identifying handwriting, including her own.

Recall from the case presented at the beginning of this chapter that P. M. also had difficulty in recognizing faces. His view on his difficulty was that, although he could see the different bits of the face quite clearly, he had trouble putting it all together because, unless a person was a long way off, the entire face was not in the visual field all at once. You can imagine what it would be like to try to recognize people by looking at snapshots of different parts of their faces.

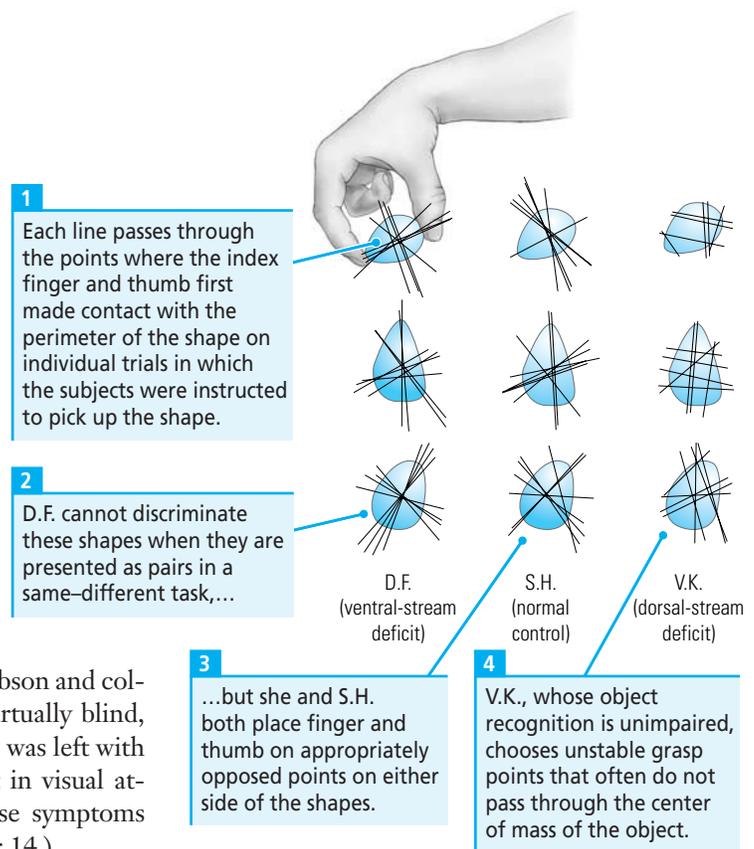


Figure 13.14 The brain has different systems for visual object recognition and visual guidance of movement. Representative “grasping” axes for three different shapes by patient D. F. with visual form agnosia (ventral-stream deficit), by control subject S. H. with no brain damage and by V. K., a patient with bilateral occipitoparietal damage resulting in optic ataxia (dorsal-stream deficit). Even though D. F. does not recognize the object, she perceives enough information about shape to control her grasp as she picks it up. In contrast, V. K. recognizes objects but cannot control her movements in relation to them. (Adapted from Milner and Goodale, 1995.)

The facial-recognition deficit, **prosopagnosia**, is particularly interesting because many prosopagnosics cannot recognize even their own faces in a mirror. Although D. could not recognize faces, she could make use of information in faces. For example, when given various tests of lip reading, she appeared completely normal. Furthermore, she could imitate the facial movements and expressions of another person.

Case T. provides an interesting contrast to case D. Case T. has a left occipitotemporal lesion with a right hemianopia. She had great difficulty reading (**alexia**) and was unable to name colors, even though she could discriminate them. In contrast with D., T. had no difficulty in recognizing familiar faces but was impaired in lip reading.

Taken together, cases D. and T. indicate that face identification and the extraction of speech information from faces do not call on the same cortical systems. In addition, the fact that D. has a lesion on the right and a deficit in face identification and that T. has a lesion on the left and a deficit in lip reading suggests a relative asymmetry in some aspects of occipital-lobe functions. Exactly what visual processes are impaired in the two cases and what the necessary lesions for deficits in facial recognition and lip reading might be remain to be shown.

Conclusions from Case Studies

Several conclusions can be extracted from the behavior and pathology of these cases:

- There are clearly distinct syndromes of visual disturbance.
- Some symptoms can be taken as evidence of a fundamental dissociation between vision for guiding movements (the dorsal stream) and visual recognition (the ventral stream).
- The dissociability of the symptoms in the various patients implies that our introspective view of a unified visual experience is false. The fact that objects can be seen when they are still but not when they are moving is particularly disturbing, because it seems to defy the commonsense view that an object is the same object whether it is moving or still. Clearly the brain does not treat objects in the same way in the two conditions.
- Neuroscientists have at least suggestive evidence of an asymmetry in occipital-lobe functions.

Visual Agnosia

A difficulty in describing the symptomatology and pathology of agnosia is the bewildering variety of patients and symptoms discussed in the neurological literature. Another, as Farah has pointed out, is that there is no agreement on a taxonomy of agnosia, which makes classifying different patterns of symptoms very difficult. We shall separate visual agnosias into object agnosias and other agnosias.

Object Agnosias

The traditional way to classify visual-object agnosia is to distinguish two broad forms: apperceptive agnosia and associative agnosia.

Apperceptive Agnosia

Any failure of object recognition in which relatively basic visual functions (acuity, color, motion) are preserved is apperceptive. This agnosia category has been applied to an extremely heterogeneous set of patients, but the fundamental deficit is an inability to develop a percept of the structure of an object or objects. In the simplest case, patients are simply unable to recognize, copy, or match simple shapes, much like case D. F.

Many patients have another unusual symptom, too—often referred to as **simultagnosia**. In this case, patients can perceive the basic shape of an object, but they are unable to perceive more than one object at a time. Thus, if two objects are presented together, only one is perceived. Such patients often act as though they were blind, possibly because they are simply overwhelmed by the task at hand. Imagine trying to see the world one object at a time.

Apperceptive agnosia does not result from a restricted lesion but usually follows gross bilateral damage to the lateral parts of the occipital lobes, including regions sending outputs to the ventral stream. Such injuries are probably most commonly associated with carbon monoxide poisoning, which appears to produce neuronal death in “watershed” regions—that is, regions lying in the border areas between territories of different arterial systems.

Associative Agnosia

The inability to recognize an object despite an apparent perception of the object is associative agnosia. Thus, the associative agnosic can copy a drawing rather accurately, indicating a coherent percept, but cannot identify it. Associative agnosia is therefore conceived as being at a “higher cognitive” level of processing that is associated with stored information about objects—that is, with memory.

In effect, failure of object recognition is a defect in memory that affects not only past knowledge about the object but also the acquisition of new knowledge. Associative agnosias are more likely with damage to regions in the ventral stream that are farther up the processing hierarchy, such as the anterior temporal lobe.

Other Agnosias

A critical point in understanding the nature of visual agnosia is that the most commonly affected region is the tissue at the occipitotemporal border, which is part of the ventral visual pathway. Visual agnosias do not appear to result from damage to the dorsal stream. Note, however, that agnosias are at least partly dissociable, which means that there must be different streams of visual information processing within the ventral pathway. We now briefly consider three other visual agnosias.

Prosopagnosia

Patients with facial agnosia (recall cases D. and P. M.) cannot recognize any previously known faces, including their own as seen in a mirror or photograph. They can recognize people by face information, however, such as a birthmark, mustache, or characteristic hairdo.

Prosopagnosics may not accept the fact that they cannot recognize their own faces, probably because they know who must be in the mirror and thus see themselves. We saw one young woman who was convinced of the severity of her problem only when she was presented with her identical twin sister. When asked who her twin was, she indicated that she had never seen the woman before. Imagine her amazement to discover that the person was her twin sister.

According to Damasio and colleagues, most facial agnosics can tell human from nonhuman faces and can recognize facial expressions normally. All post-mortem studies on facial agnosics have found bilateral damage, and the results of imaging studies in living patients confirm the bilateral nature of the injury in most patients, with the damage centered in the region below the calcarine fissure at the temporal junction. These results imply that the process of facial recognition is probably bilateral, but asymmetrical.

Alexia

An inability to read has often been seen as the complementary symptom to facial-recognition deficits. Alexia is most likely to result from damage to the left fusiform and lingual areas. Either hemisphere can read letters, but only the left hemisphere appears able to combine the letters to form lexical representations (that is, words). Alexia can be conceived to be a form of object agnosia in which there is an inability to construct perceptual wholes from parts or to be a form of associative agnosia, in which case word memory (the lexical store) is either damaged or inaccessible.

Visuospatial Agnosia

Among this variety of disorders of spatial perception and orientation, one disruptive form is *topographical disorientation*—the inability to find one's way around familiar environments such as one's neighborhood. People with this deficit seem unable to recognize landmarks that would indicate the appropriate direction in which to travel. Most people with topographical disorientation have other visual deficits, especially defects in facial recognition. Thus, it is not surprising to find that the critical area for this disorder lies in the right medial occipitotemporal region, including the fusiform and lingual gyri.

Why Are Faces Special?

Most of us probably spend more time looking at faces than at any other single stimulus. Infants prefer to look at faces almost from birth, and adults are excellent at identifying familiar faces despite large variations in expression and viewing angles, even when the faces are disguised with beards, spectacles, or hats. Faces also convey a wealth of social information, and we humans are unique among primates in spending a good deal of time looking directly at the faces of other members of our species.



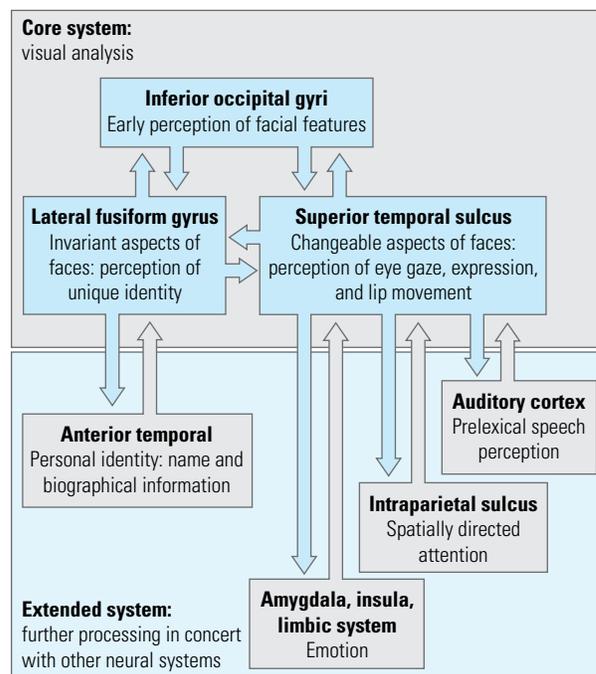
Figure 13.15 The “Thatcher illusion.” Look at the face of former British Prime Minister Margaret Thatcher as presented (upside down) and then invert the page and look again. There is a compelling illusion of normalcy in the inverted face but, in the upright view, the reconfigured face appears hideous. Lady Thatcher was the original subject of the illusion that now bears her name.

The importance of faces as visual stimuli has led to the idea that a special pathway exists in the visual system for the analysis of faces (see Farah, 1998, for a review). Several lines of evidence support this view. In the first place, the results of studies of monkeys show neurons in the temporal lobe that are specifically tuned to different faces, with some cells attuned to facial identity and others to facial expression. (We return to these cells in Chapter 15.) In the second place, inverting a photograph of any object that has a usual right side up makes it harder to recognize, but the effect on faces is disproportionate (see a review by Valentine).

Similarly, we are particularly sensitive to the configuration of upright faces. Consider the illusion shown in Figure 13.15, which illustrates this effect. The importance of an upright orientation to facial perception is also seen in imaging studies. For example, Haxby and his colleagues showed that inverted faces are processed by the same cortical regions as are other visual stimuli, whereas upright faces are processed in a separate face-perception system. This face-perception system is surprisingly extensive and includes regions not only in the occipital lobe but also in several different regions of the temporal lobe.

Figure 13.16 summarizes a model by Haxby and colleagues in which different aspects of facial perception (such as facial expression versus identity) are analyzed in core visual areas in the temporal part of the ventral stream. The model also includes other cortical regions as an “extended system” that includes the analysis of other facial characteristics such as emotion and lip reading. The key point here is that the analysis of faces is unlike that of other visual stimuli.

Figure 13.16 A model of the distributed human neural system for face perception. The model is divided into a core system, consisting of occipital and temporal regions, and an extended system, including regions that are part of neural systems for other cognitive functions. The fusiform gyrus is an occipital region lying on the ventral surface of the temporal lobe. (After Haxby, Hoffman, and Gobbini, 2000.)



(A) Original face



(B) Composite of right sides



(C) Composite of the left sides



Figure 13.17 The split-faces test. Subjects were asked which of the two pictures, B or C, most closely resembles picture A. Control subjects chose picture C significantly more often than picture B. Picture C corresponds to that part of picture A falling in a subject's left visual field. The woman pictured chose B, the view that she is accustomed to seeing in the mirror. (After Kolb, Milner, and Taylor, 1983.)

Finally, a clear asymmetry exists in the role of the temporal lobes in the analysis of faces. Right temporal lesions have a greater effect on facial processing than do similar left temporal lesions. Even in control subjects, researchers can see an asymmetry in face perception.

We presented subjects with photographs of faces, as illustrated in Figure 13.17. Photographs B and C are composites of the right or the left sides, respectively, of the original face shown in photograph A. Asked to identify which composite most resembled the original, normal subjects consistently matched the left side of photograph A to its composite in photograph C, whether the photographs were presented upright or inverted. Furthermore, patients with either right temporal or right parietal removals failed to consistently match either side of the face in either the upright or the inverted presentation.

The results of this split-faces test not only show an asymmetry in facial processing but also speak to the nature of our perceptions of our own faces. Self-perception provides a unique example of visual perception, because your own image of your face comes largely from looking in a mirror, where the image is reversed, whereas the image that others have of your face comes from direct view. Inspection of Figure 13.17 illustrates the implications of this difference. Photograph A is the image that other people see of this woman and, because there is a left-visual-field bias in our perception, most right-handers choose photograph C as the picture most resembling the original. Consider the choice of the woman herself, however. Her common view of her face (in the mirror) is the reverse of ours, and hence she is more likely to choose (and in fact did choose) composite photograph B as most resembling her own face.

An intriguing consequence of our biased self-facial image is our opinion of personal photographs. Many people complain about not being photogenic, that their photographs are never taken at the correct angle, that their hair wasn't just right, and so on. The problem may be rather different: we are accustomed to seeing ourselves in a mirror image and hence, when we view a photograph, we are biased to look at the side of the face that we do not nor-

mally perceive selectively in the mirror. Indeed, we appear not to see ourselves as others see us. The more asymmetrical the face, the less flattering the person will see his or her image to be.

Visual Imagery

Our ability to conjure up mental images of things that cannot be perceived is central to human thought. Visualization is crucial in problem-solving tasks such as mental arithmetic, map reading, and mechanical reasoning. How crucial can be seen in a patient such as D. E., who was unable to copy drawings or to recognize actual objects but who could nonetheless produce drawings of the same objects from memory (see Figure 13.12).

Behrmann and colleagues described another such patient, C. K. The curious thing about C. K. is that, although he cannot recognize objects, he can imagine them and can draw them in considerable detail from memory. This ability implies some dissociation between the neural system dealing with object perception and that dealing with the generation of images. We can conclude that neural structures mediating the perception and visualization of objects are unlikely to be completely independent, but it is clear that a deficit in object perception cannot be due simply to a loss of mental representations (that is, memory) of objects.

There has been considerable controversy over whether mental rotation of objects might be localized to some region of the right hemisphere. In her review of this literature, Farah concludes that the studies have been “distressingly inconsistent.” She proposes that mental rotation probably entails both hemispheres, with some degree of right-hemisphere superiority. (For more detail, see both Farah and Kosslyn.)

Nonetheless, it does seem likely that mental rotation implicates structures related to the dorsal stream. We can imagine that, before a brain could visualize rotating an object, it would first have to have actually rotated it manually. It is a small step to presume that visualizing an object rotating requires the activation of at least part of the motor cortex—the regions needed to actually do it.

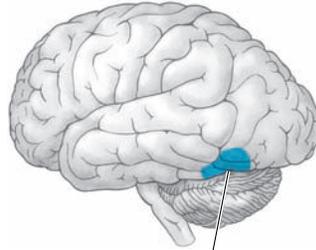
In the past two decades, cognitive neuroscientists have conducted a flurry of imaging studies designed to identify the neural events underlying the generation of a mental image. Farah concludes that, although the data are noisy, a reasonably consistent answer is emerging from the results of imaging studies such as the one described in the Snapshot on page 342. Mental imagery appears to be a top-down activation of a subset of the brain’s visual areas. In other words, at least some cortical areas are used both for perception and for visualization.

These common areas carry the same representational functions for both purposes, carrying information specifically about color, shape, spatial location, and so on. There is evidence for a distinct mechanism for image generation as well, one separate from the processes needed for perception. Farah notes that the evidence, although mixed, points to a region in the left temporo-occipital region as the key location for this mechanism.

Generating Mental Images

What is the neural basis for visual imagery? It may result from activity in the same visual areas that are active when an image is actually viewed. Another possibility is that some other region of the brain is selectively active when we imagine.

D'Esposito and colleagues addressed this question in an fMRI study by asking subjects to generate mental images from memory, cued by an aurally presented word such as "tree." These cues were common objects rather than abstract representations ("tree" rather than "love," for example). The subjects kept their eyes closed throughout the experiment so that any neural activation could be attributed to imagery rather than to direct activation of the visual pathways. In the baseline condition, the subjects heard abstract words that would not easily allow any image formation, and they were asked simply to listen to the words.



Left temporo-occipital region
(fusiform gyrus, area 37)

The results (illustrated here) show that visualizing concrete words increases activation in the left posterior temporo-occipital region, corresponding to the fusiform gyrus (area 37). There was no activation in area V1. The fMRI data are consistent with those of other imaging studies, as well as with a case history of a patient with a left-occipital lobectomy (including area 37) who had a hemianopia in both real and imagined stimuli. The pronounced asymmetry is consistent with Farah's hypothesis that, in most people, the left hemisphere is specialized for image generation.

(M. D'Esposito, J. A. Detre, G. K. Aguirre, M. Stallcup, D. C. Alsop, L. J. Tippet, and M. J. Farah. A functional MRI study of mental image generation. *Neuropsychologia* 35:725–730, 1997.)

Summary

The function of the occipital lobe is vision, but visual functions extend beyond the occipital lobe. Separate anatomical regions within the occipital lobe take part in the perception of form, movement, and color. Occipital structures are merely the beginning of visual processing because multiple visual systems can be divided into at least three major routes, one going ventrally into the temporal lobe, another going dorsally into the parietal lobe, and a middle route going to the superior temporal sulcus. The ventral stream is most certainly implicated in various aspects of stimulus recognition. The dorsal stream is for the guidance of movement in space. The representation of spatial information relies on the recognition of cues within the environment, which would therefore make visuospatial recognition dependent on processing in the ventral stream. An important aspect of the dorsal–ventral distinction in visual processing is that neither route is a single system. Rather, clearly dissociable subsystems take part in various functions. Finally, some occipital regions, especially those adjoining the temporal cortex, may be functionally asymmetrical. In particular, there appears to be some specialization for word recognition on the left and facial recognition and mental rotation on the right.

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