The Skull Protects the Eye

The external anatomy of the eye is shown in Figure 10-29. Like sensory elements of the ears, the eyes are protected by a bony cavity, the orbit, which is formed by facial bones of the skull. Accessory structures associated with the eye include six extrinsic eye muscles, skeletal muscles that attach to the outer surface of the eyeball and control eye movements. Cranial nerves III, IV, and VI innervate these muscles.

The upper and lower eyelids close over the anterior surface of the eye, and the lacrimal apparatus, a system of glands and ducts, keeps a continuous flow of tears washing across the exposed surface so that it remains moist and free of debris. Tear secretion is stimulated by parasympathetic neurons from cranial nerve VII.

The eye itself is a hollow sphere divided into two compartments (chambers) separated by a lens (Fig. 10-30a). The lens, suspended by ligaments called zonules, is a transparent disk that focuses light. The anterior chamber in front of the lens is filled with aqueous humor [humidus, moist], a low-protein plasma-like fluid secreted by the ciliary epithelium supporting the lens. Behind the lens is a much larger chamber, the vitreous chamber, filled mostly with the vitreous body [vitreus, glass; also called the vitreous humor], a clear, gelatinous matrix that helps maintain the shape of the eyeball. The outer wall of the eyeball, the sclera, is composed of connective tissue.

GLAUCOMA

The eye disease glaucoma, characterized by degeneration of the optic nerve, is the leading cause of blindness worldwide. Many people associate glaucoma with increased intraocular (within the eyeball) pressure, but scientists have discovered that increased pressure is only one risk factor for the disease. A significant number of people with glaucoma have normal intraocular pressure, and not everyone with elevated pressure develops glaucoma. Many cases of elevated eye pressure are associated with excess aqueous humor, a fluid that is secreted by the ciliary epithelium near the lens. Normally the fluid drains out through the canal of Schlemm in the anterior chamber of the eye, but if outflow is blocked, the aqueous humor accumulates, causing pressure to build up inside the eye. Treatments to decrease intraocular pressure include drugs that inhibit aqueous humor production and surgery to reopen the canal of Schlemm. Research suggests that the optic nerve degeneration in glaucoma may be due to nitric oxide or apoptosis-inducing factors, and studies in these areas are underway.
Light enters the anterior surface of the eye through the cornea, a transparent disk of tissue that is a continuation of the sclera. After passing through the opening of the pupil, it strikes the lens, which has two convex surfaces. The cornea and lens together bend incoming light rays so that they focus on the retina, the light-sensitive lining of the eye that contains the photoreceptors.

When viewed through the pupil with an ophthalmoscope (ophthalmos, eye), the retina is seen to be crisscrossed with small arteries and veins that radiate out from one spot, the optic disk (Fig. 10-30b). The optic disk is the location where neurons of the visual pathway form the optic nerve (cranial nerve II) and exit the eye. Lateral to the optic disk is a small dark spot, the fovea. The fovea and a narrow ring of tissue surrounding it, the macula, are the regions of the retina with the most acute vision.

Neural pathways for the eyes are illustrated in Figure 10-31. The optic nerves from the eyes go to the optic chiasm in the brain, where some of the fibers cross to the opposite side. After synapsing in the lateral geniculate body (lateral geniculate nucleus) of the thalamus, the vision neurons of the tract terminate in the occipital lobe at the visual cortex. Collateral pathways go from the thalamus to the midbrain, where they synapse with efferent neurons of cranial nerve III that control the diameter of the pupils.

**CONCEPT CHECK**

24. What functions does the aqueous humor serve? Answers: p. 383

**Light Enters the Eye Through the Pupil**

In the first step of the visual pathway, light from the environment enters the eye. Before it strikes the retina, however, the light is modified two ways. First, the amount of light that reaches photoreceptors is modulated by changes in the size of the pupil. Second, the light is focused by changes in the shape of the lens.

The human eye functions over a 100,000-fold range of light intensity. Most of this ability comes from the sensitivity of the photoreceptors, but the pupils assist by regulating the amount of light that falls on the retina. In bright sunlight, the pupils narrow to about 1.5 mm in diameter when a parasympathetic pathway constricts the circular pupillary muscles. In the dark, the opening of the pupil dilates to 8 mm, a 28-fold increase in pupil area. Dilation occurs when radial muscles lying perpendicular to the circular muscles contract under the influence of sympathetic neurons.

Testing pupillary reflexes is a standard part of a neurological examination. Light hitting the retina in one eye activates the reflex. Signals travel through the optic nerve to the thalamus,
then to the midbrain, where efferent neurons constrict the pupils in both eyes (Fig. 10-31c). This response is known as the consensual reflex and is mediated by parasympathetic fibers running through cranial nerve III.

**CONCEPT CHECK**

25. Use the neural pathways in Figure 10-31c to answer the following questions.

(a) Why does shining light into one eye cause pupillary constriction in both eyes?

(b) If you shine a light in the left eye and get pupillary constriction in the right eye but not in the left eye, what can you conclude about the afferent path from the left eye to the brain? About the efferent pathways to the pupils?

26. Parasympathetic fibers constrict the pupils, and sympathetic fibers dilate them. This is an example of what kind of control?

In addition to regulating the amount of light that hits the retina, the pupils create what is known as depth of field. A simple example comes from photography. Imagine a picture of a puppy sitting in the foreground amid a field of wildflowers. If only the puppy and the flowers immediately around her are in focus, the picture is said to have a shallow depth of field. If the puppy and the wildflowers all the way back to the horizon are in focus, the picture has full depth of field. Full depth of field is created by constricting the pupil (or the diaphragm on a camera) so that only a narrow beam of light enters the eye. In this way, a greater depth of the image is focused on the retina.

**The Lens Focuses Light on the Retina**

When light enters the eye, it passes through the cornea and lens prior to striking the retina. When light rays pass from air into a medium of different density, such as glass or water, they bend, or refract. Light entering the eye is refracted twice: first when it passes through the cornea, and again when it passes through the lens. About two-thirds of the total refraction (bending) occurs at the cornea and the remaining one-third occurs at the lens. Here we consider only the refraction that
The otolaryngologist strongly suspects that Anant has Ménière's disease, with excessive endolymph in the vestibular apparatus and cochlea. Many treatments are available, from simple dietary changes to surgery. For now, the physician suggests that Anant limit his salt intake and take diuretics, drugs that cause the kidneys to remove excess fluid from the body.

**Question 5:** Why is limiting salt (NaCl) intake suggested as a treatment for Ménière's disease? (Hint: What is the relationship between salt, osmolarity, and fluid volume?)

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**RUNNING PROBLEM**

occurs as light passes through the lens because the lens is capable of changing its shape to focus light.

When light passes from one medium into another, the angle of refraction (how much the light rays bend) is influenced by two factors: (1) the difference in density of the two media and (2) the angle at which the light rays meet the surface of the medium into which it is passing. For light passing through the lens of the eye, we assume that the density of the lens is the same as the density of the air so that this factor can be ignored. The angle at which light meets the face of the lens depends on the curvature of the lens surface and the direction of the light beam.

Imagine parallel light rays striking the surface of a transparent lens. If the lens surface is perpendicular to the rays, the light passes through without bending. If the surface is not perpendicular, however, the light rays bend. Parallel light rays striking a concave lens, such as that shown in Figure 10-32a, are refracted into a wider beam. Parallel rays striking a convex lens bend inward and focus to a point—**convex lenses converge light waves** (Fig. 10-32b). You can demonstrate the properties of a convex lens by using a magnifying glass to focus sunlight onto a piece of paper or other surface.

When parallel light rays pass through a convex lens, the single point where the rays converge is called the focal point (Fig. 10-32b). The distance from the center of a lens to its focal point is known as the focal length (or focal distance) of the lens. For any given lens, the focal length is fixed. For the focal length to change, the shape of the lens must change.

When light from an object passes through the lens of the eye, the focal point and object image must fall precisely on the retina if the object is to be seen in focus. In Figure 10-33a, parallel light rays strike a lens whose surface is relatively flat. For this lens, the focal point falls on the retina. The object is therefore in focus. For the human eye, any object that is 20 feet or more from the eye creates parallel light rays.

What happens, though, when an object is closer than 20 feet to the lens? In that case, the light rays from the object are not parallel and strike the lens at an oblique angle that changes the distance from the lens to the object's image (Fig. 10-33b). The focal point now lies behind the retina, and the object image becomes fuzzy and out of focus.

To keep a near object in focus, the lens must become more rounded to increase the angle of refraction (Fig. 10-33c). Making a lens more convex shortens its focal length. In this example, rounding the lens causes light rays to converge on the retina instead of behind it, and the object comes into focus.

The process by which the eye adjusts the shape of the lens to keep objects in focus is known as accommodation, and the closest distance at which it can focus an object is known as the near point of accommodation. You can demonstrate changing focus with the accommodation reflex easily by closing one eye and holding your hand up about 8 inches in front of your open eye, fingers spread apart.

Focus your eye on some object in the distance that is visible between your fingers. Notice that when you do so, your fingers remain visible but out of focus. Your lens is flattened for distance vision, so the focal point for near objects falls behind the retina. Those objects appear out of focus. Now shift your gaze to your fingers and notice that they come into focus. The light rays coming off your fingers have not changed their
Parallel light rays pass through a flattened lens and the focal point falls on the retina.

For close objects, the light rays are no longer parallel.

Rounding a lens shortens its focal length.

**FIGURE QUESTION**

The relationship between the focal length of a lens (F), the distance between an object and the lens (P), and the distance from the lens to the object’s image (Q) is expressed as $1/F = 1/P + 1/Q$.

(a) If the focal length of a lens does not change but an object moves closer to the lens, what happens to the image distance Q?

(b) If an object moves closer to the lens and the image distance Q must stay the same for the image to fall on the retina, what happens to the focal length F of the lens? For this change in F to occur, should the lens become flatter or more rounded?

**FIGURE 10-33 Optics of the eye**

angle, but your lens has become more rounded, and the light rays now converge on the retina.

How can the lens, which is clear and does not have any muscle fibers in it, change shape? The answer lies in the ciliary muscle, a ring of smooth muscle that surrounds the lens and is attached to it by the inelastic ligaments called zonules (Fig. 10-34). If no tension is placed on the lens by the ligaments, the lens assumes its natural rounded shape because of the elasticity of its capsule. If the ligaments pull on the lens, it flattens out and assumes the shape required for distance vision.

Tension on the ligaments is controlled by the ciliary muscle. When this circular muscle contracts, the muscle ring gets smaller, releasing tension on the ligaments so that the lens rounds. When the ciliary muscle is relaxed, the ring is more open and the lens is pulled into a flatter shape.

Young people can focus on items as close as 8 cm, but the accommodation reflex diminishes from the age of 10 on. By age 40, accommodation is only about half of what it was at age 10, and by age 60, many people lose the reflex completely because the lens has lost flexibility and remains in its flatter shape for distance vision. The loss of accommodation, presbyopia, is the reason most people begin to wear reading glasses in their 40s.

Two other common vision problems, near-sightedness (myopia) and far-sightedness (hyperopia), occur when the focal point falls either in front of the retina or behind the retina, respectively (Fig. 10-35). These conditions are caused by abnormally curved or flattened corneas or by eyeballs that are too long or too short. Placing a lens with the appropriate curvature in front of the eye changes the refraction of light entering the eye and corrects the problem. A third common vision problem,
astigmatism, is usually caused by a cornea that is not a perfectly shaped dome, resulting in distorted images.

CONCEPT CHECK

27. If a person's cornea, which helps focus light, is more rounded than normal (has a greater curvature), is this person more likely to be hyperopic or myopic? (Hint: See Figure 10-35.)

Answers: p. 383

Phototransduction Occurs at the Retina

In the second step of the visual pathway, photoreceptors of the retina convert light energy into electrical signals. Light energy is part of the electromagnetic spectrum, which ranges from high-energy, very-short-wavelength waves such as X-rays and gamma rays to low-energy, lower-frequency microwaves and radio waves (Fig. 10-36). However, our brains can perceive only a small portion of this broad energy spectrum. For humans, visible light is limited to electromagnetic energy with waves that have a frequency of $4.0-7.5 \times 10^{14}$ cycles per second (hertz, Hz) and a wavelength of 400-750 nanometers (nm). Electromagnetic energy is measured in units called photons.

Our unaided eyes see visible light but do not respond to ultraviolet and infrared light, whose wavelengths border the ends of our visible light spectrum. On the other hand, the eyes of some other animals can see these wavelengths. For example, bees use ultraviolet “runways” on flowers to guide them to pollen and nectar.

RUNNING PROBLEM

Anant's condition does not improve with the low-salt diet and diuretics, and he continues to suffer from disabling attacks of vertigo with vomiting. In severe cases of Ménière's disease, surgery is sometimes performed as a last resort. In one surgical procedure for the disease, the vestibular nerve is severed. This surgery is difficult to perform, as the vestibular nerve lies near many other important nerves, including facial nerves and the auditory nerve. Patients who undergo this procedure are advised that the surgery can result in deafness if the cochlear nerve is inadvertently severed.

Question 6:
Why would severing the vestibular nerve alleviate Ménière's disease?
Phototransduction is the process by which animals convert light energy into electrical signals. In humans, phototransduction takes place when light hits the retina, the sensory organ of the eye. The retina develops from the same embryonic tissue as the brain, and (as in the cortex of the brain) neurons in the retina are organized into layers (Fig. 10-37d). There are five types of neurons in the retinal layers: photoreceptors, bipolar cells, ganglion cells, amacrine cells, and horizontal cells.

Backing the photosensitive portion of the human retina is a dark pigment epithelium layer. Its function is to absorb any light rays that escape the photoreceptors, preventing distracting light from reflecting inside the eye and distorting the visual image. The black color of these epithelial cells comes from granules of the pigment melanin.

Photoreceptors are the neurons that convert light energy into electrical signals. There are two main types of photoreceptors, rods and cones, as well as a recently discovered photoreceptor that is a modified ganglion cell (see Emerging Concepts Box: Melanopsin). You might expect photoreceptors to be on the surface of the retina facing the vitreous chamber, where light will strike them first, but the retinal layers are actually in reverse order. The photoreceptors are the bottom layer, with their photosensitive tips against the pigment epithelium. Most light entering the eye must pass through several relatively transparent layers of neurons before striking the photoreceptors.

One exception to this organizational pattern occurs in a small region of the retina known as the fovea [pit]. In this area, photoreceptors receive light directly because the intervening neurons are pushed off to the side (Fig. 10-37c). The fovea is also free of blood vessels that would block light reception. As noted earlier, the fovea and the macula immediately surrounding it are the areas of most acute vision, and they form the center of the visual field.

When you look at an object, the lens focuses the object image on the fovea. For example, in Figure 10-38, the eye is focused on the green-yellow border of the color bar. Light from that section of the visual field falls on the fovea and is in sharp focus. Notice also that the image falling on the retina is upside down. Subsequent visual processing by the brain reverses the image again so that we perceive it in the correct orientation.

Sensory information about light passes from the photoreceptors to bipolar neurons, then to a layer of ganglion cells. The axons of ganglion cells form the optic nerve, which leaves the eye at the optic disk. Because the optic disk has no photoreceptors, images projected onto this region cannot be seen, creating what is called the eye’s blind spot.

**CONCEPT CHECK**

28. Animals that see well in very low light, such as cats and owls, lack a pigment epithelium and instead have a layer called the tapetum lucidum behind the retina. What property might this layer have that would enhance vision in low light?

29. How is the difference in visual acuity between the fovea and the edge of the visual field similar to the difference in touch discrimination between the fingertips and the skin of the arm?

30. Macular degeneration is the leading cause of blindness in Americans over the age of 55. Impaired function of the macula causes vision loss in which part of the visual field?

**Answers:** p. 383

**Photoreceptors Transduce Light into Electrical Signals**

There are two types of photoreceptors in the eye: rods and cones. **Rods** function well in low light and are used in night
(a) Dorsal view of a section of the left eye.

(b) Axons from the retina exit via the optic nerve.

(c) Light strikes the photoreceptors in the fovea directly because overlying neurons are pushed aside.

(d) Retinal photoreceptors are organized into layers.

(e) Convergence in the retina

**FIGURE QUESTION**

How many rods converge on the ganglion cell in (e)?

vision, when objects are seen in black and white rather than in color. They outnumber cones by a 20:1 ratio, except in the fovea, which contains only cones.

**Cones** are responsible for **high-acuity** vision and color vision during the daytime, when light levels are higher. **Acuity** means keenness and is derived from the Latin *acuere*, meaning “to sharpen.” The fovea, which is the region of sharpest vision, has a very high density of cones.

The two types of photoreceptors have the same basic structure (Fig. 10-39): (1) an outer segment whose tip touches the pigment epithelium of the retina, (2) an inner segment that contains the cell nucleus and organelles for ATP and protein synthesis, and (3) a basal segment with a synaptic terminal that releases glutamate onto bipolar cells.

**FIGURE 10-39** Photoreceptors: rods and cones. The dark pigment epithelium absorbs extra light and prevents that light from reflecting back and distorting vision. Light transduction takes place in the outer segment of the photoreceptor. Changes in photoreceptor membrane potential alter neurotransmitter release onto bipolar cells.
In the outer segment, the cell membrane has deep folds that form disk-like layers, like candy mints stacked in a wrapper. Toward the tip of the outer segments in rods, these layers actually separate from the cell membrane and form free-floating membrane disks. In the cones, the disks stay attached.

Light-sensitive **visual pigments** are bound to the disk membranes in outer segments of photoreceptors. These visual pigments are transducers that convert light energy into a change in membrane potential. Rods have one type of visual pigment, rhodopsin. Cones have three different pigments that are closely related to rhodopsin.

The visual pigments of cones are excited by different wavelengths of light allowing us to see in color. White light is a combination of colors, as revealed when you separate white light by passing it through a prism. The eye contains cones for red, green, and blue light. Each cone type is stimulated by a range of light wavelengths but is most sensitive to a particular wavelength (Fig. 10-40). Red, green, and blue are the three primary colors that make the colors of visible light, just as red, blue, and yellow are the three primary colors that make different colors of paint.

The color of any object we are looking at depends on the wavelengths of light reflected by the object. Green leaves reflect green light, and bananas reflect yellow light. White objects reflect most wavelengths. Black objects absorb most wavelengths, which is one reason they heat up in sunlight while white objects stay cool.

Our brain recognizes the color of an object by interpreting the combination of signals coming to it from the three different color cones. The details of color vision are still not fully understood, and there is some controversy about how color is processed in the cerebral cortex. **Color-blindness** is a condition in which a person inherits a defect in one or more of the three types of cones and has difficulty distinguishing certain colors. Probably the best-known form of color-blindness is red-green, in which people have trouble telling red and green apart.

**CONCEPT CHECK**

31. Why is our vision in the dark in black and white rather than in color?

**Phototransduction** The process of phototransduction is similar for rhodopsin (in rods) and the three color pigments (in cones). Rhodopsin is composed of two molecules: **opsin**, a protein embedded in the membrane of the rod disks, and **retinal**, a vitamin A derivative that is the light-absorbing portion of the pigment (see Fig. 10-39). In the absence of light, retinal binds snugly into a binding site on the opsin (Fig. 10-41a). When activated by as little as one photon of light, retinal changes shape to a new configuration. The activated retinal no longer binds to opsin and is released from the pigment in the process known as **bleaching** (Fig. 10-41b).

How does rhodopsin bleaching lead to action potentials traveling through the optical pathway? To understand the pathway, we must look at other properties of the rods. As you learned in Chapters 5 and 8, electrical signals in cells occur as a result of ion movement between the intracellular and extracellular compartments. Rods contain three main types of ion channels: cyclic nucleotide-gated channels (CNG channels) that allow Na⁺ and Ca²⁺ to enter the rod, K⁺ channels that allow K⁺ to leave out of the rod, and voltage-gated Ca²⁺ channels in the synaptic terminal that help regulate exocytosis of neurotransmitter.

When a rod is in darkness and rhodopsin is not active, cyclic GMP (cGMP) levels in the rod are high, and both CNG and K⁺ channels are open. Sodium and Ca²⁺ ion influx is greater than K⁺ efflux, so the rod stays depolarized to an average membrane potential of −40 mV (instead of the more usual −70 mV). At this slightly depolarized membrane potential, the voltage-gated Ca²⁺ channels are open and there is tonic (continuous) release of the neurotransmitter glutamate from the synaptic portion of the rod onto the adjacent bipolar cell (Fig. 10-41a).

When light activates rhodopsin, a second-messenger cascade is initiated through the G protein **transducin** (Fig. 10-41b). (Transducin is closely related to gustducin, the G protein
In darkness, rhodopsin is inactive, cGMP is high, and CNG and K+ channels are open.

\[ \text{Pigment epithelium cell} \]
\[ \text{Transducin (G protein)} \]
\[ \text{Inactive rhodopsin (opsin and retinal)} \]

\[ \text{cGMP levels high} \]
\[ \text{CNG channel open} \]
\[ \text{Membrane potential in dark = -40 mV} \]

\[ \text{Tonic release of neurotransmitter onto bipolar neurons} \]

\[ \text{FIGURE 10-41 Phototransduction in rods uses the visual pigment rhodopsin.} \]

One rod contains about 10,000 CNG channels open in the dark. One photon of light activates 1 rhodopsin. Each rhodopsin activates 800 transducin. Each transducin cascade removes 6 cGMP. A decrease of 24 cGMP closes one CNG channel. How many photons are needed to close all the CNG channels in one rod?

Signal Processing Begins in the Retina

We now move from the cellular mechanism of light transduction to the processing of light signals by the retina and brain, the third and final step in our vision pathway. Signal processing in the
The retina is an excellent example of convergence [p. 282], in which multiple neurons synapse onto a single postsynaptic cell (Fig. 10-37e). Depending on location in the retina, as many as 15 to 45 photoreceptors may converge on one bipolar neuron. Multiple bipolar neurons in turn innervate a single ganglion cell, so that the information from hundreds of millions of retinal photoreceptors is condensed down to a mere 1 million axons leaving the eye in each optic nerve. Convergence is minimal in the fovea, where some photoreceptors have a 1:1 relationship with their bipolar neurons, and greatest at the outer edges of the retina.

Signal processing in the retina is modulated by input from two additional sets of cells that we will not discuss (Fig. 10-37d). Horizontal cells synapse with photoreceptors and bipolar cells. Amacrine cells modulate information flowing between bipolar cells and ganglion cells.

**Bipolar Cells** After glutamate is released from photoreceptors onto bipolar neurons, signal processing begins. There are two types of bipolar cells, light-on and light-off. Light-on bipolar cells are inhibited by glutamate release in the dark and are activated (released from inhibition) in the light. Light-off bipolar cells are excited by glutamate release in the dark and inhibited in the light. Whether glutamate is excitatory or inhibitory depends on the type of glutamate receptor on the bipolar neuron. In this fashion, one stimulus (light) creates two responses with a single neurotransmitter. Bipolar cells then form either excitatory or inhibitory synapses with ganglion cells, the next neurons in the pathway.

**Ganglion Cells** We know more about ganglion cells because they lie on the surface of the retina, where their axons are the most accessible to researchers. Extensive studies have been done in which researchers stimulated the retina with carefully placed light and evaluated the response of the ganglion cells.

Each ganglion cell receives information from a particular area of the retina. These areas, known as *visual fields*, are similar to receptive fields in the somatic sensory system [p. 336]. The visual field of a ganglion cell near the fovea is quite small. Only a few photoreceptors are associated with each ganglion cell, and so visual acuity is greatest in these areas. At the edge of the retina, multiple photoreceptors converging onto a single ganglion cell results in vision that is not as sharp.

An analogy for this arrangement is to think of pixels on your computer screen. Assume that two screens have the same number of “photoreceptors,” as indicated by a maximal screen resolution of $1280 \times 1024$ pixels. If screen A has one photoreceptor becoming one “ganglion cell” pixel, the actual screen resolution is $1280 \times 1024$, and the image is very clear. If eight photoreceptors on screen B converge into one ganglion cell pixel, then the actual screen resolution falls to $160 \times 128$, resulting in a very blurry and perhaps indistinguishable image.

Visual fields of ganglion cells are roughly circular (unlike the irregular shape of somatic sensory receptive fields) and they are divided into sections: a round center and its doughnut-shaped surround (Fig. 10-42). This organization allows each ganglion cell to use contrast between the center and its surround to interpret visual information. Strong contrast between the center and surround elicits a strong excitatory response (a series of action potentials) or a strong inhibitory response (no action potentials) from the ganglion cell. Weak contrast between center and surround gets an intermediate response.

There are two types of ganglion cell visual fields. In an *on-center/off-surround field*, the associated ganglion cell responds most strongly when light is brightest in the center of the field (Fig. 10-42). If light is brightest in the off-surround region of the field, the ganglion cell is inhibited and stops firing action potentials. The reverse happens with *off-center/on-surround fields*.

What happens if light is uniform across a visual field? In that case, the ganglion cell responds weakly. Thus, the retina uses contrast rather than absolute light intensity to recognize objects in the environment. One advantage of using contrast is that it allows better detection of weak stimuli.

Scientists have now identified multiple types of ganglion cells in the primate retina. The two predominant types, which account for 80% of retinal ganglion cells, are M cells and P cells. Large magnocellular ganglion cells, or M cells, are more sensitive to information about movement. Smaller parvocellular ganglion cells, or P cells, are more sensitive to signals that pertain to form and fine detail, such as the texture of objects in the retina.