10.17: A_Vision

Learning Objectives

By the end of this section, you will be able to do the following:

- Explain how electromagnetic waves differ from sound waves
- Trace the path of light through the eye to the point of the optic nerve
- Explain tonic activity as it is manifested in photoreceptors in the retina

Vision is the ability to detect light patterns from the outside environment and interpret them into images. Animals are bombarded with sensory information, and the sheer volume of visual information can be problematic. Fortunately, the visual systems of species have evolved to attend to the most-important stimuli. The importance of vision to humans is further substantiated by the fact that about one-third of the human cerebral cortex is dedicated to analyzing and perceiving visual information.

Light

As with auditory stimuli, light travels in waves. The compression waves that compose sound must travel in a medium—a gas, a liquid, or a solid. In contrast, light is composed of electromagnetic waves and needs no medium; light can travel in a vacuum (Figure 36.17). The behavior of light can be discussed in terms of the behavior of waves and also in terms of the behavior of the fundamental unit of light—a packet of electromagnetic radiation called a photon. A glance at the electromagnetic spectrum shows that visible light for humans is just a small slice of the entire spectrum, which includes radiation that we cannot see as light because it is below the frequency of visible red light and above the frequency of visible violet light.

Certain variables are important when discussing perception of light. Wavelength (which varies inversely with frequency) manifests itself as hue. Light at the red end of the visible spectrum has longer wavelengths (and is lower frequency), while light at the violet end has shorter wavelengths (and is higher frequency). The wavelength of light is expressed in nanometers (nm); one nanometer is one billionth of a meter. Humans perceive light that ranges between approximately 380 nm and 740 nm. Some other animals, though, can detect wavelengths outside of the human range. For example, bees see near-ultraviolet light in order to locate nectar guides on flowers, and some non-avian reptiles sense infrared light (heat that prey gives off).

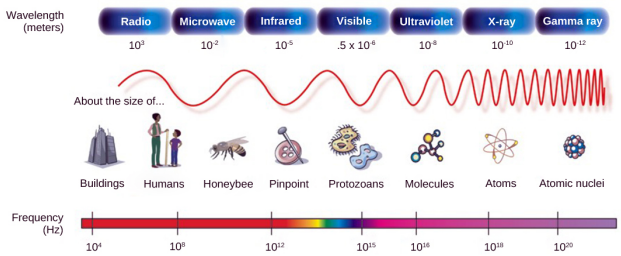


Figure 36.17 In the electromagnetic spectrum, visible light lies between 380 nm and 740 nm. (credit: modification of work by NASA)

Wave amplitude is perceived as luminous intensity, or brightness. The standard unit of intensity of light is the candela, which is approximately the luminous intensity of one common candle.

Light waves travel 299,792 km per second in a vacuum, (and somewhat slower in various media such as air and water), and those waves arrive at the eye as long (red), medium (green), and short (blue) waves. What is termed “white light” is light that is perceived as white by the human eye. This effect is produced by light that stimulates equally the color receptors in the human eye. The apparent color of an object is the color (or colors) that the object reflects. Thus a red object reflects the red wavelengths in mixed (white) light and absorbs all other wavelengths of light.

Anatomy of the Eye

The photoreceptive cells of the eye, where transduction of light to nervous impulses occurs, are located in the retina (shown in Figure 36.18) on the inner surface of the back of the eye. But light does not impinge on the retina unaltered. It passes through other layers that process it so that it can be interpreted by the retina (Figure 36.18b). The cornea, the front transparent layer of the eye, and the crystalline lens, a transparent convex structure behind the cornea, both refract (bend) light to focus the image on the retina.

The iris, which is conspicuous as the colored part of the eye, is a circular muscular ring lying between the lens and cornea that regulates the amount of light entering the eye. In conditions of high ambient light, the iris contracts, reducing the size of the pupil at its center. In conditions of low light, the iris relaxes and the pupil enlarges.

Visual Connection

Visual Connection

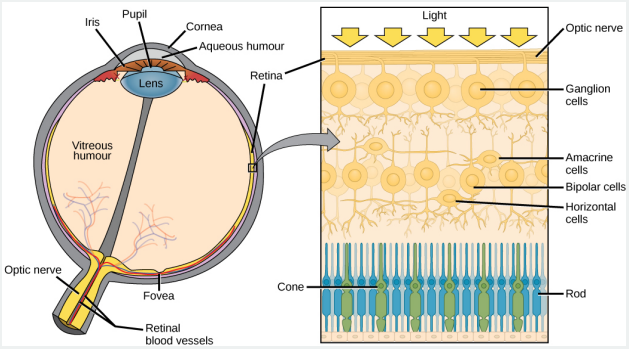


Figure 36.18 (a) The human eye is shown in cross section. (b) A blowup shows the layers of the retina.

Which of the following statements about the human eye is false?

a. Rods detect color, while cones detect only shades of gray.
b. When light enters the retina, it passes the ganglion cells and bipolar cells before reaching photoreceptors at the rear of the eye.
c. The iris adjusts the amount of light coming into the eye.
d. The cornea is a protective layer on the front of the eye.

The main function of the lens is to focus light on the retina and fovea centralis. The lens is dynamic, focusing and re-focusing light as the eye rests on near and far objects in the visual field. The lens is operated by muscles that stretch it flat or allow it to thicken, changing the focal length of light coming through it to focus it sharply on the retina. With age comes the loss of the flexibility of the lens, and a form of farsightedness called presbyopia results. Presbyopia occurs because the image focuses behind the retina. Presbyopia is a deficit similar to a different type of farsightedness called hyperopia caused by an eyeball that is too short. For both defects, images in the distance are clear but images nearby are blurry. Myopia (nearsightedness) occurs when an eyeball is elongated and the image focus falls in front of the retina. In this case, images in the distance are blurry but images nearby are clear.

There are two types of photoreceptors in the retina: rods and cones, named for their general appearance as illustrated in Figure 36.19. Rods are strongly photosensitive and are located in the outer edges of the retina. They detect dim light and are used primarily for peripheral and nighttime vision. Cones are weakly photosensitive and are located near the center of the retina. They respond to bright light, and their primary role is in daytime, color vision.

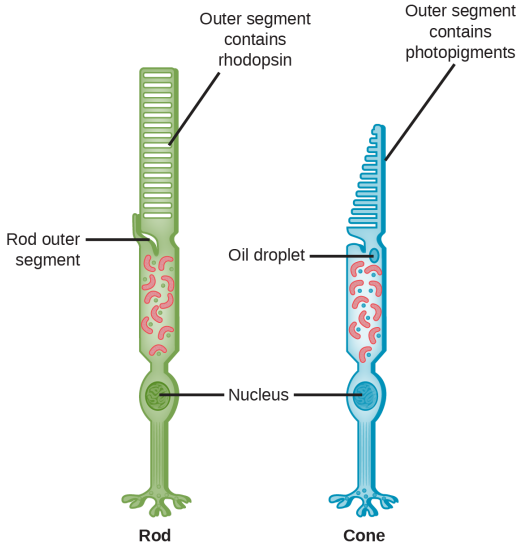


Figure 36.19 Rods and cones are photoreceptors in the retina. Rods respond in low light and can detect only shades of gray. Cones respond in intense light and are responsible for color vision. (credit: modification of work by Piotr Sliwa)

The fovea is the region in the center back of the eye that is responsible for acute vision. The fovea has a high density of cones. When you bring your gaze to an object to examine it intently in bright light, the eyes orient so that the object's image falls on the fovea. However, when looking at a star in the night sky or other object in dim light, the object can be better viewed by the peripheral vision because it is the rods at the edges of the retina, rather than the cones at the center, that operate better in low light. In humans, cones far outnumber rods in the fovea.

Link to Learning

Link to Learning

Review the anatomical structure of the eye, clicking on each part to practice identification.

Transduction of Light

The rods and cones are the site of transduction of light to a neural signal. Both rods and cones contain photopigments. In vertebrates, the main photopigment, rhodopsin, has two main parts (Figure 36.20): an opsin, which is a membrane protein (in the form of a cluster of α-helices that span the membrane), and retinal—a molecule that absorbs light. When light hits a photoreceptor, it causes a shape change in the retinal, altering its structure from a bent (*cis*) form of the molecule to its linear (*trans*) isomer. This isomerization of retinal activates the rhodopsin, starting a cascade of events that ends with the closing of Na^+ channels in the membrane of the photoreceptor. Thus, unlike most other sensory neurons (which become depolarized by exposure to a stimulus) visual receptors become hyperpolarized and thus driven away from threshold (Figure 36.21).

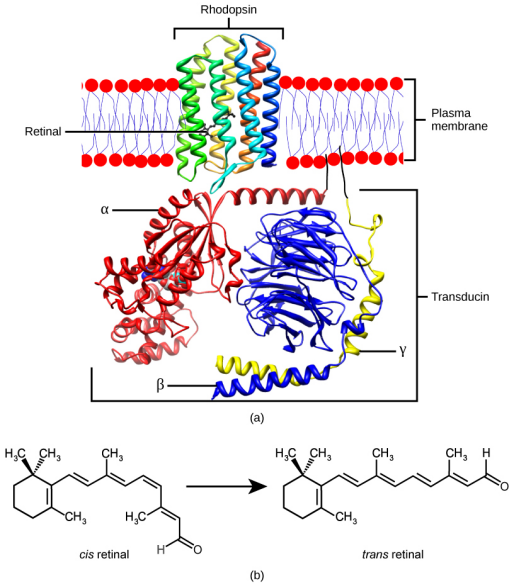


Figure 36.20 (a) Rhodopsin, the photoreceptor in vertebrates, has two parts: the trans-membrane protein opsin, and retinal. When light strikes retinal, it changes shape from (b) a *cis* to a *trans* form. The signal is passed to a G-protein called transducin, triggering a series of downstream events.

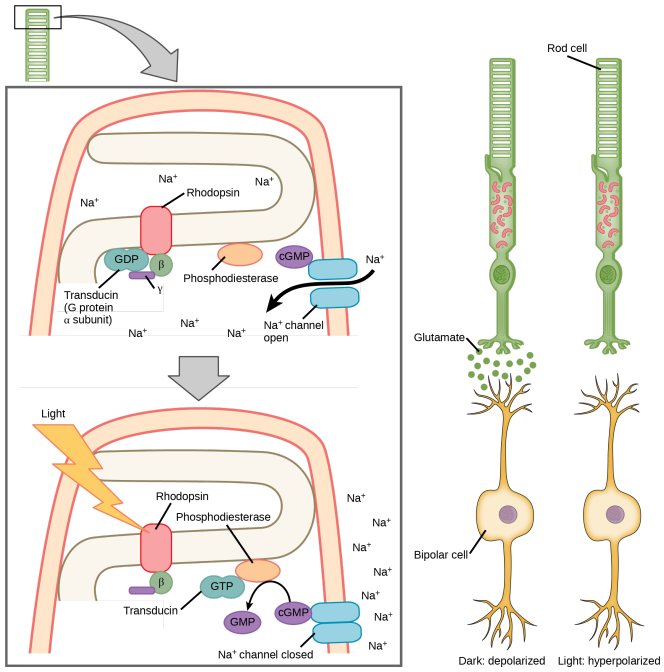


Figure 36.21 When light strikes rhodopsin, the G-protein transducin is activated, which in turn activates phosphodiesterase. Phosphodiesterase converts cGMP to GMP, thereby closing sodium channels. As a result, the membrane becomes hyperpolarized. The hyperpolarized membrane does not release glutamate to the bipolar cell.

Trichromatic Coding

There are three types of cones (with different photopsins), and they differ in the wavelength to which they are most responsive, as shown in Figure 36.22. Some cones are maximally responsive to short light waves of 420 nm, so they are called S cones (“S” for “short”); others respond maximally to waves of 530 nm (M cones, for “medium”); a third group responds maximally to light of longer wavelengths, at 560 nm (L, or “long” cones). With only one type of cone, color vision would not be possible, and a two-cone (dichromatic) system has limitations. Primates use a three-cone (trichromatic) system, resulting in full color vision.

The color we perceive is a result of the ratio of activity of our three types of cones. The colors of the visual spectrum, running from long-wavelength light to short, are red (700 nm), orange (600 nm), yellow (565 nm), green (497 nm), blue (470 nm), indigo (450 nm), and violet (425 nm). Humans have very sensitive perception of color and can distinguish about 500 levels of brightness, 200 different hues, and 20 steps of saturation, or about 2 million distinct colors.

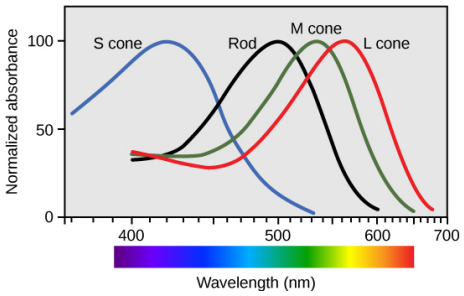


Figure 36.22 Human rod cells and the different types of cone cells each have an optimal wavelength. However, there is considerable overlap in the wavelengths of light detected.

Retinal Processing

Visual signals leave the cones and rods, travel to the bipolar cells, and then to ganglion cells. A large degree of processing of visual information occurs in the retina itself, before visual information is sent to the brain.

Photoreceptors in the retina continuously undergo tonic activity. That is, they are always slightly active even when not stimulated by light. In neurons that exhibit tonic activity, the absence of stimuli maintains a firing rate at a baseline; while some stimuli increase firing rate from the baseline, and other stimuli decrease firing rate. In the absence of light, the bipolar neurons that connect rods and cones to ganglion cells are continuously and actively inhibited by the rods and cones. Exposure of the retina to light hyperpolarizes the rods and cones and removes their inhibition of bipolar cells. The now active bipolar cells in turn stimulate the ganglion cells, which send action potentials along their axons (which leave the eye as the optic nerve). Thus, the visual system relies on change in retinal activity, rather than the absence or presence of activity, to encode visual signals for the brain. Sometimes horizontal cells carry signals from one rod or cone to other photoreceptors and to several bipolar cells. When a rod or cone stimulates a horizontal cell, the horizontal cell inhibits more distant photoreceptors and bipolar cells, creating lateral inhibition. This inhibition sharpens edges and enhances contrast in the images by making regions receiving light appear lighter and dark surroundings appear darker. Amacrine cells can distribute information from one bipolar cell to many ganglion cells.

You can demonstrate this using an easy demonstration to “trick” your retina and brain about the colors you are observing in your visual field. Look fixedly at Figure 36.23 for about 45 seconds. Then quickly shift your gaze to a sheet of blank white paper or a white wall. You should see an afterimage of the Norwegian flag in its correct colors. At this point, close your eyes for a moment, then reopen them, looking again at the white paper or wall; the afterimage of the flag should continue to appear as red, white, and blue. What causes this? According to an explanation called opponent process theory, as you gazed fixedly at the green, black, and yellow flag, your retinal ganglion cells that respond positively to green, black, and yellow increased their firing dramatically. When you shifted your gaze to the neutral white ground, these ganglion cells abruptly decreased their activity and the brain interpreted this abrupt downshift as if the ganglion cells were responding now to their “opponent” colors: red, white, and blue, respectively, in the visual field. Once the ganglion cells return to their baseline activity state, the false perception of color will disappear.

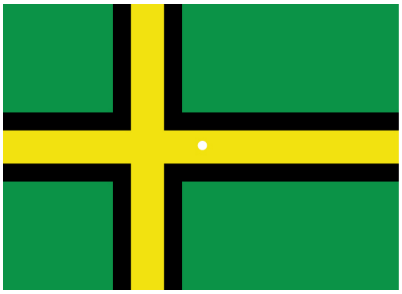


Figure 36.23 View this flag to understand how retinal processing works. Stare at the center of the flag (indicated by the white dot) for 45 seconds, and then quickly look at a white background, noticing how colors appear.

Higher Processing

The myelinated axons of ganglion cells make up the optic nerves. Within the nerves, different axons carry different qualities of the visual signal. Some axons constitute the magnocellular (big cell) pathway, which carries information about form, movement, depth, and differences in brightness. Other axons constitute the parvocellular (small cell) pathway, which carries information on color and fine detail. Some visual information projects directly back into the brain, while other information crosses to the opposite side of the brain. This crossing of optical pathways produces the distinctive optic chiasma (Greek, for “crossing”) found at the base of the brain and allows us to coordinate information from both eyes.

Once in the brain, visual information is processed in several places, and its routes reflect the complexity and importance of visual information to humans and other animals. One route takes the signals to the thalamus, which serves as the routing station for all incoming sensory impulses except olfaction. In the thalamus, the magnocellular and parvocellular distinctions remain intact, and there are different layers of the thalamus dedicated to each. When visual signals leave the thalamus, they travel to the primary visual cortex at the rear of the brain. From the visual cortex, the visual signals travel in two directions. One stream that projects to the parietal lobe, in the side of the brain, carries magnocellular (“where”) information. A second stream projects to the temporal lobe and carries both magnocellular (“where”) and parvocellular (“what”) information.

Another important visual route is a pathway from the retina to the superior colliculus in the midbrain, where eye movements are coordinated and integrated with auditory information. Finally, there is the pathway from the retina to the suprachiasmatic nucleus (SCN) of the hypothalamus. The SCN is a cluster of cells that is considered to be the body’s internal clock, which controls our circadian (day-long) cycle. The SCN sends information to the pineal gland, which is important in sleep/wake patterns and annual cycles.

Link to Learning

Link to Learning

View this interactive presentation to review what you have learned about how vision functions.

The human eye is wrapped in three layers of tissue:

- the **sclerotic coat.** This tough layer creates the "white" of the eye except in the front where it forms the transparent **cornea**. The corneaThe surface of the cornea is kept moist and dust-free by secretions from the tear glands.
  - admits light to the interior of the eye and
  - bends the light rays to that they can be brought to a focus.
- the **choroid coat.** This middle layer is deeply pigmented with **melanin**. It reduces reflection of stray light within the eye. The choroid coat forms the **iris** in the front of the eye. This, too, is pigmented and is responsible for eye "color". The size of its opening, the **pupil**, is variable and under the control of the autonomic nervous system. In dim light (or when danger threatens), the pupil opens wider letting more light into the eye. In bright light the pupil closes down. This not only reduces the amount of light entering the eye but also improves its image-forming ability (as does "stopping down" the iris diaphragm of a camera).
- the **retina** The retina is the inner layer of the eye. It contains the light receptors, the **rods** and **cones** (and thus serves as the "film" of the eye). The retina also has many interneurons that process the signals arising in the rods and cones before passing them back to the brain. **(Note:** the rods and cones are **not at the surface** of the retina but lie underneath the layer of interneurons.)

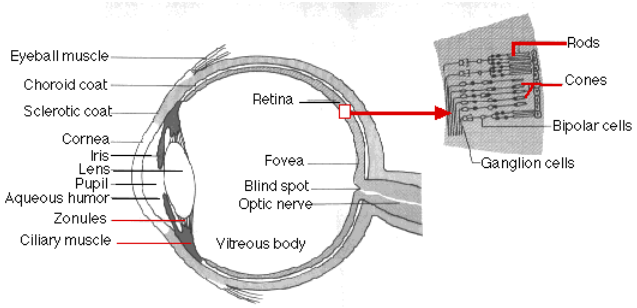


Figure 15.9.3.1 Human eye

The blind spot

All the nerve impulses generated in the retina travel back to the brain by way of the axons in the optic nerve (above). At the point on the retina where the approximately 1 million axons converge on the optic nerve, there are no rods or cones. This spot, called the blind spot, is thus insensitive to light.

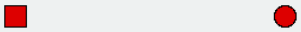


Figure 15.9.3.2 Blind spot

You can demonstrate the presence of the blind spot. Cover your right eye with your hand and stare at the red circle as you move closer to the screen (the square will disappear). Or cover your left eye and stare at the red square as you move.

The Lens

The lens is located just behind the iris. It is held in position by **zonules** extending from an encircling ring of muscle. When this **ciliary muscle** is **relaxed**, its diameter increases, the zonules are put under tension, and the lens is flattened and when **contracted**, its diameter is reduced, the zonules relax, and the lens becomes more spherical. These changes enable the eye to adjust its focus between far objects and near objects.

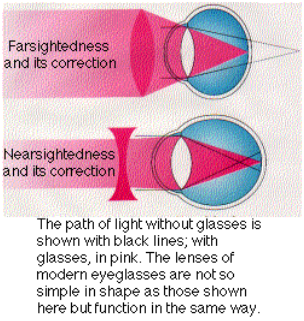


Figure 15.9.3.3 Eye corrections

Farsightedness. If the eyeball is too short or the lens too flat or inflexible, the light rays entering the eye — particularly those from nearby objects — will not be brought to a focus by the time they strike the retina. Eyeglasses with convex lenses can correct the problem. Farsightedness is called **hypermetropia**.

Nearsightedness. If the eyeball is too long or the lens too spherical, the image of distant objects is brought to a focus in front of the retina and is out of focus again before the light strikes the retina. Nearby objects can be seen more easily. Eyeglasses with concave lenses correct this problem by diverging the light rays before they enter the eye. Nearsightedness is called **myopia**.

Cataracts One or both lenses often become cloudy as one ages. When a cataract seriously interferes with seeing, the cloudy lens is easily removed and a plastic one substituted. The entire process can be done in a few minutes as an outpatient under local anesthesia.

The iris and lens divide the eye into two main chambers:

- the front chamber is filled with a watery liquid, the **aqueous humor**
- the rear chamber is filled with a jellylike material, the **vitreous body**

The Retina

Four kinds of light-sensitive receptors are found in the retina:

- **rods**
- three kinds of **cones**, each "tuned" to respond best to light from a portion of the spectrum of visible light
  - cones that absorb long-wavelength light (red)
  - cones that absorb middle-wavelength light (green)
  - cones that absorb short-wavelength light (blue)

This scanning electron micrograph (courtesy of Scott Mittman and David R. Copenhagen) shows rods and cones in the retina of the tiger salamander. Each type of receptor has its own special pigment for absorbing light. Each consists of a transmembrane protein called **opsin** coupled to the prosthetic group **retinal**. Retinal is a derivative of vitamin A (which explains why night blindness is one sign of vitamin A deficiency) and is used by all four types of receptors.

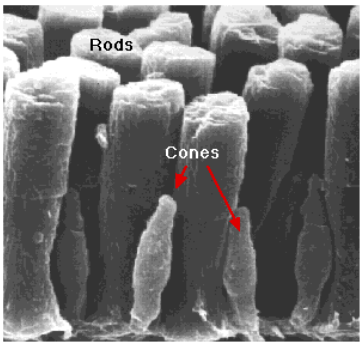


Figure 15.9.3.4 The retina

The amino acid sequence of each of the four types of opsin are similar, but the differences account for their differences in absorption spectrum. The retina also contains a complex array of interneurons:

- **bipolar cells** and **ganglion cells** that together form a path from the rods and cones to the brain
- a complex array of other interneurons that form synapses with the bipolar and ganglion cells and modify their activity.

Ganglion cells are always active. Even in the dark they generate trains of action potentials and conduct them back to the brain along the **optic nerve**. Vision is based on the modulation of these nerve impulses. There is not the direct relationship between visual stimulus and an action potential that is found in the senses of hearing, taste, and smell. In fact, action potentials are not even generated in the rods and cones.

Rod Vision

Rhodopsin is the light-absorbing pigment of the rods. This G-protein-coupled receptor (GPCR) is incorporated in the membranes of disks that are neatly stacked (some 1000 or more of them) in the outer portion of the rod. This arrangement is reminiscent of the organization of thylakoids, another light-absorbing device.

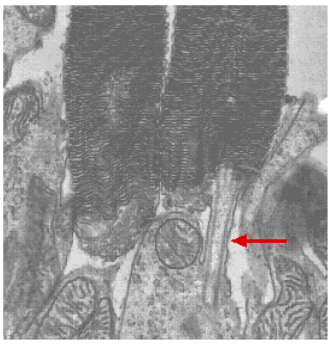


Fig.15.9.3.5 Rod cells of kangaroo bat

The electron micrograph (courtesy of Keith Porter) shows the rod cells of the kangaroo rat. The outer segments of the rods contain the orderly stacks of membranes which incorporate rhodopsin. The inner portion contain many mitochondria. The two parts of the

rod are connected by a stalk (arrow) that has the same structure as a primary cilium. Although the disks are initially formed from the plasma membrane, they become separated from it. Thus signals generated in the disks must be transmitted by a chemical mediator (a "second messenger" called **cyclic GMP** (cGMP) to alter the potential of the plasma membrane of the rod. Rhodopsin consists of an opsin of 348 amino acids coupled to **retinal**. Like all G-protein-coupled receptors, opsin has 7 segments of alpha helix that pass back and forth through the lipid bilayer of the disk membrane.

Retinal

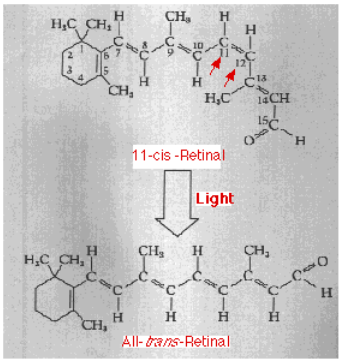
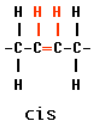
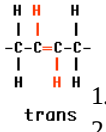


Figure 15.9.3.6 Retinal

Retinal consists of a system of alternating single and double bonds. In the dark, the hydrogen atoms attached to the #11 and #12 carbon atoms of retinal (red arrows) point in the same direction producing a kink in the molecule. This configuration is designated *cis*. When light is absorbed by retinal, the molecule straightens out forming the all-*trans* isomer.





This physical change in retinal triggers the following chain of events culminating in a change in the pattern of impulses sent back along the optic nerve.

1. Formation of all-*trans* retinal activates its **opsin**.
2. Activated rhodopsin, in turn, activates many molecules of a G protein called **transducin**.
3. Transducin activates an enzyme that breaks down **cyclic GMP**.
4. The drop in cGMP **closes** Na^+ channels in the plasma membrane of the rod. Because these positive ions can no longer enter, the interior of the cell becomes more negative (hyperpolarized) increasing its membrane potential from about −30 to some −70 mV.
5. This **slows** the release of the neurotransmitter glutamate at synapses between the rod and interneurons (e.g., bipolar cells).
6. This reduction in glutamate release activates some interneuron pathways, inhibits others.
7. The interplay of excited and inhibited interneurons modulates the spontaneous firing of the ganglion cells to which they are connected and gives rise to the ability of the retina to discriminate shapes.

So the retina is not simply a sheet of photocells, but a tiny brain center that carries out complex information processing before sending signals back along the optic nerve. In fact, the retina really **is** part of the brain and grows out from it during embryonic development.

Rod vision is acute but coarse

Rods do not provide a sharp image for several reasons.

- Adjacent rods are connected by gap junctions and so share their changes in membrane potential.
- Several nearby rods often share a single circuit to one ganglion cell.
- A single rod can send signals to several different ganglion cells.

So if only a single rod is stimulated, the brain has no way of determining exactly where on the retina it was. However, rods are extremely sensitive to light. A single photon (the minimum unit of light) absorbed by a small cluster of adjacent rods is sufficient to send a signal to the brain. So although rods provide us with a relatively grainy, colorless image, they permit us to detect light that is over a billion times dimmer than what we see on a bright sunny day.

Cone Vision

Although cones operate only in relatively bright light, they provide us with our sharpest images and enable us to see colors. Most of the 3 million cones in each retina are confined to a small region just opposite the lens called the **fovea**. So our sharpest and colorful

images are limited to a small area of view. Because we can quickly direct our eyes to anything in view that interests us, we tend not to be aware of just how poor our peripheral vision is.

The three types of cones provide us the basis of color vision. Cones are "tuned" to different portions of the visible spectrum.

- red absorbing cones; those that absorb best at the relatively long wavelengths peaking at 565 nm
- green absorbing cones with a peak absorption at 535 nm
- blue absorbing cones with a peak absorption at 440 nm.

Retinal is the prosthetic group for each pigment. Differences in the amino acid sequence of their opsins accounts for the differences in absorption. The response of cones is not all-or-none. Light of a given wavelength (color), say 500 nm (green), stimulates all three types of cones, but the green-absorbing cones will be stimulated most strongly. Like rods, the absorption of light does not trigger action potentials but modulates the membrane potential of the cones.

Color Blindness

The term color blindness is something of a misnomer. Very few (~1 in 10^5) people cannot distinguish colors at all. Most "color-blind" people actually have abnormal color vision such as confusing the red and green of traffic lights. As high as 8% of the males in some populations have an inherited defect in their ability to discriminate reds and greens. These defects are found almost exclusively in males because the genes that encode the red-absorbing and green-absorbing opsins are on the X chromosome.

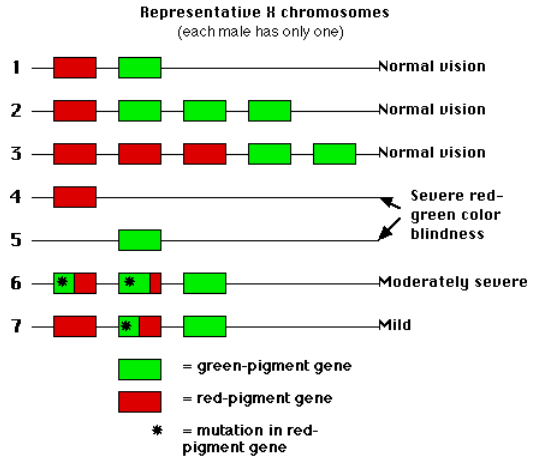


Figure 15.9.3.7 Red - Green genes

The X chromosome normally carries a cluster of from 2 to 9 opsin genes. The minimum basis for normal red-green vision is one gene whose opsin absorbs efficiently in the red and one that absorbs well in the green (chromosome **1** in the figure). Multiple copies of these genes are also fine (**2** and **3**). Males with either a "green gene" or "red gene" missing are severely color blind (**4** and **5**). However, if all the red genes carry mutations (this seldom seems to be the case for the green genes — nobody knows why), then they may have red-green color blindness that ranges from mild to severe depending on the particular mutations involved (**6**). The rule seems to be that the more the mutations shift the pigment towards green, the more serious the defect. However, a large number of mutations don't always produce serious defects. Multiple mutations in a single gene may offset each other producing only mild defects. And as long as one normal copy of each gene is present, the presence of additional mutated genes seldom produce a serious problem (**7**).

Why do some males have as many as 9 copies of genes encoding the red and green opsins, when two are enough? The sequences of the red and green genes are the same at 98% of their nucleotides. This high degree of similarity creates the risk of mismatches in synapsis during meiosis with unequal crossing over.

Blue vision

Abnormal blue sensitivity occasionally occurs in humans but is much rarer than abnormalities in red-green vision. The gene for the blue-cone opsin is located on chromosome 7. Thus this trait shows an autosomal pattern of inheritance being found in females as often as in males.