A **Closer Look**

The Retina and Color Sensitivity

Structure of the Retina

Light entering the retina first passes through outer layers, consisting of nerve endings and connecting cells, before reaching the receptor cells, where an image is formed and detected by photosensitive molecules. There are two types of receptor cells, called "rods" and "cones" because of the rod or cone shapes of the ends of these cells (Fig. 25-A).

Receptor cells are not connected directly to nerve fibers. Between the receptor cells and the nerve fibers is a layer of "bipolar" cells. One end of these cells interacts electrically with receptor cells across small gaps, or "synapses"; the other end interacts across synapses with nerve fibers (Fig. 25-B). It is the complexity of this electrical network that gives the retina its brainlike capacity to analyze visual images.

Fig. 25-A A scanning electron micrograph of the receptor ends of rods and cones.

Intensity Range: Scotopic and Photopic Vision

The eye is able to adapt to an enormously wide range of light intensities. For example, you can read a book in bright sunlight or look at the stars at night. The intensity of starlight reaching your eyes is only about 10^{-6} W/m^2, but light reflected from a book in direct sunlight has an intensity at the eye on the order of 10 W/m^2. So given time to adapt to different lighting conditions, the eye is effective over a range of intensities varying by a factor of at least 10^7. Actually the entire range of sensitivity is much greater than this. Experiments on the threshold of vision for the dark-adapted eye have shown a sensitivity to light much weaker than starlight. Light can be detected when as few as 100 photons* enter the eye in an interval of 0.001 s. When the eye is exposed to a scene in bright sunlight, in an interval of 0.001 s the eye receives on the order of 10^{32} photons—roughly 10^{30} times the number at the threshold of vision.

Fig. 25-B Typical connection of foveal cones with nerve fibers through bipolar cells.

Part of the eye's adaptation between light and dark involves the size of the pupil, but the pupil diameter can vary only from about 2 mm to about 6 mm. This means that the area of the pupil can vary only by a factor of $3^2 = 9$. This accounts for only a small part of the eye's ability to adapt. Most of it comes from the way the retina responds to vastly different intensities.

The eye possesses a dual system for detecting light over two intensity ranges. Light-adapted vision, called photopic vision, utilizes only cones. Dark-adapted vision, called scotopic vision, utilizes only rods. Pure scotopic vision occurs in light of intensity less than about 10^{-3} W/m^2 (a little less bright than a moonlit night). The cones are then completely inoperative, and light is detected solely through absorption of photons by the rhodopsin molecules, located at the ends of the rod cells. With scotopic vision there is no color sense; although the eye is sensitive to various frequencies, these are sensed not as colors but as shades of gray, as in a

*Only about 5 of these 100 photons are actually absorbed by receptors in the retina. Absorption of a single photon by a photosensitive molecule is enough to produce an electrical response in the receptor cell, but the circuitry of the bipolar layer needs about five photons to produce a nerve impulse. This mechanism apparently prevents the retina from responding to the few thermal photons that are present.

Continued.

A Closer Look

black and white photograph. Visual acuity, the ability to see fine details, is very limited under scotopic conditions. For example, it is impossible to read fine print under these conditions.

The Visible Spectrum

Although "visible light" constitutes only that part of the electromagnetic spectrum with vacuum wavelengths between about 400 nm to 700 nm, the retina is actually somewhat sensitive to ultraviolet light, with wavelengths shorter than 400 nm. These shorter wavelengths are not normally sensed because most such light is absorbed by other parts of the eye before reaching the retina. The cornea absorbs wavelengths below 300 nm, and the lens absorbs almost all light of wavelength below 400 nm. The lens thus protects the retina from the potentially damaging UV light from 300 nm to 400 nm.*

Spectral Sensitivity

For scoptic vision, the eye's sensitivity to various frequencies is not the same as for photopic vision (shown at the beginning of Chapter 23). Fig. 25-C shows both scotopic and photopic sensitivities in a single graph. Notice that under photopic conditions the eye has maximum sensitivity to yellow-green light, but under scotopic conditions the eye has maximum sensitivity to the blue-green part of the spectrum (though of course it is not sensed as blue-green) and is completely blind to the red end of the spectrum. This is known as the Purkinje effect and can be observed in a garden at night, where red flowers may appear black and blue flowers appear white or gray.

Rhodopsin molecules have been chemically extracted from rod cells. When exposed to light of various wavelengths, these molecules absorb some wavelengths more readily than others. The "absorption spectrum," which shows the relative amount of each wavelength absorbed, is nearly identical to the eye's scotopic sensitivity curve. Thus it is the rhodopsin molecule that is responsible for the eye's spectral sensitivity under scotopic conditions.

After absorbing light in the retina, rhodopsin is regenerated in a complex chemical process involving vitamin A and requiring about 5 minutes for half of a large sample of molecules to be regenerated. After about 30 minutes the regeneration is nearly complete. Apparently the time required for the eye's adaptation to the dark, after exposure to bright light, is related to this regeneration time, and a severe deficiency in vitamin A will prevent it and result in night blindness.

It is much more difficult to extract the photosensitive molecules from cone cells than it is to extract the photosensitive rhodopsin molecule from rod cells. However, beginning in the 1960s delicate experiments were performed, using a technique in which a narrow light beam was directed onto individual cone cells in retinal segments taken from either human, monkey, or goldfish retinas. The frequency of the light was varied, and the fraction of light absorbed was measured as a function of frequency. In all these experiments three distinct kinds of cells were identified, each with its own absorption spectrum. Approximate absorption curves for human cones are shown in Fig. 25-D. Each of these curves covers a broad spectral range, with maximum absorption at 450 nm, 540 nm, and

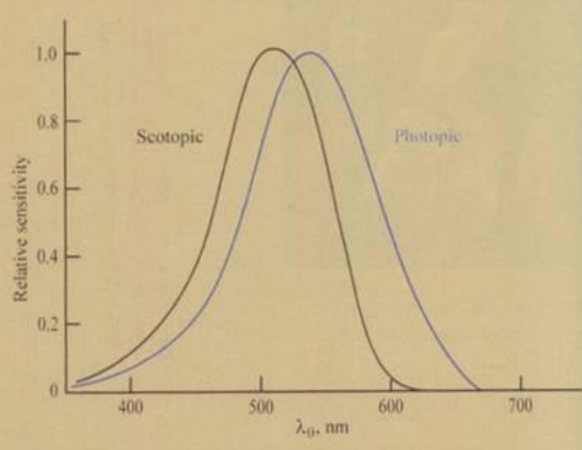

Fig. 25-C Spectral sensitivity of the eye for photopic (light-adapted) and scotopic (dark-adapted) vision.

*In time the lens itself may be damaged by the absorption of UV light. (This often occurs in older individuals who have spent a lifetime exposed to sunlight, especially in tropical areas where sunlight is most intense, or in the Arctic zone where much sunlight is reflected from snow and ice.) As the damage increases, the lens gradually becomes opaque. This is called a "cataract." A person with a cataract may have the lens surgically removed. It is then found that the eye has considerable sensitivity to ultraviolet light. Some people have even reported seeing X-rays.

580 nm. These maxima correspond to blue, green, and yellow light respectively.

This spectrometry work verifies a theory proposed by Thomas Young in 1802. Young believed that human perception of color comes from three distinct color receptors in the human eye, sensitive respectively to blue, green, and red light,* and that all color sensations were combinations of excitations of these receptors. Maxwell and Helmholtz further developed this "trichromatic" theory, which is very successful in accounting for color-mixing phenomena. Any spectral color can be matched when the right combination of blue, green, and red light—the "primary colors"—are mixed (Fig. 25-E). For example, you see yellow when your red and green cones are equally stimulated and your blue cones are not stimulated. You can accomplish this either by looking at monochromatic yellow light or by looking at a combination of green light and red light. In either case, the perception is yellow.

You should not confuse the primary colors of light with the primary paint colors used by an artist who mixes paints. The primary paint colors are yellow, cyan (a brilliant shade of blue), and magenta (a purplish red). Paint pigments create color by absorbing or subtracting out other colors in the light that illuminates them. For example, when blue paint is illuminated by white light, the pigment absorbs the red end of the spectrum and reflects the blue end. Yellow paint illuminated by white light absorbs the blue part of the light and reflects red and green light equally. If you mix yellow and blue paints, you get green paint, since the yellow pigment absorbs the blue light and the blue pigment absorbs the red light. On the other hand, if you mix yellow light and blue light, you get white light!

*Although the third pigment peaks in the yellow, rather than red, it does extend far enough into the red to account for detection of this color.

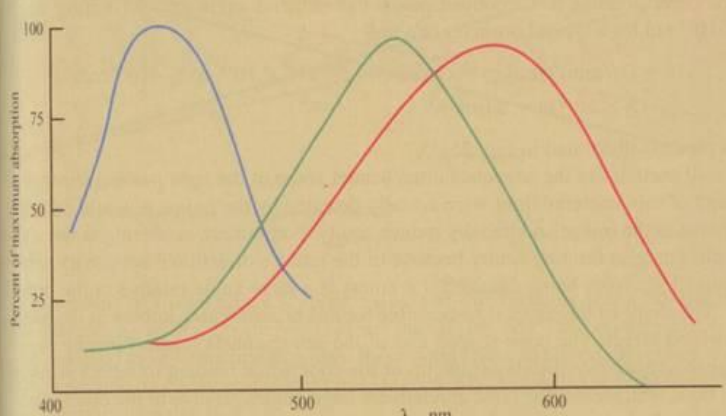

Fig. 25-D Absorption of light by the three types of cones in the retina of the human eye.

Fig. 25-E Colors produced by the addition of the primary colors of red, blue, and green.

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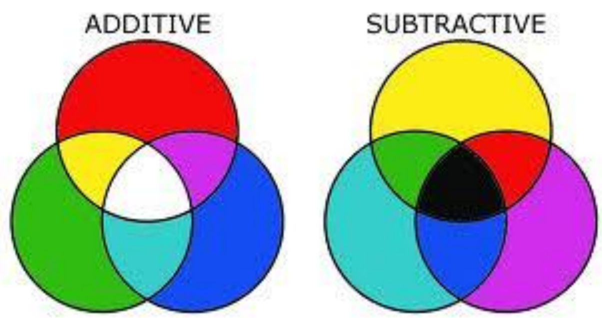
A Closer Look

Color blindness occurs when one or more of the cones are missing, or, more commonly, when the absorption spectra of the red and green cones are somewhat different from those shown in Fig. 25-D. "Red-green" color blindness is about 10 times more common in men than in women, occurring in about 6% of all males. Other kinds of color blindness are more rare. Only about one person in 30,000 is completely blind to colors. Those who are red-green color blind can distinguish bright primary colors but have difficulty with certain shades of color.

Although the idea of three distinct kinds of color receptors now seems to be well established, it seems certain that color perception does not consist merely of receptor cells sending one of three messages (blue, green, or red) along the optic nerve directly to the brain. There is an abundance of color phenomena that is impossible to explain in this way. For example, Land has performed a series of experiments that dramatically illustrate how the human eye is able to maintain a constant determination of the color of an object, independent of the frequency of the illuminating light and also therefore independent of the frequency of the light reflected by the object. Apparently the eye is able to compare the light reflected from various objects in the visual field and to somehow determine from these data the "true" color of each object. This is just one indication of the processing of visual information that takes place both within the retina in the network of receptors, bipolar cells, and nerve fibers and in the visual cortex of the brain.

1. Look at the picture of cones and rods. Do cones look like you expected? Why? Have you seen an image of cones and rods before? If so where?
2. Is the sensitivity range of our eyes as phenomenal as the range for our ears? What are you basing this answer on?
3. What is scotopic vision?
4. What is photopic vision?
5. Sit in a dark room (no more light than moonlight) for 5+ minutes and then make some observations. Are you able to see detail of objects around you, can you identify colors, are you comfortable functioning at this level of light? Do your observations match the article, why or why not?
6. Now try reading normal size text. Are you able to do this after sitting in the room for 5+ minutes?
7. Why do questions 4 and 5 ask you to sit for 5+ minutes before making your final observations? Be very specific in your answer.
8. Does the sensitivity of our three types of cones appear to be equally spaced across the visible spectrum? Explain? Does this fit with the description in lab about the fovea not containing blue cones? Why?



9. Consider primary colors of light and primary paint colors. The colors on the right are demonstrating subtractive color combinations which are used in art. For example, red and green make black. However, when considering how light combines, additive combinations, you can see that red and green make yellow!

Use page three to fill in the following table to see how this works:

Color / substance	Absorbs	Reflects
Blue paint		
Yellow paint		
Yellow and Blue paint mixed		
Yellow and Blue light		