visual information, different regions of the brain and different kinds of processing are required.

There is more. Consider your coffee mug. It has a shape and it has a color pattern. Yet you are not consciously aware of each of these attributes separately, as depicted in Figure 8-1B. Instead, you perceive the patterned mug to be a single object. It may therefore surprise you to learn that your brain produces this unified perception after analyzing color separately from shape, each analysis in a different neural location. Consequently, people can have brain damage that allows them to see the color of an object but to have no idea of what the object is, because its shape is indecipherable.

Conversely, a person with another sort of brain damage might see the shape of an object clearly but have no clue to its color. The brain essentially dissects the object, analyzes the various parts separately, and then produces what appears to be a unified perception of the whole. Yet there is no “picture” of the entire object in one place in the brain. How, then, do we perceive a single object if we have only multiple mental versions of it with which to work? You may recall from Chapter 2 that we referred to this conundrum as the binding problem. We will return to this fascinating question later.

**In Review**

We identified two key points about sensation and perception. First, our perceptions of the world are entirely a creation of the brain. Different species and, to a lesser extent, different individual members of a species have different perceptions of what the world is really like. Neither is right or wrong, but both are imaginary. Second, the brain does not analyze sensory information as though it were uniform. Rather, sensory information entering the brain is dissected and passed to specialized regions that analyze particular characteristics. We only have the impression that we perceive a unified sensory world. This binding problem is one of the puzzles of how the brain works. Before returning to that puzzle, we must first identify how the visual system breaks down visual stimuli.

**ANATOMY OF THE VISUAL SYSTEM**

Vision is our primary sensory experience. Far more of the human brain is dedicated to vision than to any of our other senses. Understanding the organization of the visual system is therefore key to understanding human brain function. To build this understanding, we begin by following the routes that visual information takes to the brain and within it. This exercise is a bit like traveling a road to discover where it goes. The first step is to consider what the visual system analyzes—namely, light.

**Light: The Stimulus for Vision**

Simply put, light is electromagnetic energy that we see. This energy comes either directly from a source, such as a lamp or the sun, that produces it or indirectly after having been reflected off one or more objects. In either case, light energy travels from the outside world, through the pupil, and into the eye, where it strikes a light-sensitive surface on the back of the eye called the **retina**. From this stimulation of receptors on the retina, we start the process of creating a visual world.
A useful way to represent light is as a continuously moving wave. Not all light waves are the same length, however. **Figure 8-2** shows that, within the rather narrow range of electromagnetic energy visible to humans, the wavelength varies from about 400 nanometers (violet) to 700 nanometers (red). (A nanometer, abbreviated nm, is one-billionth of a meter.)

The range of visible light is constrained not by the properties of light waves but rather by the properties of our visual receptors. If our receptors could detect light in the ultraviolet or infrared range, we would see additional colors. In fact, bees detect light in both the visible and the ultraviolet range and so have a broader range of color perception than we do.

**Structure of the Eye**

How do the cells of the retina absorb light energy and initiate the processes leading to vision? To answer this question, we first consider the structure of the eye as a whole so that you can understand how it is designed to capture and focus light. Only then do we consider the photoreceptor cells.

The functionally distinct parts of the eye are shown in **Figure 8-3**. They include the *sclera*, the white part that forms the eyeball; the *cornea*, the eye's clear outer covering;
the iris, which opens and closes to allow more or less light in; the lens, which focuses light; and the retina, where light energy initiates neural activity. As light enters the eye, it is bent first by the cornea, travels through the hole in the iris called the pupil, and is then bent again by the lens. The curvature of the cornea is fixed, and so the bending of light waves there is fixed, whereas small muscles adjust the curvature of the lens.

The shape of the lens adjusts to bend the light to greater or lesser degrees. This ability allows near and far images to be focused on the retina. When images are not properly focused, we require a corrective lens, as discussed in “Optical Errors of Refraction and Visual Illuminance.”

Figure 8-4 includes a photograph of the retina, which is composed of photoreceptors beneath a layer of neurons connected to them. Although the neurons lie in front of the photoreceptor cells, they do not prevent incoming light from being absorbed by those receptors, because the neurons are transparent and the photoreceptors are extremely sensitive to light. (The neurons in the retina are insensitive to light and so are unaffected by the light passing through them.)

Together, the photoreceptor cells and the neurons of the retina perform some amazing functions. They translate light into action potentials, discriminate wavelengths so that we can distinguish colors, and work in a range of light intensities from very bright to very dim. These cells afford visual precision sufficient for us to see a human hair lying on the page of this book from a distance of 18 inches.

As in a camera, the image of objects projected onto the retina is upside down and backward. This flip-flopped orientation poses no problem for the brain. Remember that the brain is creating the outside world, and so it does not really care how the image is oriented initially. In fact, the brain can make adjustments regardless of the orientation of the images that it receives.

In fact, if you were to put on glasses that invert visual images and kept those glasses on for several days, the world would first appear upside down but then would suddenly appear right side up again because your brain would correct the distortion (Held, 1968). Curiously, when you removed the glasses, the world would temporarily seem upside down once more, because your brain at first would be unaware that you had tricked it another time. Eventually, though, your brain would solve this puzzle, too, and the world would flip back in the right orientation.

THE BLIND SPOT

Try this experiment. Stand with your head over a tabletop and hold a pencil in your hand. Close one eye. Stare at the edge of the tabletop nearest you. Now hold the pencil in a horizontal position and move it along the edge of the table, with the eraser on the table. Beginning at a point approximately below your nose, move the pencil slowly along the table in the direction of the open eye.

When you have moved the pencil about 6 inches, the eraser will vanish. You have found your blind spot, a small area of the retina that is also known as the optic disc. As shown on the far right in Figure 8-3, the optic disc is the area where blood vessels enter and exit the eye and where fibers leading from retinal neurons form the optic nerve that
Optical Errors of Refraction and Visual Illuminance

The eye, like a camera, works correctly only when sufficient light passes through the lens and is focused on the receptor surface—the retina of the eye or the film in the camera. Too little light entering the eye or the camera produces a problem of visual illuminance: it is hard to see any image at all. If the focal point of the light is slightly in front of the receptor surface or slightly behind it, a refractive error causes objects to appear blurry.

Refractive errors in the eye are of two basic types. Most common in young people (afflicting about 50 percent of the population) is myopia (nearsightedness), an inability to bring distant objects into clear focus. Myopia is most commonly caused by the normally round eyeball being elongated instead. Myopia can also be caused by excessive curvature of the front of the cornea. In either case, the focal point of light falls short of the retina.

In hyperopia (farsightedness), a less common refractive error in which people are unable to focus on near objects, the focal point of light falls beyond the retina. Whereas the myopic eyeball may be too long, the hyperopic eyeball may be too short. Farsightedness may also result because the lens is too flat and does not adequately refract light. As people age, the lens loses its elasticity and consequently becomes unable to refract light from nearby objects correctly.

This form of hyperopia is called presbyopia (old sightedness). Presbyopia is so common that it is rare to find people older than 50 who do not need glasses to see up close, especially for reading. Fortunately, this error and other errors of refraction can be cured by corrective lenses.

An additional complication to the aging eye cannot be cured by corrective lenses. As we age, the eye’s lens and cornea allow less light through, and so less light strikes the retina—a problem of visual illuminance. Don Kline (1994) estimated that, between ages 20 and 40, there is a drop of 50 percent in visual illuminance in dim lighting and a further drop of 50 percent over every 20 additional years. As a result, it becomes increasingly difficult to see in dim light, especially at night.

Corrective lenses do not compensate for this reduced visual illuminance; the only solution is to increase lighting. Night vision is especially problematic. Not surprisingly, statistics show a marked drop in the number of people driving at night in each successive decade after age 40.

These photographs represent the drop in visual illuminance that occurs between age 20 (left) and age 60 (right).
goes to the brain. There are therefore no photoreceptors in this part of the retina, and so you cannot see with it. Figure 8-5 enables you to demonstrate your own blind spot.

Fortunately, your visual system solves the blindspot problem by locating the optic disc in a different location in each of your eyes. The optic disc is lateral to the fovea in each eye, which means that it is left of the fovea in the left eye and right of the fovea in the right eye. Because the visual world of the two eyes overlaps, the blind spot of the left eye can be seen by the right eye and visa versa.

Thus, using both eyes together, you can see the whole visual world. People with blindness in one eye have a greater problem, however, because the sightless eye cannot compensate for the blind spot in the functioning eye. Still, the visual system compensates for the blind spot in several other ways, and so people who are blind in one eye have no sense of a hole in their field of vision.

The optic disc that produces a blind spot is of particular importance in neurology. It allows neurologists to indirectly view the condition of the optic nerve that lies behind it while providing a window onto events within the brain.

If there is an increase in intracranial pressure, such as occurs with a tumor or brain abscess (infection), the optic disc swells, leading to a condition known as papilloedema (swollen disc). The swelling occurs in part because, like all neural tissue, the optic nerve is surrounded by cerebrospinal fluid. Pressure inside the cranium can displace this fluid around the optic nerve, causing swelling at the optic disc.

Another reason for papilloedema is inflammation of the optic nerve itself, a condition known as optic neuritis. Whatever the cause, a person with a swollen optic disc usually loses vision owing to pressure on the optic nerve. If the swelling is due to optic neuritis, probably the most common neurological visual disorder, the prognosis for recovery is good.

THE FOVEA

Now try another experiment. Focus on the print at the left edge of this page. The words will be clearly legible. Now, while holding your eyes still, try to read the words on the right side of the page. It will be very difficult and likely impossible, even though you can see that words are there.

The lesson is that our vision is better in the center of the visual field than at the margins, or periphery. This difference is partly due to the fact that photoreceptors are more densely packed at the center of the retina, in a region known as the fovea. Figure 8-4 shows that the surface of the retina is depressed at the fovea. This depression is formed because many of the fibers of the optic nerve skirt the fovea to facilitate light access to its receptors.

Photoreceptors

The retina's photoreceptor cells convert light energy first into chemical energy and then into neural activity. When light strikes a photoreceptor, it triggers a series of chemical reactions that lead to a change in membrane potential. This change in turn leads to a change in the release of neurotransmitter onto nearby neurons.

**Fovea.** Region at the center of the retina that is specialized for high acuity; its receptive fields are at the center of the eye's visual field.

**Rod.** Photoreceptor specialized for functioning at low light levels.

**Cone.** Photoreceptor specialized for color and high visual acuity.
Rods and cones, the two types of photoreceptors, differ in many ways. As you can see in Figure 8-6, they are structurally different. Rods are longer than cones and cylindrically shaped at one end, whereas cones have a tapered end. **Rods**, which are more numerous than cones, are sensitive to low levels of brightness (luminance), especially in dim light, and are used mainly for night vision. **Cones** do not respond to dim light, but they are highly responsive in bright light. Cones mediate both color vision and our ability to see fine detail.

Rods and cones are not evenly distributed over the retina. The fovea has only cones, but their density drops dramatically at either side of the fovea. For this reason, our vision is not so sharp at the edges of the visual field, as demonstrated earlier.

A final difference between rods and cones is in their light-absorbing pigments. Although both rods and cones have pigments that absorb light, all rods have the same pigment, whereas cones have three different pigment types. Any given cone has one of these three cone pigments. The four different pigments, one in the rods and three in the cones, form the basis of our vision.

The three types of cone pigments absorb light over a range of frequencies, but their maximum absorptions are at about 419, 531, and 559 nm, respectively. The small range of wavelengths to which each cone pigment is maximally responsive is shown in Figure 8-7. Cones that contain these pigments are called “blue,” “green,” and “red,” respectively, loosely referring to colors in their range of peak sensitivity.

Note, however, that if you were to look at lights with wavelengths of 419, 531, and 559 nm, they would not appear blue, green, and red but rather violet, blue green, and yellow green, as you can see on the background spectrum in Figure 8-7. Remember, though, that you are looking at the lights with all three of your cone types and that each cone pigment is responsive to light across a range of frequencies, not just to its frequency of maximum absorption. So the terms blue, green, and red cones are not that far off the mark. Perhaps it would be more accurate to describe these three cone types as responsive to short, middle, and long visible wavelengths, referring to the relative length of light waves at which their sensitivities peak.

Not only does the presence of three different cone receptors contribute to our perception of color, so does the relative number and distribution of cone types across the retina. As Figure 8-8 shows, the three cone types are distributed more or less randomly across the retina, making our ability to perceive different colors fairly constant across the visual field. Although there are approximately equal...
numbers of red and green cones, there are fewer blue cones, which means that we are not as sensitive to wavelengths in the blue part of the visible spectrum.

Other species that have color vision similar to that of humans also have three types of cones, with three color pigments. But, because of slight variations in these pigments, the exact frequencies of maximum absorption differ among different species. For humans, the exact frequencies are not identical with the numbers given earlier, which were an average across mammals. They are actually 426 and 530 nm for the blue and green cones, respectively, and 552 or 557 nm for the red cone. There are two peak sensitivity levels given for red because humans, as stated earlier, have two variants of the red cone. The difference in these two red cones appears minuscule, but recall that it does make a functional difference in color perception.

This functional difference between the two human variants of red cone becomes especially apparent in some women. The gene for the red cone is carried on the X chromosome. Because males have only one X chromosome, they have only one of these genes and so only one type of red cone. The situation is more complicated for women. Although most women have only one type of red cone, some have both, with the result that they are more sensitive than the rest of us to color differences at the red end of the spectrum. Their color receptors create a world with a richer range of red experiences. However, these women also have to contend with peculiar-seeming color coordination by others.

## Retinal Neuron Types

Figure 8-9 shows that the photoreceptors in the retina are connected to two layers of retinal neurons. In the procession from the rods and cones toward the brain, the first layer contains three types of cells: bipolar cells, horizontal cells, and amacrine cells. Two cell types in the first neural layer are essentially linkage cells. The horizontal cells link photoreceptors with bipolar cells, whereas the amacrine cells link bipolar cells with cells of the second neural layer, the retinal ganglion cells. The axons of the ganglion cells collect in a bundle at the optic disc and leave the eye to form the optic nerve.

Retinal ganglion cells are not all the same in regard to the brain cells to which they connect. They fall into two major categories, which in the primate retina are called M and P cells. The designations M and P derive from the distinctly different populations of cells in the visual thalamus to which these two classes of ganglion cells send their axons.

As shown in Figure 8-10, one of these populations consists of magnocellular cells (hence M), whereas the other consists of parvocellular cells (hence P). M cells, which are larger (magno means "large" in Latin), receive their input primarily from rods and so are sensitive to light but not to color. P cells, which are smaller (parvo means "small" in Latin), receive their input primarily from cones and so are sensitive to color.

M cells are found throughout the retina, including the periphery, where we are sensitive to movement but not to color or fine details. P cells are found largely in
Visual Pathways

Imagine leaving your house and finding yourself on an unfamiliar road. Because the road is not on any map, the only way to find out where it goes is to follow it. You soon discover that the road divides in two, and so you must follow each branch sequentially to figure out its end point. Suppose you learn that one branch goes to a city, whereas the other goes to a national park. By knowing the end point of each branch, you can conclude something about their respective functions—that one branch carries people to work, whereas the other carries them to play, for example.

The same strategy can be used to follow the paths of the visual system. The retinal ganglion cells form the optic nerve, which is the road into the brain. This road travels to several places, each with a different function. By finding out where the branches go, we can begin to guess what the brain is doing with the visual input and how the brain creates our visual world.

Let us begin with the optic nerves, one exiting from each eye. You may know that they are formed by the axons of ganglion cells leaving the retina. Just before entering the brain, the optic nerves partly cross, forming the optic chiasm (from the shape of the Greek letter χ).

About half the fibers from each eye cross in such a way that the left half of each optic nerve goes to the left side of the brain, whereas the right halves go to the brain's right side, as diagrammed in Figure 8-11. The medial path of each retina, the nasal retina, crosses to the opposite side. The lateral path, the temporal retina, goes straight back on the same side. Because the light that falls on the right half of the retina actually comes from the left side of the
Flow of Visual Information into the Brain

The optic nerve has two principal branches: (1) the geniculostriate system through the LGN in the thalamus to the primary visual cortex and (2) the tectopulvinar system through the superior colliculus of the tectum to the pulvinar region of the thalamus and thus to the temporal and parietal lobes.

Figure 8-13

Striate Cortex

The primary visual cortex is referred to as striate cortex because it appears to have striations (stripes) when stained with either a cell-body stain (left) or a myelin stain (right) in these sections from a rhesus monkey brain.

Geniculostriate system

Projections from the retina to the lateral geniculate nucleus of the thalamus.

Striate cortex

Primary visual cortex in the occipital lobe; its striped appearance when stained gives it this name.

Tectopulvinar system

Projections from the retina to the superior colliculus to the pulvinar (thalamus) to the parietal and temporal visual areas.

Brain

Visual information from the visual field, information from the left visual field goes to the brain’s right hemisphere, whereas information from the right visual field goes to the left hemisphere. Thus, half of each retina’s visual field is represented on each side of the brain.

Having entered the brain, the axons of the ganglion cells separate, forming two distinct pathways, charted in Figure 8-12. All the axons of the P ganglion cells and some of the M ganglion cells form a pathway called the geniculostriate system. This pathway goes from the retina to the lateral geniculate nucleus (LGN) of the thalamus and then to layer IV of the primary visual cortex, which is in the occipital lobe.

As Figure 8-13 shows, the primary visual cortex appears to have a broad stripe across it in layer IV and so is known as striate cortex. The term geniculostriate therefore means a bridge between the thalamus (geniculate) and the striate cortex. From the striate cortex, the axon pathway now splits, with one route going to vision-related regions of the parietal lobe and another route going to vision-related regions of the temporal lobe.

The second pathway leading from the eye is formed by the axons of the remaining M ganglion cells. These cells send their axons to the superior colliculus (located in the tectum of the midbrain; see Chapter 2). The superior colliculus sends connections to a region of the thalamus known as the pulvinar. This pathway is therefore known as the tectopulvinar system because it goes from the eye through the tectum to the pulvinar (see Figure 8-12). The pulvinar then sends connections to the parietal and temporal lobe.

To summarize, two principal pathways extend into the visual brain—namely, the geniculostriate and tectopulvinar systems. Each pathway eventually travels either to the parietal or the temporal lobe. Our next task is to determine the respective roles of the parietal lobe and the temporal lobe in creating our visual world.

Dorsal and Ventral Visual Streams

Identification of the temporal- and parietal-lobe visual pathways led researchers on a search for the possible functions of each. One way to examine these functions is to ask why evolution would produce two different destinations for the pathways in the brain. The answer is that each route must create visual knowledge for a different purpose.

David Milner and Mel Goodale (1995) proposed that these two purposes are to identify what a stimulus is (the “what” function) and to use visual information to control movement (the “how” function). Many authors have emphasized the role of the lateral geniculate nucleus (LGN) in the control of visual processing.
pathway as a “where” function. The problem is that “where” is a property of “what” a stimulus is as well as a cue for “how” to control movement to a place. We therefore will use the “what–how” distinction suggested by Milner and Goodale.

This “what” versus “how” distinction came from an analysis of where visual information goes when it leaves the striate cortex. Figure 8-14 shows the two distinct visual pathways that originate in the striate cortex, one progressing to the temporal lobe and the other to the parietal lobe. The pathway to the temporal lobe has become known as the ventral stream, whereas the pathway to the parietal lobe has become known as the dorsal stream.

To understand how these two streams function, we need to return to the details of how the visual input from the eyes contributes to them. Both the geniculostriate and the tectopulvinar systems contribute to the dorsal and ventral streams.

**GENICULOSTRIATE PATHWAY**

The retinal ganglion-cell fibers from the two eyes distribute their connections to the two lateral geniculate nuclei (left and right) of the thalamus in what at first glance appears to be an unusual arrangement. As seen in Figure 8-11, the fibers from the left half of each retina go to the left LGN, whereas those from the right half of each retina go to the right LGN. But the fibers from each eye do not go to exactly the same place in the LGN.

Each LGN has six layers, and the projections from the two eyes go to different layers, as illustrated in anatomical context in Figure 8-10 and alone in Figure 8-15. Layers 2, 3, and 5 receive fibers from the ipsilateral eye (i.e., the eye on the same side), whereas layers 1, 4, and 6 receive fibers from the contralateral eye (i.e., the eye on the opposite side). This arrangement provides for combining the information from the two eyes and for segregating the information from the P and M ganglion cells.

Axons from the P cells go only to layers 3 through 6 (referred to as the parvocellular layers), whereas axons from the M cells go only to layers 1 and 2 (referred to as the magnocellular layers). Because the P ganglion cells are responsive to color and fine detail, layers 3 through 6 of the LGN must be processing information about color and form. In contrast, the M cells mostly process information about movement, and so layers 1 and 2 must deal with movement.

Before we continue, you should be aware that just as there are six layers of the LGN (numbered 1 through 6), there are also six layers of the striate cortex (numbered I through VI). That there happen to be six layers in each of these locations is an accident of evolution found in all primate brains. Let us now see where these LGN cells send their connections in the visual cortex.

You learned in Chapter 2 that layer IV is the main afferent (incoming) layer of the cortex. Layer IV of the visual cortex has several sublayers, two of which are known as IVCα and IVCβ. LGN layers 1 and 2 go to IVCα, and layers 3 through 6 go to IVCβ. As a result, a distinction between the P and M functions continues in the cortex.

As illustrated in Figure 8-16, input from the two eyes also remains separated in the cortex but through a different mechanism. The input from the ipsilaterally
connected LGN cells (that is, layers 2, 3, and 5) and the input from the contralaterally connected LGN cells (layers 1, 4, and 6) go to adjacent strips of cortex. These strips, which are about 0.5 millimeter across, are known as cortical columns. We return to the concept of cortical columns shortly.

In summary, the P and M ganglion cells of the retina send separate pathways to the thalamus, and this segregation remains in the striate cortex. The left and right eyes also send separate pathways to the thalamus, and these pathways, too, remain segregated in the striate cortex.

TEC Topulvinar PATHWAY
As already noted, the tectopulvinar pathway is formed by the axons of the remaining M ganglion cells. These cells send their axons to the superior colliculus in the midbrain’s tectum, which functions to detect the location of stimuli and to shift the eyes toward stimuli. The superior colliculus sends connections to the region of the thalamus known as the pulvinar.

The pulvinar has two main divisions: medial and lateral. The medial pulvinar sends connections to the parietal lobe, whereas the lateral pulvinar sends connections to the temporal lobe. One type of information that these connections are conveying is related to “where,” which, as noted earlier, is important in both “what” and “how” functions.

The “where” function of the tectopulvinar system is useful in understanding blindsight in D.B. His geniculostriate system was disrupted but his tectopulvinar system was not, thus allowing him to identify the location of stimuli that he could not identify. Let us now look at how visual information proceeds from the striate cortex through the rest of the occipital lobe to the dorsal and ventral streams.

OCCIPITAL CORTEX
As shown in Figure 8-17, the occipital lobe is composed of at least six different visual regions, known as V1, V2, V3, V3A, V4, and V5. Region V1 is the striate cortex, which, as already mentioned, is sometimes also referred to as the primary visual cortex. The remaining visual areas of the occipital lobe are called the extrastriate cortex or secondary visual cortex. Because each of these occipital regions has a unique cellular structure (cytoarchitecture) and has unique inputs and outputs, we can infer that each must be doing something different from the others.

You already know that a remarkable feature of region V1 is its distinct layers, which extend throughout V1. These seemingly homogeneous layers are deceiving, however. When Margaret Wong-Riley and her colleagues (1993) stained the cortex for the enzyme cytochrome oxidase, which has a role in cell metabolism, they were surprised to
find an unexpected heterogeneity in region V1. So they sectioned the V1 layers in such a way that each cortical layer was in one plane of section, much like peeling off the layers of an onion and laying them flat on a table. The surface of each flattened layer can then be viewed from above.

As Figure 8-18 illustrates, the heterogeneous cytochrome staining now appeared as random blobs in the layers of V1. In fact, these darkened regions have become known as **blobs**, and the less-dark regions separating them have become known as **interblobs**. Blobs and interblobs serve different functions. Neurons in the blobs take part in color perception, whereas neurons in the interblobs participate in form and motion perception. So, within region V1, input that arrives in the parvo- and magnocellular pathways of the geniculostriate system is segregated into three separate types of information: color, form, and movement.

This information is then sent to region V2, which lies next to region V1. Here the color, form, and movement inputs remain segregated. This segregation can again be seen through the pattern of cytochrome oxidase staining, but the staining pattern is different from that in region V1. Figure 8-19 shows that region V2 has a pattern of thick and thin stripes that are intermixed with pale zones. The thick stripes receive input from the
movement-sensitive neurons in region V1; the thin stripes receive input from V1's color-sensitive neurons; and the pale zones receive input from V1's form-sensitive neurons.

As diagrammed in Figure 8-19, the visual pathways proceed from region V2 to the other occipital regions and then to the parietal and temporal lobes, forming the dorsal and ventral streams. Although many parietal and temporal regions take part, the major regions are region G in the parietal lobe (thus called region PG) and region E in the temporal lobe (thus called region TE).

Within the dorsal and ventral streams, the function of the visual pathways becomes far more complex than a simple record of color, form, and movement. Rather, the color, form, and movement information is put together to produce a rich, unified visual world made up of complex objects, such as faces and paintings, and complex visuomotor skills, such as catching a ball. The functions of the dorsal and ventral streams are therefore complex, but they can be thought of as consisting of "how" functions and "what" functions. "How" is action to be visually guided toward objects, whereas "what" identifies what an object is.

**In Review**

Vision begins when photoreceptors in the retina at the back of the eye convert light energy into neural activity in neighboring ganglion cells, the axons of which form the optic nerve leading to the brain. P ganglion cells receive input mostly from cones and carry information about color and fine detail, whereas M ganglion cells receive input mostly from rods and carry information about light but not color. Visual input takes two routes into the brain. The geniculostriate pathway travels through the LGN of the thalamus to layer IV of the striate cortex in the occipital lobe. The tectopulvinar pathway is from the tectum of the midbrain to the pulvinar of the thalamus and then to visual cortical areas. Both pathways contribute to the dorsal and ventral visual streams that project to the parietal and temporal lobes, respectively. The dorsal stream to the parietal lobe processes the visual guidance of movements (the how), whereas the ventral stream to the temporal lobe processes the visual perception of objects (the what).

**LOCATION IN THE VISUAL WORLD**

One aspect of visual information that we have not yet considered is location. As we move around, going from place to place, we encounter objects in specific locations. Indeed, if we had no sense of location, the world would be a bewildering mass of visual information. Our next task, then, is to look at how the brain constructs a spatial map from this complex array of visual input.

The coding of location begins in the retina and is maintained throughout all the visual pathways. To understand how this spatial coding is accomplished, you need to imagine your visual world as seen by your two eyes. Imagine the large red and blue rectangles in Figure 8-20 as a wall. Focus your gaze on the black cross in the middle of the wall.

All of the wall that you can see without moving your head is your visual field. The visual field can be divided into two halves, the left and right visual fields, by drawing a vertical line down the middle of the black cross. Now recall from Figure 8-11 that the left half of each retina looks at the right side of the visual field, whereas the right half of each retina looks at the visual field's left side. This means that input from the right visual field, which is on the left side, and the left visual field, which is on the right side, are coded separately.
visual field goes to the left hemisphere, whereas input from the left visual field goes to the right hemisphere.

Therefore the brain can easily determine whether visual information is located to the left or right of center. If input goes to the left hemisphere, the source must be in the right visual field; if input goes to the right hemisphere, the source must be in the left visual field. This arrangement tells you nothing about the precise location of an object in the left or right side of the visual field, however. To understand how precise spatial localization is accomplished, we must return to the retinal ganglion cells.

**Coding Location in the Retina**

Look again at Figure 8-9 and you can see that each retinal ganglion cell receives input through bipolar cells from several photoreceptors. In the 1950s, Stephen Kuffler, a pioneer in studying the physiology of the visual system, made an important discovery about how photoreceptors and ganglion cells are linked. By shining small spots of light on the receptors, he found that each ganglion cell responds to stimulation on just a small circular patch of the retina. This patch became known as the ganglion cell's receptive field.

A ganglion cell's receptive field is therefore the region of the retina on which it is possible to influence that cell's firing. Stated differently, the receptive field represents the outer world as seen by a single cell. Each ganglion cell sees only a small bit of the world, much as you would if you looked through a narrow cardboard tube. The visual field is composed of thousands of such receptive fields.

Now let us consider how receptive fields enable the visual system to interpret the location of objects. Imagine that the retina is flattened like a piece of paper. When a tiny light is shone on different parts of the retina, different ganglion cells respond. For example, when a light is shone on the top-left corner of the flattened retina, a particular ganglion cell responds because that light is in its receptive field. Similarly, when a light is shone on the top-right corner, a different ganglion cell responds.

By using this information, we can identify the location of a light on the retina by knowing which ganglion cell is activated. We can also interpret the location of the light in the outside world because we know where the light must come from to hit a particular place on the retina. For example, light from above hits the bottom of the retina after passing through the eye’s lens, whereas light from below hits the top of the retina. (Refer to Figure 8-3 to see why this is so.) Information at the top of the visual field will stimulate ganglion cells on the bottom of the retina, whereas information at the bottom of the field will stimulate ganglion cells on the top of the retina.

**Location in the LGN and Cortical Region VI**

Now consider the connection from the ganglion cells to the lateral geniculate nucleus. In contrast with the retina, the LGN is not a flat sheet; rather, it is a three-dimensional structure in the brain. We can compare it to a stack of cards, with each card representing a layer of cells.
Topographic map. A spatially organized neural representation of the external world.

**Figure 8-21**

Receptive Field Projection The information from a receptive field retains its spatial relation when it is sent to the lateral geniculate nucleus (LGN). In this example, information at the top of the visual field goes to the top of the LGN and information from the bottom of the visual field goes to the bottom of the LGN. Similarly, information from the left or right goes to the left or right of the LGN, respectively.

**Figure 8-22**

Topographic Organization of the Visual Cortex (V1) In the right occipital lobe, the area of left central vision (the fovea) is represented at the back of the brain, whereas the more peripheral visual areas are represented more anteriorly. The fovea also occupies a disproportionately large part of the cortex, which is why visual acuity is best in the central part of the visual field.

Figure 8-21 shows how the connections from the retina to the LGN can represent location. A retinal ganglion cell that responds to light in the top-left corner of the retina connects to the left side of the first card. A retinal ganglion cell that responds to light in the bottom-right corner of the retina connects to the right side of the last card. In this way, the location of left–right and top–bottom information is maintained in the LGN.

Like the ganglion cells, each of the LGN cells has a receptive field, which is the region of the retina that influences its activity. If two adjacent retinal ganglion cells synapse on a single LGN cell, the receptive field of that LGN cell will be the sum of the two ganglion cells’ receptive fields. As a result, the receptive fields of LGN cells can be bigger than those of retinal ganglion cells.

The LGN projection to the striate cortex (region V1) also maintains spatial information. As each LGN cell, representing a particular place, projects to region V1, a topographic representation, or topographic map, is produced in the cortex. As illustrated in Figure 8-22, this representation is essentially a map of the visual world.

The central part of the visual field is represented at the back of the brain, whereas the periphery is represented more anteriorly. The upper part of the visual field is represented at the bottom of region V1, the lower part at the top of V1. The other regions of the visual cortex (such as V3, V4, and V5) also have topographical maps similar to that of V1. Thus the V1 neurons must project to the other regions in an orderly manner, just as the LGN neurons project to region V1 in an orderly way.

Within each visual cortical area, each neuron has a receptive field corresponding to the part of the retina to which the neuron is connected. As a rule of thumb, the cells in the cortex have much larger receptive fields than those of retinal ganglion cells. This increase in receptive-field size means that the receptive field of a cortical neuron must be composed of the receptive fields of many retinal ganglion cells, as illustrated in Figure 8-23.

There is one additional wrinkle to the organization of topographic maps. Jerison’s principle of proper mass, which
The receptive fields of many retinal ganglion cells... combine to form the receptive field of a single LGN cell. The receptive fields of many LGN cells combine to form the receptive field of a single V1 cell.

Figure 8-23
Receptive Field Hierarchy
The receptive fields of region V1 neurons are constructed from those of lateral geniculate (LGN) cells, which, in turn, are constructed from those of ganglion cells. The receptive field of a single ganglion cell is small. In this example, the receptive fields of the LGN cells are the summation of the fields of four ganglion cells. The receptive field of the V1 cell is the sum of the four LGN cells.

Figure 8-24
Callosal Connections
The darker areas indicate regions of the cortex of a rhesus monkey that receive projections from the opposite hemisphere by means of the corpus callosum. Most of the occipital lobe has no such connections.

The visual corpus callosum

The creation of tophographic maps based on the receptive fields of neurons is an effective way for the brain to code the location of objects. But, if the left visual field is represented in the right cerebral hemisphere and the right visual field is represented in the left cerebral hemisphere, how are the two halves of the visual field ultimately bound together in a unified representation of the world? After all, we have the subjective impression not of two independent visual fields, but rather of a single, continuous field of vision. The answer to how this unity is accomplished lies in the corpus callosum, which binds the two sides of the visual field at the midline.

Until the 1950s, the function of the corpus callosum was largely a mystery. Physicians had occasionally cut it to control severe epilepsy, as described in “Epilepsy” on page 111, or to reach a very deep tumor, but patients did not appear to be much affected by this surgery. The corpus callosum clearly linked the two hemispheres of the brain, but exactly which parts were connected was not yet known.

We now realize that the corpus callosum connects only certain brain structures. Whereas much of the frontal lobes have callosal connections, the occipital lobes have almost none, as shown in Figure 8-24. If you think about it, there is no reason for a neuron in the visual cortex that is “looking at” one place in the visual field to be concerned with what another neuron in the opposite hemisphere is “looking at” in another part of the visual field.

Cells that lie along the midline of the visual field are an exception, however. These cells would...
be “looking at” adjacent places in the field of vision, one slightly to the left of center and one slightly to the right. If connections existed between such cells, we could zip the two visual fields together by combining their receptive fields to cross at the midline, which is exactly what happens. Cortical cells with receptive fields that lie along the midline of your field of vision are connected to one another through the corpus callosum so that their receptive fields overlap the midline. The two fields thus become one.

**In Review**

The brain can determine the location of a particular stimulus because each neuron of the visual system connects to only a small part of the retina, known as that neuron’s receptive field. Each receptive field, in turn, receives input from only a small part of the visual field, and so which part of the retina is stimulated effectively detects exactly where the light source is positioned in the environment. This location-detecting method is maintained at different levels in the visual system, from the ganglion cells of the retina to the neurons of the LGN in the thalamus to the neurons of the primary visual cortex. Inputs to different parts of cortical region V1 from different parts of the retina essentially form a topographic map of the visual world within the brain. Cells with receptive fields that lie along the midline of the field of vision are connected by the corpus callosum, binding the two sides of the visual world together as one.

**NEURAL ACTIVITY**

The pathways of the visual system are made up of individual neurons. By studying how these cells behave when their receptive fields are stimulated, we can begin to understand how the brain processes different features of the visual world beyond just the locations of light. To illustrate, we examine how neurons from the retina to the temporal cortex respond to shapes and colors. We then briefly consider how neurons in the dorsal stream behave.

**Seeing Shape**

Imagine that we have placed a microelectrode near a neuron somewhere in the visual pathway from retina to cortex and are using that electrode to record changes in the neuron’s firing rate. This neuron occasionally fires spontaneously, producing action potentials with each discharge. Let us assume that the neuron discharges, on the average, once every 0.08 second. Each action potential is brief, on the order of 1 millisecond.

If we plot action potentials spanning a second, we see only spikes in the record because the action potentials are so brief. (Refer to Figure 4-12 for an illustration of this effect.) Figure 8-25A is a single-cell recording in which there are 12 spikes in the span of 1 second. If the firing rate of this cell increases, we will see more spikes (Figure 8-25B). If the firing rate decreases, we will see fewer spikes (Figure 8-25C). The increase in firing represents excitation of the cell, whereas the decrease represents inhibition. Excitation and inhibition, as you know, are the principal mechanisms of information transfer in the nervous system.

Now suppose we present a stimulus to the neuron by illuminating its receptive field in the retina, perhaps by shining a light stimulus on a blank screen within the cell’s visual field. We might place before the eye a straight line positioned at a 45° angle. The cell...
could respond to this stimulus either by increasing or decreasing its firing rate. In either case, we would conclude that the cell is creating information about the line.

Note that the same cell could show excitation to one stimulus, inhibition to another stimulus, and no reaction at all. For instance, the cell could be excited by lines oriented 45° to the left and inhibited by lines oriented 45° to the right. Similarly, the cell could be excited by stimulation in one part of its receptive field (such as the center) and inhibited by stimulation in another part (such as the periphery).

Finally, we might find that the cell's response to a particular stimulus is selective. Such a cell would be telling us about the importance of the stimulus to the animal. For instance, the cell might fire (be excited) when a stimulus is presented with food but not fire (be inhibited) when the same stimulus is presented alone. In each case, the cell is selectively sensitive to characteristics in the visual world.

Now we are ready to move from this hypothetical example to what visual neurons actually do when they process information about shape. Neurons at each level of the visual system have distinctly different characteristics and functions. Our goal is not to look at each neuron type but rather to consider generally how some typical neurons at each level differ from one another in their contributions to processing shape. We focus on neurons in three areas: the ganglion-cell layer of the retina, the primary visual cortex, and the temporal cortex.

**PROCESSING IN RETINAL GANGLION CELLS**

Cells in the retina do not actually see shapes. Shapes are constructed by processes in the cortex from the information that ganglion cells pass on about events in their receptive fields. Keep in mind that the receptive fields of ganglion cells are very small dots. Each ganglion cell responds only to the presence or absence of light in its receptive field, not to shape.

The receptive field of a ganglion cell has a concentric circle arrangement, as illustrated in Figure 8-26A. A spot of light falling in the central circle of the receptive

![Figure 8-26](image)

**On-Off Receptivity**

(A) In the receptive field of a retinal ganglion cell with an on-center and off-surround, a spot of light placed on the center causes excitation in the neuron, whereas a spot of light in the surround causes inhibition. When the light in the surround region is turned off, firing rate increases briefly (called an "offset" response). A light shining in both the center and the surround would produce a weak increase in firing in the cell. (B) In the receptive field of a retinal ganglion cell with an off-center and on-surround, light in the center produces inhibition, whereas light on the surround produces excitation, and light across the entire field produces weak inhibition.
The receptive fields of retinal ganglion cells overlap extensively... and so any two adjacent fields look at almost the same part of the world.

**Figure 8-27** Overlapping Receptive Fields

Receptive fields of neighboring ganglion cells

Two overlapping receptive fields

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field excites some of these cells, whereas a spot of light falling in the surround (periphery) of the receptive field inhibits the cell. A spot of light falling across the entire receptive field causes a weak increase in the cell's rate of firing.

This type of neuron is called an on-center cell. Other ganglion cells, called off-center cells, have the opposite arrangement, with light in the center of the receptive field causing inhibition, light in the surround causing excitation, and light across the entire field producing weak inhibition (Figure 8-26B). The on-off arrangement of ganglion-cell receptive fields makes these cells especially responsive to very small spots of light.

This description of ganglion-cell receptive fields might mislead you into thinking that they form a mosaic of discrete little circles on the retina that do not overlap. In fact, neighboring retinal ganglion cells receive their inputs from an overlapping set of receptors. As a result, their receptive fields overlap, as illustrated in Figure 8-27. In this way, a small spot of light shining on the retina is likely to produce activity in both on-center and off-center ganglion cells.

How can on-center and off-center ganglion cells tell the brain anything about shape? The answer is that a ganglion cell is able to tell the brain about the amount of light hitting a certain spot on the retina compared with the average amount of light falling on the surrounding retinal region. This comparison is known as luminance contrast.

To understand how this mechanism tells the brain about shape, consider the hypothetical population of on-center ganglion cells represented in Figure 8-28. Their receptive fields are distributed across the retinal image of a light–dark edge. Some of the ganglion cells have receptive fields in the dark area, others have receptive fields in the light area, and still others have fields that straddle the edge of the light.

The ganglion cells with receptive fields in the dark or light areas are least affected because they experience either no stimulation or stimulation of both the excitatory and inhibitory regions of their receptive fields. The ganglion cells most affected by the stimulus are those lying along the edge. Ganglion cell B is inhibited because the light falls mostly on its inhibitory surround, and ganglion cell D is excited because its entire excitatory center is stimulated but only part of its inhibitory surround is.

Consequently, information transmitted from retinal ganglion cells to the visual areas in the brain does not give equal weight to all regions of the visual field. Rather, it emphasizes regions containing differences in luminance. Areas with differences in luminance are found along edges. So retinal ganglion cells are sending signals about edges, and edges are what form shapes.

**PROCESSING IN THE PRIMARY VISUAL CORTEX**

Now consider cells in region V1, the primary visual cortex, that receive their visual inputs from LGN cells, which in turn receive theirs from retinal ganglion cells. Because each V1 cell receives input from multiple retinal ganglion cells, the receptive fields of the V1 neurons are much larger than those of retinal neurons. Consequently, the V1 cells respond to stimuli more complex than simply “light on” or “light off.” In particular, these cells are maximally excited by bars of light oriented in a particular direction rather than by spots of light. These cells are therefore called orientation detectors.
Like the ganglion cells, some orientation detectors have an on–off arrangement in their receptive fields, but the arrangement is rectangular rather than circular. Visual cortex cells with this property are known as *simple cells*. Typical receptive fields for simple cells in the primary visual cortex are shown in Figure 8-29.

Simple cells are not the only kind of orientation detector in the primary visual cortex; several functionally distinct types of neurons populate region V1. For instance, *complex cells* such as those in Figure 8-30 have receptive fields that are maximally excited by bars of light moving in a particular direction through the visual field. A *hypercomplex cell*, like a complex cell, is maximally responsive to moving bars but also has a strong inhibitory area at one end of its receptive field. As illustrated in Figure 8-31, a bar of light
Each circle represents the receptive field of a ganglion cell.

Stimulation of a subset of on-center ganglion cells excites a V1 neuron through connections in the LGN (not shown here).

**Figure 8-31**

Receptive Field of a Hypercomplex Cell

A hypercomplex cell responds to a bar of light in a particular orientation (e.g., horizontal) anywhere in the excitatory (ON) part of its receptive field. If the bar extends into the inhibitory area (OFF), no response occurs.

**Figure 8-32**

V1 Receptivity

A V1 cell responds to a row of ganglion cells in a particular orientation on the retina. The bar of light strongly activates a row of ganglion cells, each connected through the LGN to a V1 neuron. The activity of this V1 neuron is most affected by a bar of light at a 45° angle.

landing on the right side of the hypercomplex cell’s receptive field excites the cell, but if the bar lands on the inhibitory area to the left, the cell’s firing is inhibited.

Note that each class of V1 neurons responds to bars of light in some way, yet this response results from input originating in retinal ganglion cells that respond maximally not to bars but to spots of light. How does this conversion from responding to spots to responding to bars take place? An example will help explain the process.

A thin bar of light falls on the retinal photoreceptors, striking the receptive fields of perhaps dozens of retinal ganglion cells. The input to a V1 neuron comes from a group of ganglion cells that happen to be aligned in a row, as in **Figure 8-32**. That V1 neuron will be activated (or inhibited) only when a bar of light hitting the retina strikes that particular row of ganglion cells. If the bar of light is at a slightly different angle, only some of the retinal ganglion cells in the row will be activated, and so the V1 neuron will be excited only weakly.

Figure 8-32 illustrates the connection between light striking the retina in a certain pattern and the activation of a simple cell in the primary visual cortex, one that responds to a bar of light in a particular orientation. Using the same logic, we can also diagram the retinal receptive fields of complex or hypercomplex V1 neurons. Try this as an exercise yourself by adapting the format in Figure 8-32.

A characteristic of cortical structure is that the neurons are organized into functional columns. **Figure 8-33** shows such a column, a 0.5-millimeter-diameter strip of
Figure 8-33
Neural Circuit in a Column in the Visual Cortex In this stereoscopic (3D) view, the sensory inputs terminate on stellate cells in layer IV. These stellate cells synapse in layers III and V with pyramidal cells in the same vertical column of tissue. Thus the flow of information is vertical. The axons of the pyramidal cells leave the column to join with other columns or structures. Adapted from "The 'Module-Concept' in Cerebral Architecture," by J. Szentagothai, 1975, Brain Research, 95, p. 490.

Figure 8-34
Organization of Functional Columns in the Primary Visual Cortex (A) Cells with the same orientation preference are found throughout a column. Adjacent columns have orientation preferences that are slightly different from one another. (B) Ocular-dominance columns are arranged at right angles to the orientation columns, producing a three-dimensional organization of the visual cortex. The ocular-dominance columns alternate from left (L) to right (R) across the primary visual cortex, with two such alternations illustrated here.

Adjacent columns house neurons that are responsive to slightly different line orientations, forming an array of 180°.

Every neuron in the same column has the same orientation bias.

Ocular-dominance columns receive input from the right or left eye.

Cortex that includes neurons and their connections. The pattern of connectivity in a column is vertical: inputs arrive in layer IV and then connect with cells in the other layers.

The neurons within a column have similar functions. For example, Figure 8-34A shows that neurons within the same column respond to lines oriented in the same direction. Adjacent columns house cells that are responsive to different line orientations.

Figure 8-34B shows the columns of input coming from each eye, discussed earlier, called ocular-dominance columns. So the visual cortex has both orientation columns housing neurons of similar sensitivity and ocular-dominance columns with input from one eye or the other.

PROCESSING IN THE TEMPORAL CORTEX

Finally, in regard to seeing shapes, consider neurons along the ventral stream in region E of the temporal lobe (see Figure 8-19). Rather than being responsive to spots or bars of light, these TE neurons are maximally excited by complex visual stimuli, such as faces or hands, and can be remarkably specific in their responsiveness. They may be responsive to particular faces seen head-on, to faces viewed in profile, to the posture of the head, or even to particular facial expressions.

How far does this specialized responsiveness extend? Would it be practical to have visual neurons in the temporal cortex specialized to respond to every conceivable feature
of objects? Keiji Tanaka (1993) approached this question by presenting monkeys with many three-dimensional representations of animals and plants to find stimuli that are effective in activating particular neurons of the inferior temporal cortex.

Having identified stimuli that were especially effective, such as faces or hands, he then wondered which specific features of those stimuli are critical to stimulating the neurons. Tanaka found that most neurons in area TE require rather complex features for their activation. These features include a combination of characteristics such as orientation, size, color, and texture. Furthermore, neurons with similar, although slightly different, responsiveness to particular features tend to cluster together in columns, as shown in Figure 8-35.

Apparently, then, an object is not represented by the activity of a single neuron. Rather, objects are represented by the activity of many neurons with slightly varying stimulus specificity that are grouped together in a column. This finding is important because it provides an explanation for stimulus equivalence, recognizing an object as remaining the same despite being viewed from different orientations.

Think of how the representation of objects by multiple neurons in a column can produce stimulus equivalence. If each neuron in the column module varies slightly in regard to the features to which it responds but the effective stimuli largely overlap, the effect of small changes in incoming visual images will be minimized and we will continue to perceive an object as the same thing.

Another remarkable feature of neurons of the inferior temporal cortex in monkeys is that their stimulus specificity is altered by experience. If monkeys are trained to discriminate particular shapes to obtain a food reward, not only do they improve their discriminatory ability, but neurons in the temporal lobe also modify their preferred stimuli to fire maximally to some of the stimuli used in training. This result shows that the temporal lobe’s role in visual processing is not determined genetically but is instead subject to experience, even in adults.

We can speculate that this experience-dependent characteristic evolved because it allows the visual system to adapt to different demands in a changing visual environment. Think of how different the demands on your visual recognition abilities are when you move from a dense forest to a treeless plain to a city street. The visual neurons of your temporal cortex can adapt to these differences (Tanaka, 1993). In addition, experience-dependent visual neurons ensure that people can identify visual stimuli that were never encountered as the human brain evolved.

Note that the preferred stimuli of neurons in the primary visual cortex are not modified by experience, which implies that the stimulus preferences of V1 neurons are genetically programmed. In any case, the functions of the V1 neurons provide the building blocks for the more complex and flexible characteristics of the inferior temporal cortex neurons.

### Seeing Color

Scientists have long wondered how people are able to see a world so rich in color. Recall from Chapter 1 the hypothesis that color vision evolved in primates whose diet required them to identify ripe fruits or to avoid predators or other dangers. Another explanation has its roots in the Renaissance, when painters discovered that they could obtain the entire range of colors in the visual world by mixing only three colors of paint (red, blue, and yellow), the process of **subtractive color mixing**.