Physiology of the Retina

Layers of the Retina

1- Retinal pigment epithelium
2- Layer of rods and cones
3- External limiting membrane
4- Outer nuclear layer containing the cell bodies of the rods and cones
5- Outer plexiform layer
6- Inner nuclear layer
7- Inner plexiform layer
8- Ganglionic layer
9- Layer of optic nerve fibers
10- Internal limiting membrane

After light passes through the lens system of the eye and then through the vitreous humor, it enters the retina from the inside of the eye (see Figure below); that is, it passes first through the ganglion cells and then through the plexiform and nuclear layers before it finally reaches the layer of rods and cones located all the way on the outer edge of the retina. This distance is a thickness of several hundred micrometers; visual acuity is decreased by this passage through such nonhomogeneous tissue. However, in the central foveal region of the retina, the inside layers are pulled aside to decrease this loss of acuity.

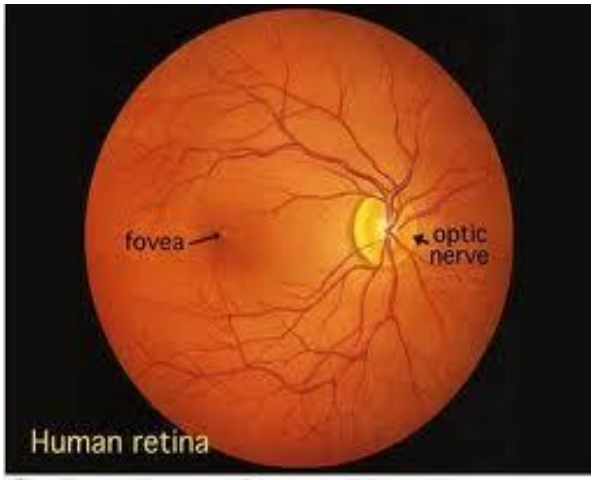
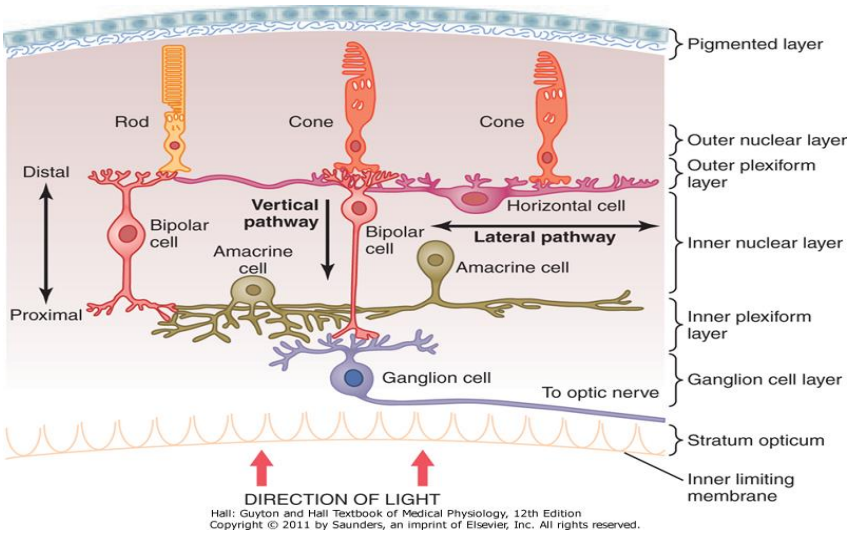


Fig. 1. Human retina as seen through an opthalmoscope.



Foveal Region of the Retina and Its Importance in Acute Vision

The f*ovea* is a minute area in the center of the retina, occupying a total area a little more than 1 square millimeter; it is especially capable of acute and detailed vision. The c*entral fovea,* only 0.3 millimeter in diameter, is composed almost entirely of cones.

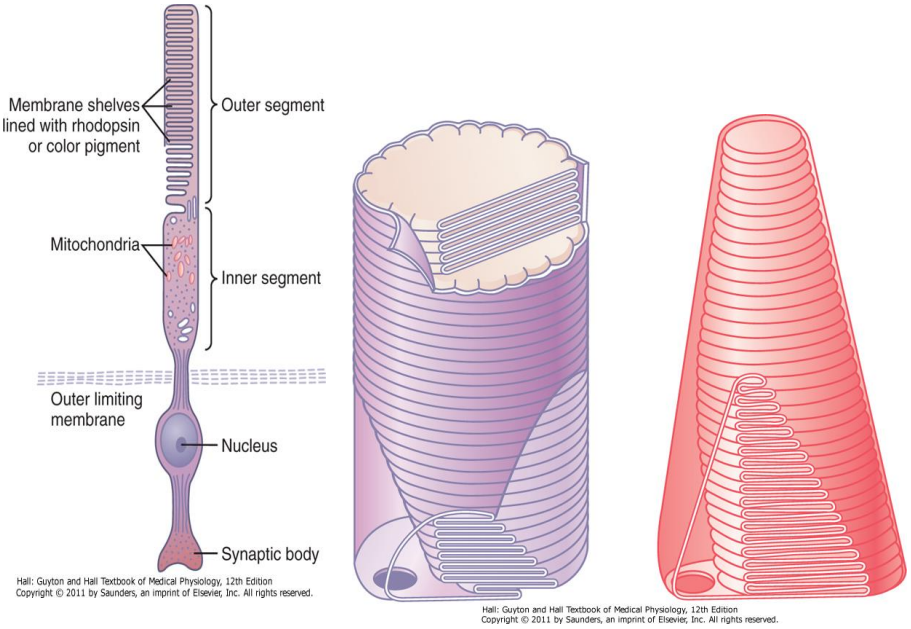
Rods and Cones

Figure below is a diagrammatic representation of the essential components of a photoreceptor (either a rod or a cone).

The major functional segments of either a rod or cone are (1) the outer segment, (2) the inner segment, (3) the nucleus, and (4) the synaptic body. The light-sensitive photochemical is found in the outer segment. In the case of the rods, this is rhodopsin; in the cones, it is one of three color pigments, that function almost exactly the same as rhodopsin except for differences in spectral sensitivity.

The inner segment of the rod or cone contains the usual cytoplasm with cytoplasmic organelles. Especially important are the mitochondria, which play the important role of providing energy for function of the photoreceptors.

The synaptic body is the portion of the rod or cone that connects with subsequent neuronal cells, the horizontal and bipolar cells, which represent the next stages in the vision chain.



Retinal pigment epithelium

The black pigment *melanin* in the pigment layer prevents light reflection throughout the globe of the eyeball; this is extremely important for clear vision. This pigment performs the same function in the eye as the black coloring inside the bellows of a camera. Without it, light rays would be reflected in all directions within the eyeball and would cause diffuse lighting of the retina rather than the normal contrast between dark and light spots required for formation of precise images.

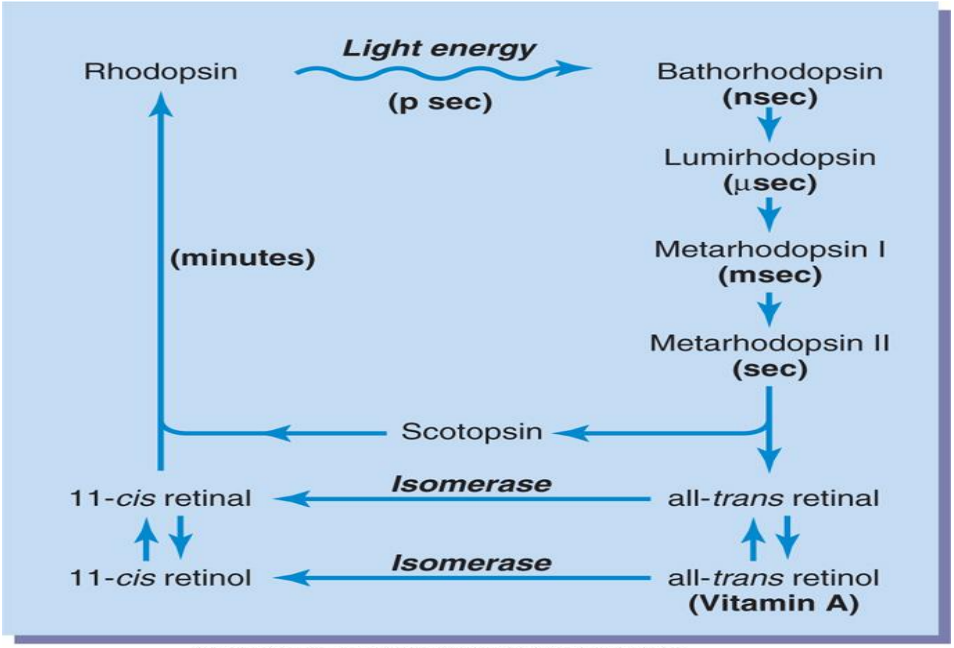
Photochemistry of Vision

The light-sensitive chemical in the r*ods* is called r*hodopsin;* the light-sensitive chemicals in the c*ones,* called c*one pigments* or c*olor pigments,* have compositions only slightly different from that of rhodopsin.This substance is a combination of the protein *scotopsin* and the carotenoid pigment *retinal* . Furthermore, the retinal is a particular type called 11-*cis* retinal. This *cis* form of retinal is important because only this form can bind with scotopsin to synthesize rhodopsin.

When light energy is absorbed by rhodopsin, the rhodopsin begins to decompose within a very small fraction of a second. The cause of this is photoactivation of electrons in the retinal portion of the rhodopsin, which leads to instantaneous change of the *cis* form of retinal into an all-*trans* form that still has the same chemical structure as the *cis* form but has a different physical structure-a straight molecule rather than an angulated molecule. Because the three-dimensional orientation of the reactive sites of the all-*trans* retinal no longer fits with the orientation of the reactive sites on the protein *scotopsin,* the all-*trans* retinal begins to pull away from the scotopsin. The immediate product is *bathorhodopsin,* which is a partially split combination of the all-*trans* retinal and scotopsin. Bathorhodopsin is extremely unstable and decays in nanoseconds to *lumirhodopsin.* This then decays in microseconds to *metarhodopsin I,* then in about a millisecond to *metarhodopsin II,* and finally, much more slowly (in seconds), into the completely split products *scotopsin* and all-*trans* retinal.
It is the metarhodopsin II, also called a*ctivated rhodopsin,* that excites electrical changes in the rods, and the rods then transmit the visual image into the central nervous system in the form of optic nerve action potential.

Re-formation of Rhodopsin
The first stage in re-formation of rhodopsin is to reconvert the all-t*rans* retinal into 11-c*is* retinal. This process requires metabolic energy and is catalyzed by the enzyme r*etinal isomerase.* Once the 11-c*is* retinal is formed, it automatically recombines with the scotopsin to re-form rhodopsin.

Role of Vitamin A for Formation of Rhodopsin
Note in Figure below that there is a second chemical route by which all-tra*ns re*tinal can be converted into 11-cis *re*tinal. This is by conversion of the all-tra*ns re*tinal first into all-tra*ns re*tinol, which is one form of vitamin A. Then the all-tra*ns re*tinol is converted into 11-cis *re*tinol under the influence of the enzyme isomerase. Finally, the 11-cis *re*tinol is converted into 11-cis *re*tinal, which combines with scotopsin to form new rhodopsin.
Vitamin A is present both in the cytoplasm of the rods and in the pigment layer of the retina. Therefore, vitamin A is normally always available to form new retinal when needed.



Color Vision

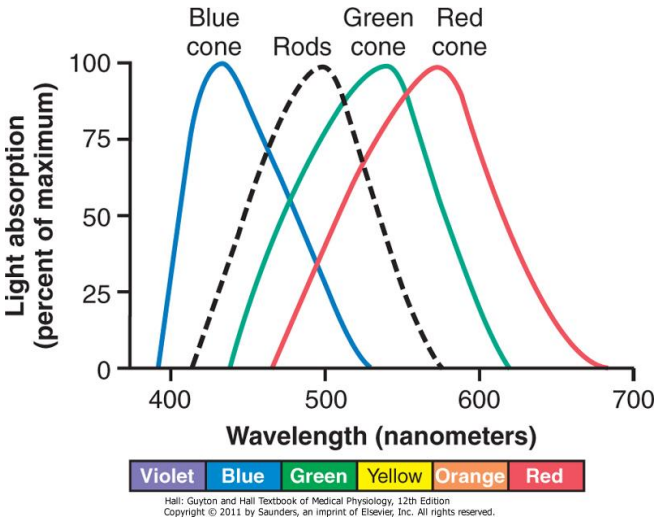
Tricolor Mechanism of Color Detection

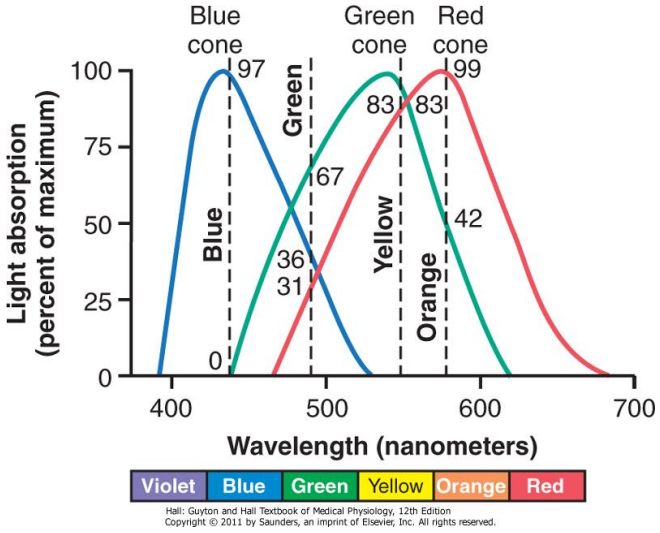
All theories of color vision are based on the well-known observation that the human eye can detect almost all gradations of colors when only red, green, and blue monochromatic lights are appropriately mixed in different combinations.

Spectral Sensitivities of the Three Types of Cones

On the basis of color vision tests, the spectral sensitivities of the three types of cones in humans have proved to be essentially the same as the light absorption curves for the three types of pigment found in the cones. These curves are shown in Figures below. They can explain most of the phenomena of color vision.

Interpretation of Color in the Nervous System





Referring to Figures above, one can see that an orange monochromatic light with a wavelength of 580 nanometers stimulates the red cones to a value of about 99 (99 percent of the peak stimulation at optimum wavelength); it stimulates the green cones to a value of about 42, but the blue cones not at all. Thus, the ratios of stimulation of the three types of cones in this instance are 99:42:0. The nervous system interprets this set of ratios as the sensation of orange. Conversely, a monochromatic blue light with a wavelength of 450 nanometers stimulates the red cones to a stimulus value of 0, the green cones to a value of 0, and the blue cones to a value of 97. This set of ratios-0:0:97-is interpreted by the nervous system as blue. Likewise, ratios of 83:83:0 are interpreted as yellow, and 31:67:36 as green.

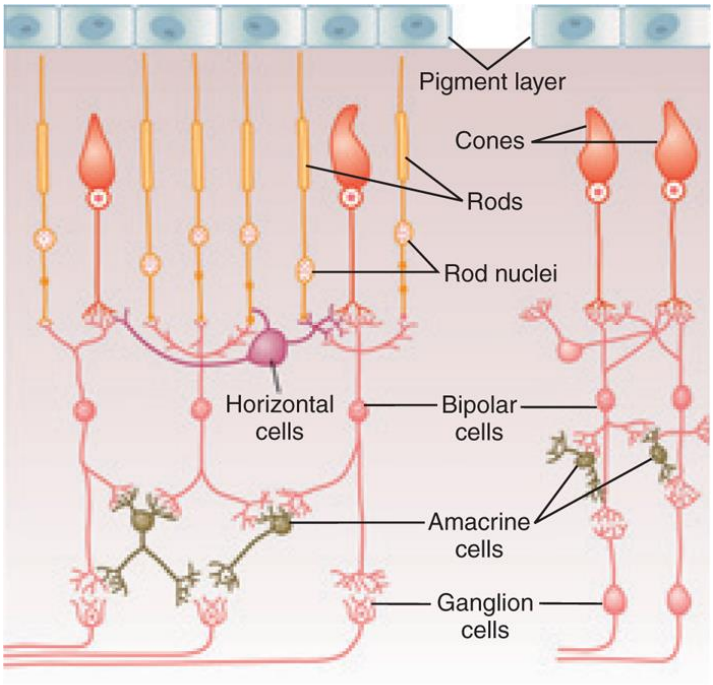
Perception of White Light

About equal stimulation of all the red, green, and blue cones gives one the sensation of seeing white. Yet there is no single wavelength of light corresponding to white; instead, white is a combination of all the wavelengths of the spectrum. Furthermore, the perception of white can be achieved by stimulating the retina with a proper combination of only three chosen colors that stimulate the respective types of cones about equally.

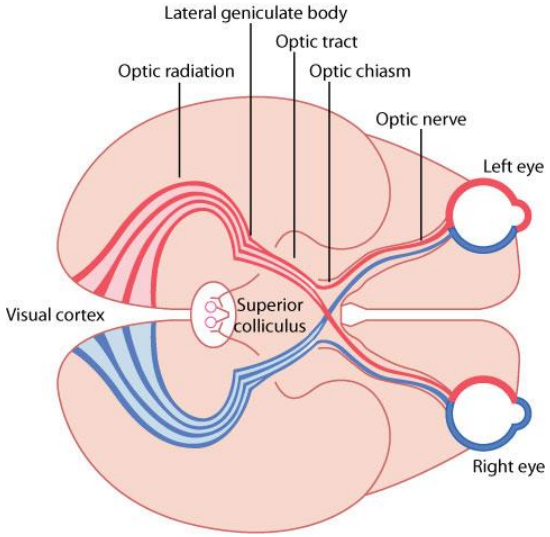
Neural Function of the Retina

Figure below presents the essentials of the retina's neural connections, showing at the left the circuit in the peripheral retina and at the right the circuit in the foveal retina. The different neuronal cell types are as follows:

1. The photoreceptors themselves-the rods and cones-which transmit signals to the outer plexiform layer, where they synapse with bipolar cells and horizontal cells
2. The horizontal cells, which transmit signals horizontally in the outer plexiform layer from the rods and cones to bipolar cells
3. The bipolar cells, which transmit signals vertically from the rods, cones, and horizontal cells to the inner plexiform layer, where they synapse with ganglion cells and amacrine cells
4. The amacrine cells, which transmit signals in two directions, either directly from bipolar cells to ganglion cells or horizontally within the inner plexiform layer from axons of the bipolar cells to dendrites of the ganglion cells or to other amacrine cells
5. The ganglion cells, which transmit output signals from the retina through the optic nerve into the brain



Central Neurophysiology of Vision



Visual Pathways

The visual nerve signals leave the retinas through the optic nerves. At the optic chiasm, the optic nerve fibers from the nasal halves of the retinas cross to the opposite sides, where they join the fibers from the opposite temporal retinas to form the optic tracts. The fibers of each optic tract then synapse in the dorsal lateral geniculate nucleus of the thalamus, and from there, geniculocalcarine fibers pass by way of the optic radiation to the primary visual cortex in the calcarine fissure area of the medial occipital lobe.

Visual fibers also pass to several older areas of the brain: (1) from the optic tracts to the suprachiasmatic nucleus of the hypothalamus, presumably to control circadian rhythms that synchronize various physiologic changes of the body with night and day; (2) into the pretectal nuclei in the midbrain, to elicit reflex movements of the eyes to focus on objects of importance and to activate the pupillary light reflex; (3) into the superior colliculus, to control rapid directional movements of the two eyes; and (4) into the ventral lateral geniculate nucleus of the thalamus and surrounding basal regions of the brain, presumably to help control some of the body's behavioral functions.

Thus, the visual pathways can be divided roughly into an old system to the midbrain and base of the forebrain and a new system for direct transmission of visual signals into the visual cortex located in the occipital lobes. In humans, the new system is responsible for perception of virtually all aspects of visual form, colors, and other conscious vision.

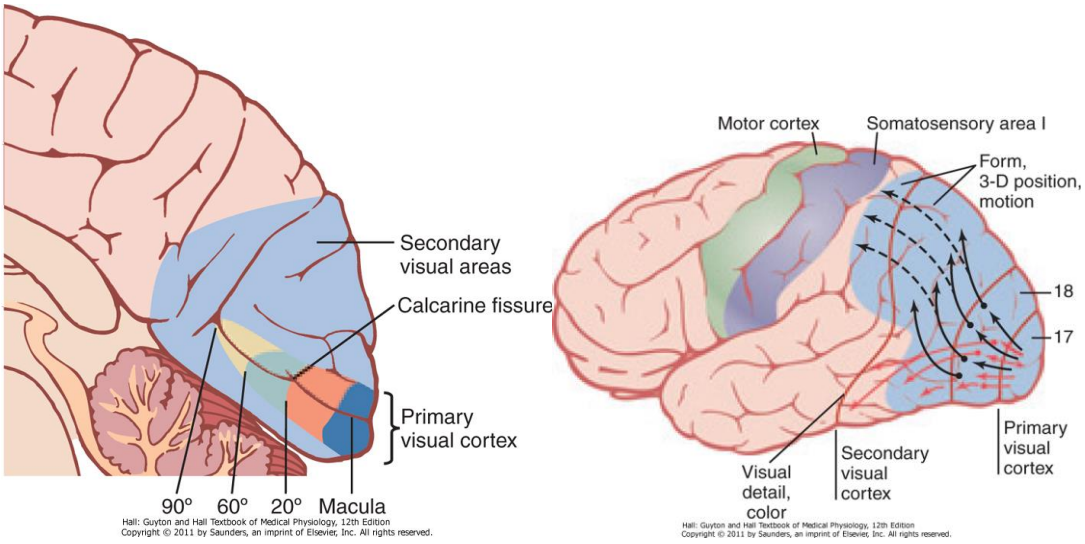
Primary Visual Cortex

The primary visual cortex lies in the cal*carine fissure area, e*xtending forward from the occ*ipital pole on* the med*ial a*spect of each occipital cortex. This area is the terminus of direct visual signals from the eyes. Signals from the macular area of the retina terminate near the occipital pole, whereas signals from the more peripheral retina terminate at or in concentric half circles anterior to the pole but still along the calcarine fissure on the medial occipital lobe. The upper portion of the retina is represented superiorly and the lower portion inferiorly.

Note in the figure the large area that represents the macula. It is to this region that the retinal fovea transmits its signals. The fovea is responsible for the highest degree of visual acuity. Based on retinal area, the fovea has several hundred times as much representation in the primary visual cortex as do the most peripheral portions of the retina.

Secondary Visual Areas of the Cortex

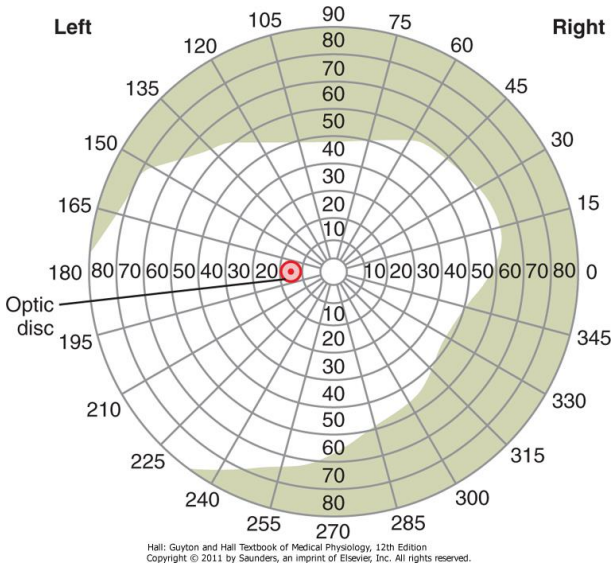
The secondary visual areas, also called visual a*ssociation areas, lie la*teral, anterior, superior, and inferior to the primary visual cortex. Most of these areas also fold outward over the lateral surfaces of the occipital and parietal cortex. Secondary signals are transmitted to these areas for analysis of visual meanings.



Fields of Vision; Perimetry

The field of vision is the visual area seen by an eye at a given instant. The area seen to the nasal side is called the nasal field of vision, and the area seen to the lateral side is called the temporal field of vision.

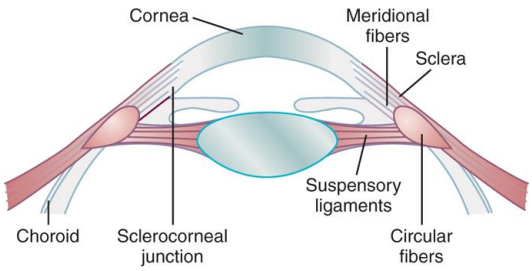
To diagnose blindness in specific portions of the retina, one charts the field of vision for each eye by a process called perimetry. This is done by having the subject look with one eye closed and the other eye looking toward a central spot directly in front of the eye. Then a small dot of light or a small object is moved back and forth in all areas of the field of vision, and the subject indicates when the spot of light or object can be seen and when it cannot. Thus, the field of vision for the left eye is plotted as shown in the Figure below. In all perimetry charts, a blind spot caused by lack of rods and cones in the retina over the optic disc is found about 15 degrees lateral to the central point of vision.

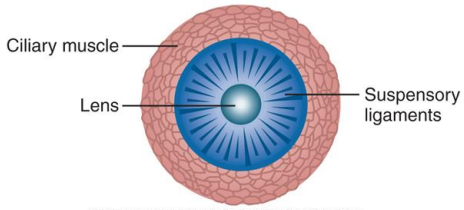


Mechanism of "Accommodation"

The shape of the lens is changed from that of a moderately convex lens to that of a very convex lens. The mechanism is as follows.

In a young person, the lens is composed of a strong elastic capsule filled with viscous, proteinaceous, but transparent fluid. When the lens is in a relaxed state with no tension on its capsule, it assumes an almost spherical shape, owing mainly to the elastic retraction of the lens capsule. However, as shown in Figure below about 70 su*spensory ligaments a*ttach radially around the lens, pulling the lens edges toward the outer circle of the eyeball. These ligaments are constantly tensed by their attachments at ciliary body. The tension on the ligaments causes the lens to remain relatively flat under normal conditions of the eye.





However, also located at the lateral attachments of the lens ligaments to the eyeball is the cil*iary muscle, wh*ich itself has two separate sets of smooth muscle fibers-mer*idional fibers an*d cir*cular fibers.* The circular fibers are arranged circularly all the way around the ligament attachments so

that when they contract, a sphincter-like action occurs, decreasing the diameter of the circle of ligament attachments; this also allows the ligaments to pull less on the lens capsule.
Thus, contraction of smooth muscle fibers in the ciliary muscle relaxes the ligaments to the lens capsule, and the lens assumes a more spherical shape, like that of a balloon, because of the natural elasticity of the lens capsule.

Accommodation Is Controlled by Parasympathetic Nerves
The ciliary muscle is controlled almost entirely by parasympathetic nerve signals transmitted to the eye through the third cranial nerve from the third nerve nucleus in the brain stem. Stimulation of the parasympathetic nerves contracts the ciliary muscle fibers, which relaxes the lens ligaments, thus allowing the lens to become thicker and increase its refractive power. With this increased refractive power, the eye focuses on objects nearer than when the eye has less refractive power. Consequently, as a distant object moves toward the eye, the number of parasympathetic impulses impinging on the ciliary muscle must be progressively increased for the eye to keep the object constantly in focus.

Control of Pupillary Diameter
Stimulation of the parasympathetic nerves also excites the pupillary sphincter muscle, thereby decreasing the pupillary aperture; this is called m*iosis.* Conversely, stimulation of the sympathetic nerves excites the radial fibers of the iris and causes pupillary dilation, called m*ydriasis.*

Pupillary Light Reflex
The major function of the iris is to increase the amount of light that enters the eye during darkness and to decrease the amount of light that enters the eye in daylight.
When light is shone into the eyes, the pupils constrict, a reaction called the pup*illary light reflex.* When light impinges on the retina, a few of the resulting impulses pass from the optic nerves to the pretectal nuclei. From here, secondary impulses pass to the *Edinger-Westphal nucleus an*d, finally, back through par*asympathetic nerves to* constrict the sphincter of the iris. Conversely, in darkness, the reflex becomes inhibited, which results in dilation of the pupil.
The function of the light reflex is to help the eye adapt extremely rapidly to changing light conditions. The limits of pupillary diameter are about 1.5 millimeters on the small side and 8 millimeters on the large side.