Chapter 14: Visual Processing: Eye and Retina

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(content provided by Chieyeko Tsuchitani, Ph.D.)

BACK NEXT

In this chapter you will learn about how the visual system initiates the processing of external stimuli. The chapter will familiarize you with measures of visual sensation by discussing the basis of form perception, visual acuity, visual field representation, binocular fusion, and depth perception. An important aspect is the regional differences in our visual perception: the central visual field is color-sensitive, has high acuity vision, operates at high levels of illumination whereas the periphery is more sensitive at low levels of illumination, is relatively color insensitive, and has poor visual acuity. You will learn that the image is first projected onto a flattened sheet of photoreceptor cells that lie on the inner surface of the eye (retina). The information gathered by millions of receptor cells is projected next onto millions of bipolar cells, which, in turn, send projects to retinal ganglion cells. These cells encode different aspects of the visual stimulus, and thus carry independent, parallel, streams of information about stimulus size, color, and movement to the visual thalamus.

14.1 Measures of Visual Sensation

The condition of the visual system can be determined by examining various aspects of visual sensation. For example, the ability to detect and identify small objects (i.e., visual acuity) can be affected by disorders in the transparent media of the eye and/or visual nervous system. The inability to detect objects in specific areas of space (i.e., visual field defects) is often related to neural damage.

Spatial Orientation and the Visual Field

The visual field is that area in space perceived when the eyes are in a fixed, static position looking straight ahead.

The **monocular visual field** (Figure 14.1)

- is that area of space visible to one eye
- can be mapped parametrically
  - Perimetry testing provides a detailed map of the visual field. The potential visual field is described as a hemisphere. However, it does not form a perfect hemisphere as the brow, nose and cheekbones obscure the view - most prominently in the nasal hemisphere
- is subdivided into two halves, the hemifields (Figure 14.1 Inset).
  - A horizontal line drawn from 0° to 180° through center of the field defines the superior & inferior hemifields.
  - A vertical line drawn from 90° to 270° through center point defines the left & right hemifields, which are often termed the nasal and temporal hemifields.
- may be further subdivided into quadrants:
  - the superior and inferior nasal quadrants
  - the superior and inferior temporal quadrants.
- contains a blind spot,
  - a small area in which objects cannot be viewed
  - which is located within the temporal hemifield.

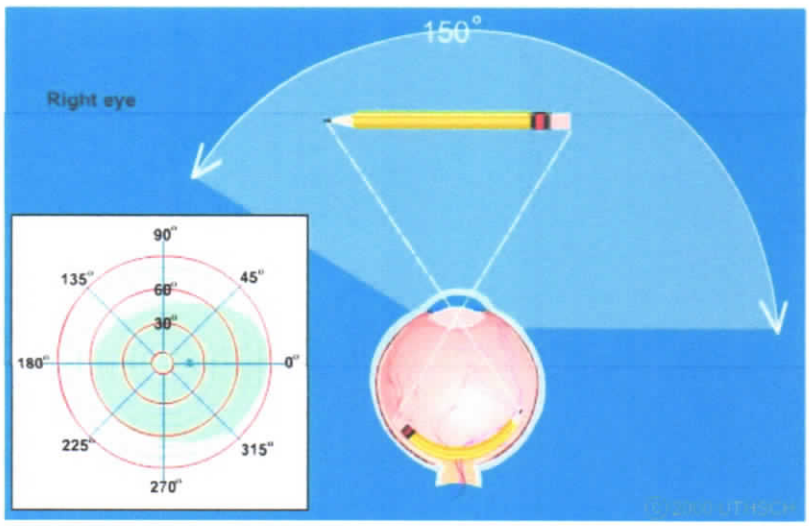


Figure 14.1
The monocular visual field is the area in space visible to one eye. As illustrated, the nose prevents the field of the right eye from covering 180 degrees in the horizontal plane. Inset. Perimetry testing provides a detailed map of the visual field. As the nose, brow and cheeks occlude the view of the most nasal, superior and inferior areas, respectively, the resulting monocular visual field occupies a limited portion (colored blue) of the potential visual space.

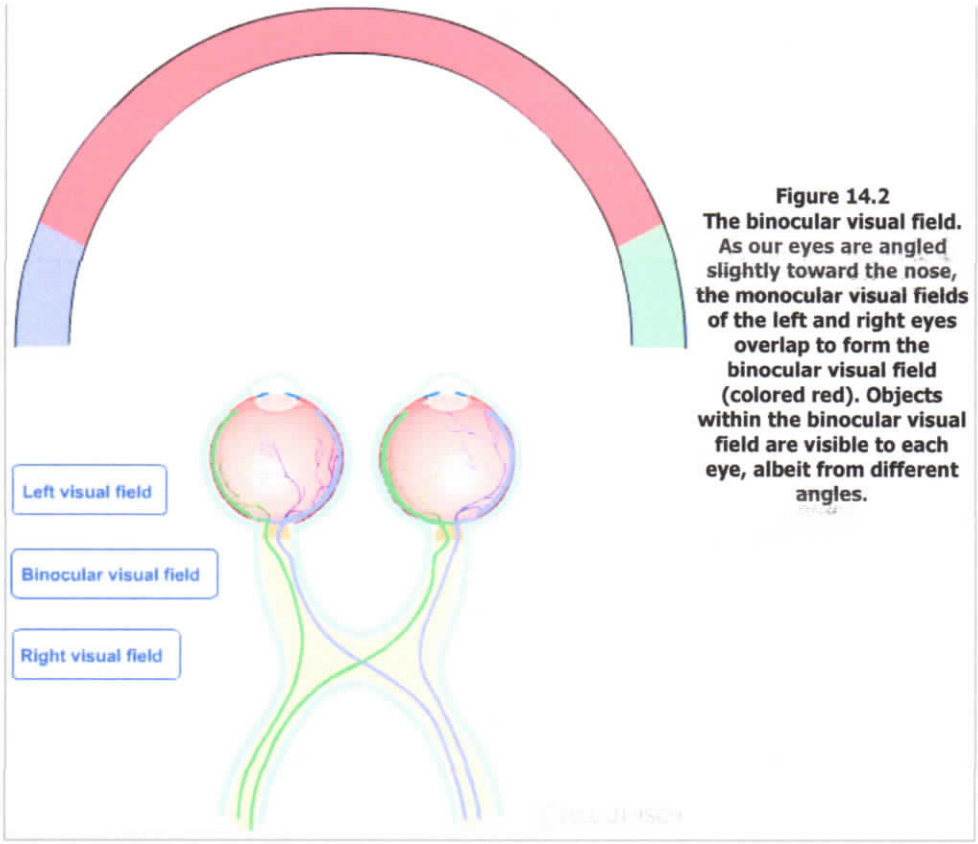


Figure 14.2
The binocular visual field. As our eyes are angled slightly toward the nose, the monocular visual fields of the left and right eyes overlap to form the binocular visual field (colored red). Objects within the binocular visual field are visible to each eye, albeit from different angles.

The monocular visual field (Figure 14.1) is determined with one eye covered. The area of overlap of the visual field of one eye with that of the opposite eye is called the binocular field (Figure 14.2). All areas of the binocular visual field are "seen" by both eyes.

The ability to locate objects in space and the ability to orient ourselves with respect to external objects are dependent upon the representation of visual space within the nervous system. The clinical examination of the visual fields most commonly used is the confrontation field test. It defines the outer limits of our subjective visual space. Neurological disorders of the visual system can often be localized based on the area of blindness within the visual field.

Visual Acuity

Visual acuity is the ability to detect and recognize small objects visually depends on the refractory (focusing) power of the eye's lens system and the cytoarchitecture of the retina.

Visual acuity is

- measured under high illumination
- the smallest size of a dark object in a light background that can be correctly identified

In the clinical setting, an eye chart

- is used to measure the patient's visual acuity.
- consists of rows of black letters on a bright white background.
- is used to measure visual acuity at a distance of 20 ft from the chart.
- reports visual acuity as the ratio of the eye chart distance (i.e., 20 ft) to the "normal distance" of the lowest row of letters correctly identified by the patient (e.g., row 3, which is 70 ft).

Color Vision

Color vision is the ability to detect differences in the wavelengths of light is called color vision. Clinically it may be tested with an Ishihara chart: a chart with spots of different colors that are spatially organized to form numbers that differ for ``normal" and color-blind eyes.

As mentioned above, the human has a trichromatic visual system, whereby visible colors can be created by a mixture of red, green and blue lights. The most common form of color blindness results in a confusion of red and green shades (i.e., red-green color blindness). Most cases of color blindness result from an absent or defective gene responsible for producing the red or green photopigment (protanopia, the lack of red; and deuteranopia, the lack of green). As these genes are located on the X chromosome, color blindness is more common in males than in females.

Regional differences: There are regional differences in color sensation, visual acuity and low-illumination sensitivity within the visual field (Figure 14.3).

A small "blindspot" is

- located in the temporal hemifield (Figure 14.3 Left)
- where objects cannot be seen.

Vision in the **visual field center**

- operates best under high illumination.
- has the greatest visual acuity and color sensitivity
- is ten times better than in the field periphery (Figure 14.3 Right)
- represents the operation of the photopic (light-adapted) subsystem

Vision in the **peripheral visual field**

- is more sensitive to dim light
- operates under low illumination.
- has little color sensitivity and poor spatial acuity (Figure 14.3 Right)
- represents the operation of the scotopic (dark-adapted) subsystem

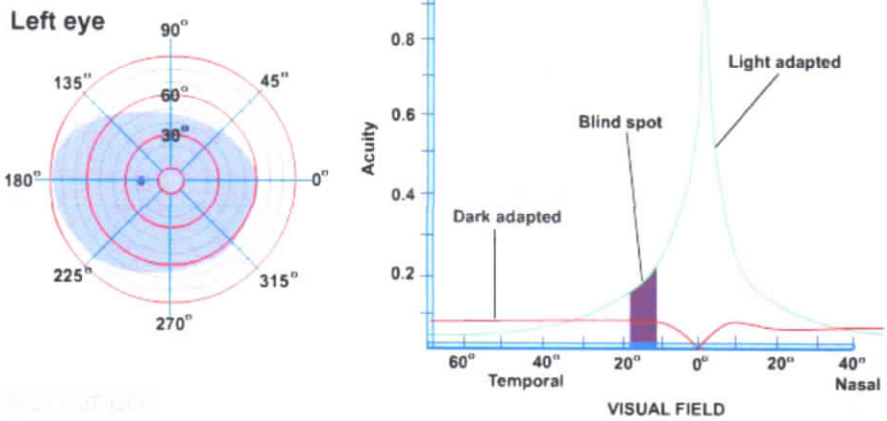


Figure 14.3
LEFT. The visual field of the left eye is mapped parametrically. The dark dot in the temporal hemifield represents the "blind spot" where nothing is seen. RIGHT. Visual acuity is plotted as a function of distance (in degrees) from the center of the visual field. The curve labeled "Light-adapted" was obtained under photopic illumination levels and the curve labeled "Dark-adapted" was obtained under scotopic illumination levels.

Binocular Fusion and Depth Perception

When a pencil is held an arm's length away with both eyes open, most individuals will see a single object and recognize it as a pencil. However, if one rapidly closes each eye alternately (i.e., left eye closed, right eye opened, then right eye opened and left eye closed); you should see the pencil "jumping" from left to right as you alternate the eye closure. This is so because the image in each eye is slightly different (disparate): Notice that because each eye is located on either side of the nose, the viewing angle of each eye is slightly different - especially when viewing near objects (Figure 14.4).

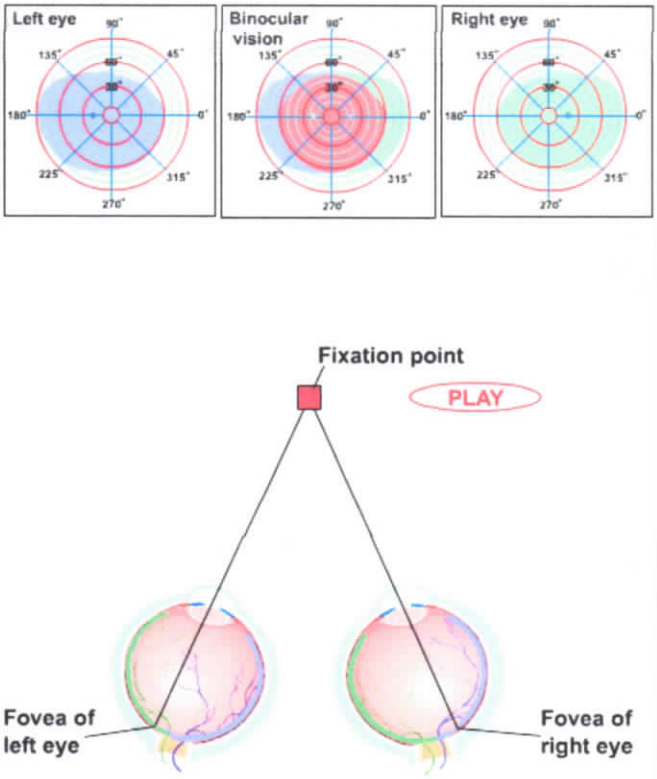


Figure 14.4
The two eyes fixated on an object view the object and objects in the background at slightly different angles. Consequently, the images on the two retinas are slightly different and must be "fused" by the visual system. The disparity in the retinal images at the two eyes also provides binocular cues for depth perception.

Although the area in space defined by the binocular visual field (Figure 14.4) represents corresponding areas of the monocular visual fields, the angle at which this space is viewed by each eye is slightly different. Consequently, the images of the corresponding (binocular) space are slightly different in each eye. The nervous system fuses these disparate binocular images to produce a single image (e.g., of the pencil located an arm's length away). The process of producing a single image from the two disparate monocular images is called **binocular fusion**.

Clinically, binocular fusion is tested by holding up one or two fingers in front of the patient and asking the patient (who should be wearing corrective lenses if they are normally worn) how many fingers they see. If the patient reports seeing four fingers when only two are presented, the patient is unable to produce binocular fusion.

Binocular fusion permits the perception a single clear image and also provides extra cues for **depth perception**. That is, the binocular disparity between the two images is used by the nervous system to allow the perception of a three-dimensional world where the approximate distance of an object can be determined. The nervous system cannot fuse disparate binocular images when the disparity is too great. When corresponding areas of the normal binocular visual field are not in alignment (e.g., in **strabismus** where one eye deviates from the normal position and/or is paralyzed), the nervous system cannot fuse the disparate images and gradually adapts by "ignoring" the image from the deviant eye. In fact, strabismus at birth, if uncorrected, may result in a form of central blindness, **amblyopia**, where the image from the deviant eye is no longer represented at cortical levels of the nervous system. The uncorrected, long-term amblyope is functionally blind in one eye and has poor depth perception.

14.2 The Image Forming Process

The transparent media of the eye function as a biconvex lens that refracts light entering the eye and focuses images of the external world onto the light sensitive retina.

Refraction

Recall that light rays will bend when passing from one transparent medium into another if the speed of light differs in the two media. However, parallel light rays will pass from air through a transparent body (e.g., flat lens) without bending if the light rays are perpendicular to the lens surface (Figure 14.5, left). If the light strikes the lens surface at an angle, the light rays will be bent in a line perpendicular to the lens surface (Figure 14.5, right).

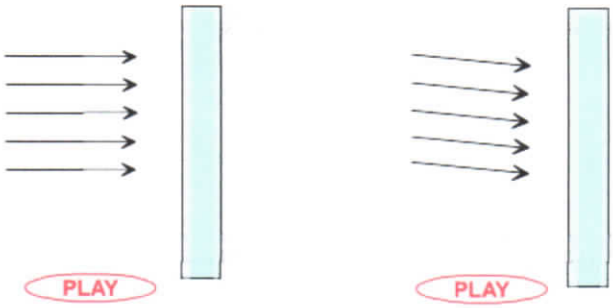


Figure 14.5
The course of light rays passing through a transparent lens are illustrated. LEFT: The light rays are entering perpendicular to the surface of the lens. RIGHT: The light rays are entering at an angle to the surface of the lens and are being refracted by the lens.

A biconvex lens, which is functionally similar to the eye's lens system, is flat only at its center. The surface of the area surrounding the center is curved and not perpendicular to parallel light rays (Figure 14.6). Consequently, the curved surfaces of a biconvex lens will bend parallel light rays to focus an image of the object emitting the light a short distance behind the lens at its focal point. The image formed is clear only if the curvature of the lens is symmetrical in all meridians and all divergent light rays emitted by a point source converge at the focal point.

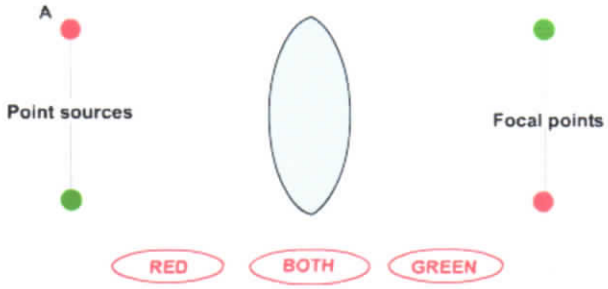


Figure 14.6
The light rays emanating from a point source take divergent paths that enter a biconvex lens at different points along the lens surface. The lens refracts the light rays bringing them together at the focal point some distance from the lens.

Note that the greater the curvature of the lens surface the greater is its refractive power and the closer is the focused image to the lens. Note also that the image formed is inverted and left-right reversed (Figure 14.7).

The image formed by eye's lens system is smaller than the object viewed, inverted (upside-down, Figure 14.6), and reversed (right-left, Figure 14.7). As the image is inverted by the lens system, the superior (top) half of each eye's visual field is projected onto the inferior (bottom) half of each eye's retina. Also, as the lens produces a reversed image, the temporal half of each visual field is projected onto the nasal half of each eye's retina[1]. Therefore, the temporal (left) hemifield of the left eye is projected onto the nasal (right) half of the left eye's retina and the nasal (left) hemifield of right eye is projected onto temporal (right) half of the right eye's retina. Consequently, the left hemifields of both eyes are projected onto the corresponding (right) halves of the two retinas. It is critical that you understand the relationship between the visual field and the retinal areas and realize that corresponding halves of the two monocular visual fields are imaged on corresponding halves of the two retinas. These relationships form the neurological basis for understanding visual field defects.

Figure 14.7
The eye's lens system functions like a biconvex lens and focuses an image on the retina that is inverted, left-right reversed and smaller than the object viewed.

Lens Accommodation

The eye must be able to change its refractive properties to focus images of both distant and nearby objects on the retina. Distant objects (greater than 30 feet or 9 meters away from the eye) emit or reflect light that can be focused on the retina in a normal relaxed eye (Figure 14.8).

PLAY

Figure 14.8
The normal eye at rest can focus on the retina images of objects more than 30 ft from the eye. When an object is brought closer to the eye (i.e., less than 30 ft from the eye), the light rays from the object take more divergent paths and each enters the cornea with a greater angle of incidence. Consequently, the

image focal point would be beyond the retina if the eye's lens system were not adjusted. During accommodation, the lens curvature increases, increasing the refractive power of the eye and focusing the image on the retina.

If a viewed object is brought closer to the eye, the light rays from the object diverge at a greater angle relative to the eye (Figure 14.8). Consequently, the nearer the object of view, the greater the angle of incidence of light rays on the cornea, and the greater the refractive power required to focus the light rays on the retina. The cornea has a fixed refractive power (i.e. it cannot change its shape). However, altering the tension of the zonules on the elastic lens capsule can alter the lens shape. The change in the refractive properties of the eye is called the accommodation or "near point" process.

In the normal eye under resting (distant vision) conditions, the ciliary muscles are relaxed and the zonules are under tension (Figure 14.9). In this case, the lens is flattened, which reduces the refractive power of the lens to focus on distant objects. When an object is closer to the eye (i.e., less than 30 ft. away), accommodation occurs to affect "near vision". The ciliary muscle contracts, pulling the ciliary processes toward the lens (remember the muscle acts as a sphincter). This action releases tension on the zonules and the lens capsule. The reduced tension allows the lens to become more spherical (i.e., increase its curvature). The increase in lens curvature increases the lens refractive power to focus on near objects. Consequently, as an object is moved closer to the viewer, his eyes accommodate to increase the lens curvature, which increases the refractive power of his eye (Figure 14.8).

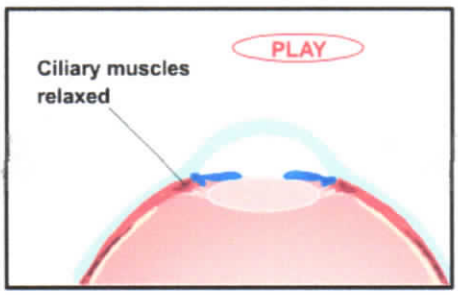


Figure 14.9
During distance vision (i.e., with the eye at rest), the ciliary muscles are relaxed and the zonules are under tension. The lens is flattened by the tension on the zonules and the lens capsule. However, in the accommodation process, the ciliary muscles contract and, acting like a sphincter muscle, decrease the tension on the zonules and lens capsule. The lens becomes more spherical with its anterior surface shifting more anteriorly into the anterior chamber.

Refractive Errors of the Eye and Corrective Lenses

Presbyopia: In presbyopia, there is normal distance vision, but lens accommodation is reduced with age. With age, the lens loses its elasticity and becomes a relatively solid mass. During accommodation, the lens is unable to assume a more spherical shape and is unable to increase its refractive power for near vision (Figure 14.10). As a result, when an object is less than 30 ft. away from the presbyopic viewer, the image is focused somewhere behind the retina.

Figure 14.10
In the presbyopic eye, when the object is moved closer to the eye, the lens is unable to accommodate and the image is focused beyond the retina. For the presbyopic eye a corrective lens that converges the light rays (i.e., a convex lens that reduces the angle of incidence of light on the cornea) will allow the presbyopic eye to view nearby objects.

A convex lens (i.e., increased refractive power) is used to correct the presbyopic eye (Figure 14.10). These lenses refract the light rays so they strike the surface of the cornea at a smaller angle. However, because the corrective lens increases the refractive power, the presbyope with convex lenses will have problems with distance vision. Consequently, the corrective lenses are often half lenses (i.e., reading glasses) which allow the presbyope to view objects in the distance unimpeded by the convex lens.

Hyperopia: In hyperopia (Figure 14.11), the refractive power of the eye's lens system is too weak or the eyeball too short. When viewing distant objects, the image is focused at a point beyond the retina.

Figure 14.11
The hyperopic eye at rest cannot focus on *the retina the image* of an object more than 30 ft from the eye. The hyperopic lens system is too weak and the image is focused beyond the retina.

The young hyperope can compensate by using lens accommodation, i.e., increase the refractive power of the eye's lens system (Figure 14.12). We call the hyperope "far-sighted" (hypermetropic) because the power of accommodation used for distance vision

cannot be used for near vision.

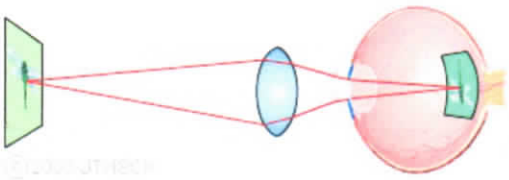


Figure 14.12
If the hyperopia is not severe; the hyperopic eye can use the lens accommodation process to increase the refractive power of the eye for distance vision.

As the hyperope ages and becomes presbyopic, the power of accommodation is diminished. Consequently, the middle aged hyperope may have a limited range (near and far) of vision. To correct this effect of aging, the refractive power of the eye is increased with convex lenses (Figure 14.12).

Myopia: In myopia (Figure 14.13), the refractive power of the eye's lens system is too strong or the eyeball too long. When viewing distant objects, the image is focused at a point in front of retina.

Figure 14.13
The myopic eye at rest cannot focus on the retina the image of an object more than 30 ft. from the eye. The refractive power of the eye's lens system is too strong and the image is focused in front of the retina.

The uncorrected myopic eye is "near-sighted" because it can focus unaided on near objects. That is, the young myope will see distant objects as blurred, poorly defined images but can see nearby small objects clearly (remember nearby objects emit divergent light rays).

For distance vision, the refractive power of the myopic eye lens system is corrected with concave lenses that diverge the light rays entering the eye (Figure 14.14). Note that as the power of accommodation diminishes with age, near vision is also affected in the presbyopic-myopic eye. The mature myope may require bifocals, the upper half of the lens diverging light rays for distance vision and the lower half with no or low converging power for near vision.

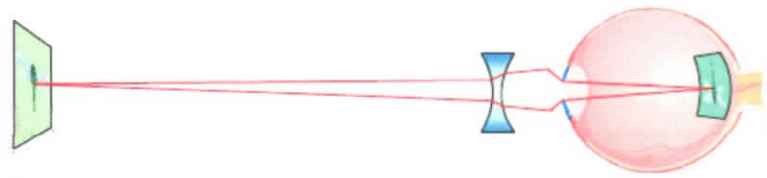


Figure 14.14
A corrective lens that diverges light rays before they enter the eye (i.e., a concave lens) will allow the myopic eye to focus the image of a distant object on the retina.

Astigmatism: An astigmatism results when the cornea surface does not resemble the surface of a sphere (e.g. is more oblong). In an eye with astigmatism, the image of distant and near objects cannot be focused on the retina (Figure 14.15). Astigmatism is corrected with a cylindrical lens having a curvature that corrects for the corneal astigmatism. The cylindrical lens directs light waves through the astigmatic cornea to focus a single, clear image on the retina.

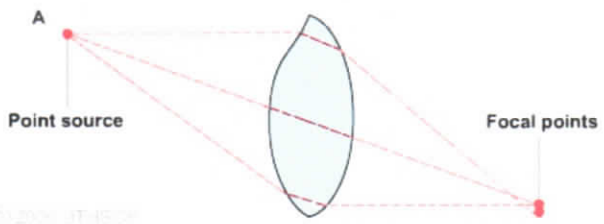


Figure 14.15
The astigmatic lens is asymmetrical and has multiple focal points, which produces multiple images of a point source.

14.3 The Retina

You will now learn about the retinal neurons and the laminar structure of the retina, and the ways in which the light-sensitive receptors of the eye convert the image projected onto the retina into neural responses. The light sensitive retina forms the innermost layer of the eye (Figure 14.16).

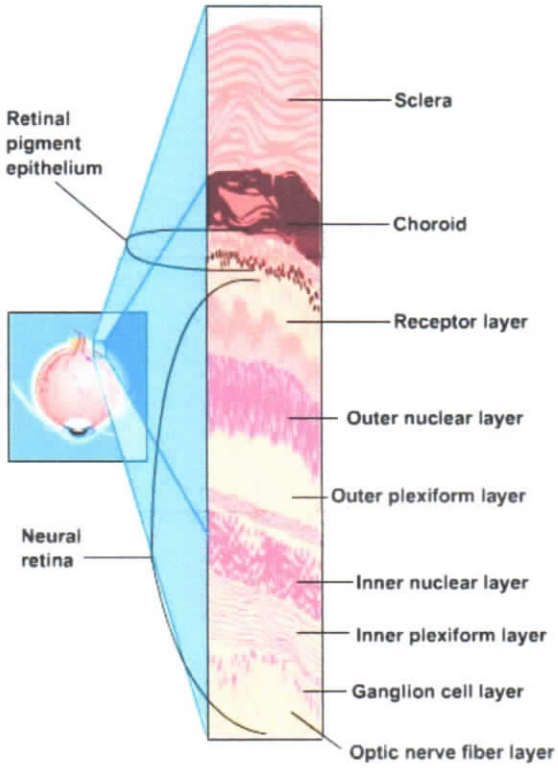


Figure 14.16
The eye, the three coats of the eye and the layers of the retina. The retina is the innermost coat of the eye and consists of the retinal pigment epithelium and neural retina.

The retina covers the choroid and extends anteriorly to just behind the ciliary body. The retina consists of neurons and supporting cells.

Components of the Retina

The **retina** is derived from the neural tube and is, therefore, part of central nervous system. It consists of two parts, the retinal pigment epithelium, which separates the middle, choroid coat of the eyeball from the other innermost component and the neural retina (Figure 14.16) – the dark pigments within the retinal pigment epithelium and choroid coat function to absorb light passing through the receptor layer, thus reducing light scatter and image distortion within the eye. The neural retina contains five types of neurons (Figure 14.17): the visual receptor cells (the rods and cones), the horizontal cells, the bipolar cells, the amacrine cells, and the retinal ganglion cells.

Retinal Layers

The **retina** is a laminated structure consisting of alternating layers of cell bodies and cell processes (Figure 14.18).

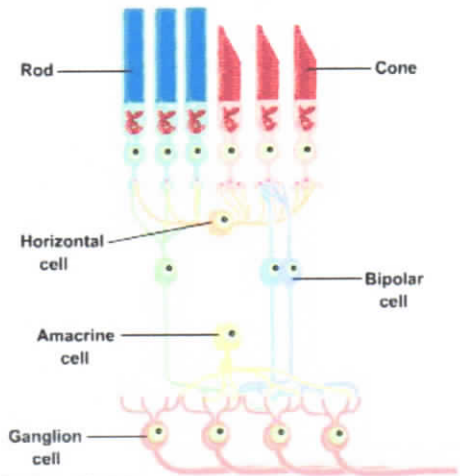


Figure 14.17
The components of the neural retina. The neural retina consists of at least five different types of neurons: the photoreceptors (rods and cones), horizontal cell, bipolar cell, amacrine cell and ganglion cell.

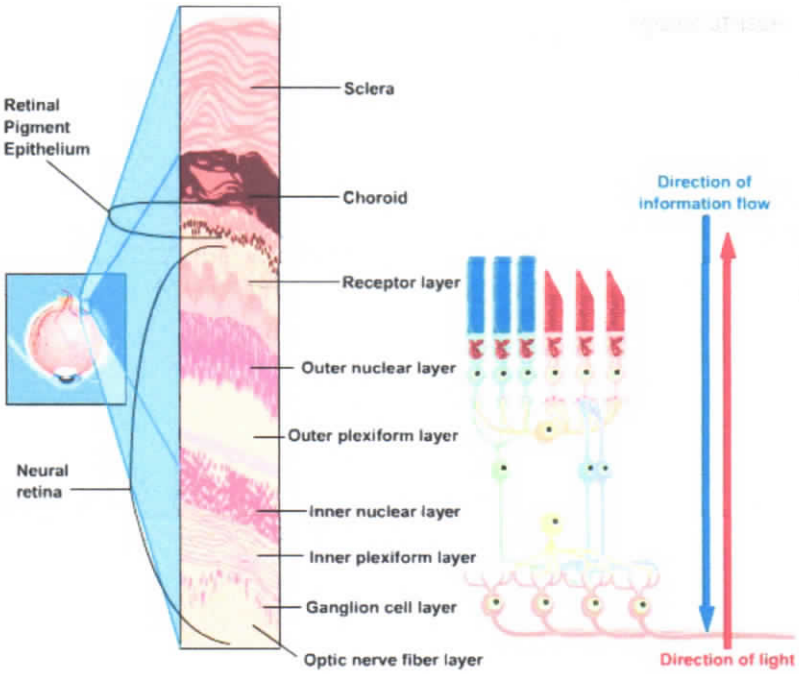


Figure 14.18
The neural retina is formed by alternating layers of neuron cell bodies that appear dark and neuron processes that appear light in Nissl stained tissue. The receptor cells synapse with bipolar and horizontal cells in the outer plexiform layer. The bipolar cells, in turn, synapse with amacrine and ganglion cells in the inner plexiform layer The axons of the retinal ganglion cells exit the eye to form the optic nerve.

The innermost layers are located nearest the vitreous chamber, whereas the outermost layers are located adjacent to the retinal pigment epithelium and choroid. The most important layers, progressing from the outer to inner layers, are:

- the **retinal pigment epithelium**, which provides critical metabolic and supportive functions to the photoreceptors;
- the **receptor layer**, which contains the light sensitive outer segments of the photoreceptors;
- the **outer nuclear layer**, which contains the photoreceptor cell bodies;
- the **outer plexiform layer**, where the photoreceptor, horizontal and bipolar cells synapse;
- the **inner nuclear layer**, which contains the horizontal, bipolar and amacrine cell bodies;
- the **inner plexiform layer**, where the bipolar, amacrine and retinal ganglion cells synapse;
- the **retinal ganglion cell layer**, which contains the retinal ganglion cell bodies; and
- the **optic nerve layer**, which contains the ganglion cell axons traveling to the optic disc.

Notice that light passing through the cornea, lens and vitreous must pass through most of the retinal layers before reaching the light-sensitive portion of the photoreceptor; the outer segment in the receptor layer. Notice also that in the region of the fovea where the image of the central visual field center is focused, the retina consists of fewer layers (Figure 14.19): thereby minimizing the obstacles to forming a clear image on the fovea. The area around the fovea, the surrounding macula, is thicker because it contains the cell bodies and processes of retinal neurons receiving information from the receptors in the fovea.

The optic disc is formed by the retinal ganglion cell axons that are exiting the retina. It is located nasal to the fovea (Figure 14.19). This region of the retina is devoid of receptor cells and composed predominantly by the optic nerve layer. Consequently, it is the structural basis for the 'blind spot" in the visual field.

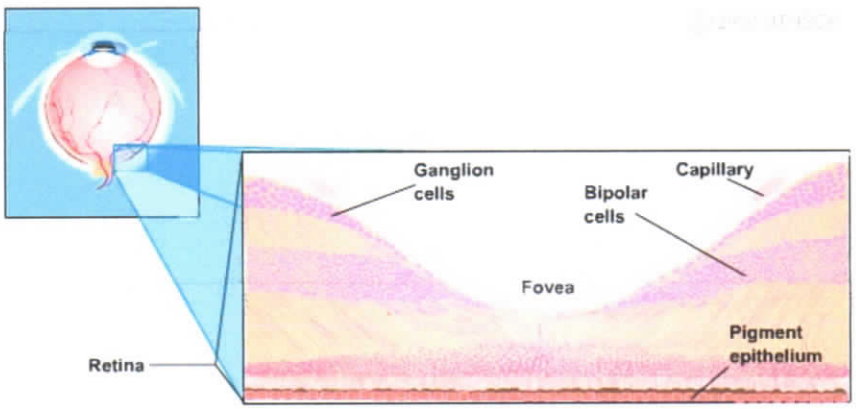


Figure 14.19
The fovea of the retina and the layers of the retina in the surrounding macula. The fovea and macula are colored as they appear when stained for Nissl substance, which is most abundant in the neuron cell body.

The Photoreceptors

The human has two types of **photoreceptors**: the **rods** and **cones** (Figure 14.20). They are distinguished structurally by the shapes of their outer segments. The photopigments of the rods and cones also differ. The rod outer segment disks contain the photopigment rhodopsin, which absorbs a wide bandwidth of light. The cones differ in the color of light their photopigments absorbs: one type of photopigment absorbs red light, another green light, and a third blue light. As each cone receptor contains only one of the three types of cone photopigment, there are three types of cones; red, green or blue. Each cone responds best to a specific color of light, whereas the rods respond best to white light[2]. The rod and cone photopigments also differ in illumination sensitivity; rhodopsin breaks down at lower light levels than that required to breakdown cone photopigments. Consequently, the rods are more sensitive - at least at low levels of illumination.

14.4 Rods and Cones Form the Basis for Scotopic and Photopic Vision

The human visual system has two subsystems that operate at different light energy levels. The *scotopic, dark-adapted system*

operates at low levels of illumination, whereas the *photopic, light-adapted system* operates at high levels of illumination.

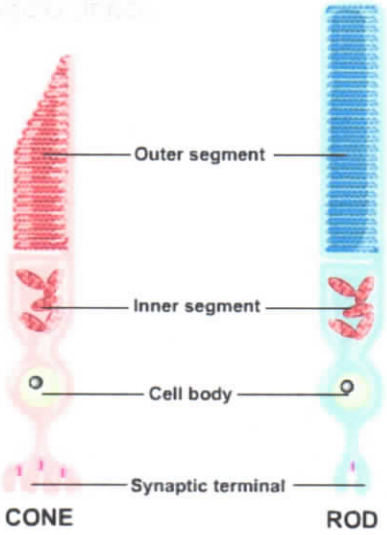


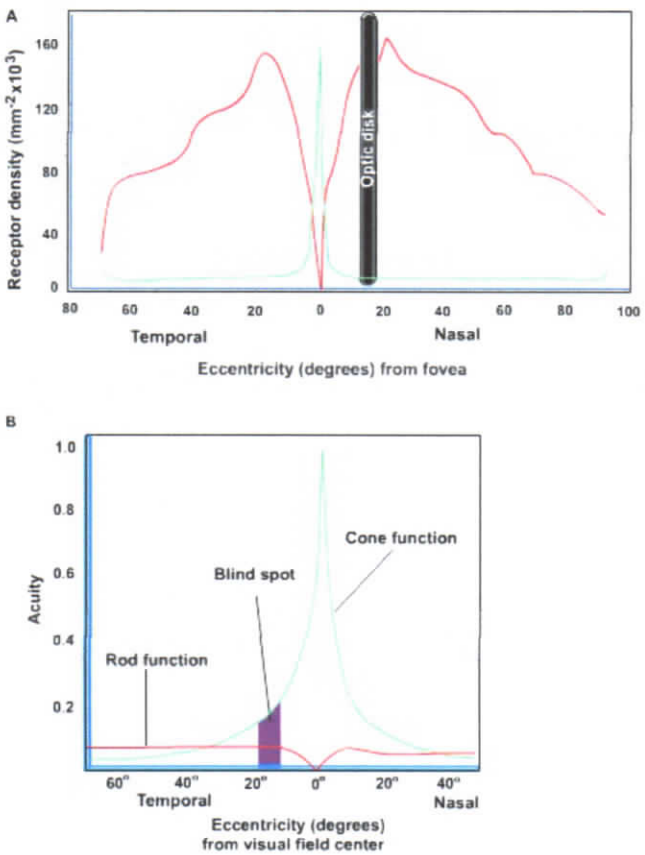
Figure 14.20
The cone and rod photoreceptors. The photoreceptors are neurons that have a dendritic component (the outer segment) and an axonal component that forms synaptic terminals.

Rods are responsible for the initiation of the scotopic visual process. Rods

- contain the photopigment *rhodopsin*, which breaks down when exposed to a wide bandwidth of light (i.e., it is achromatic).
  - Rhodopsin is also more sensitive to light and reacts at lower light levels than the color sensitive (chromatic) cone pigments.
- have longer outer segments, more outer segment disks and, consequently, contain more photopigment.
- are more sensitive to light and function at scotopic (low) levels of illumination.
- dominate in the peripheral retina (Figure 14.21A), which is color insensitive, has poor acuity (Figure 14.21B), but is sensitive to low levels of illumination.

Cones are responsible for the initiation of the photopic visual process. Cones

- contain photopigments that breakdown in the presence of a limited bandwidth of light (i.e., cone photopigments are chromatic).
- are color sensitive.
- are less sensitive to light and require high (daylight) illumination levels.
- are concentrated in the fovea (Figure 14.21A)
- in the fovea have image of the central visual field projected on them.
- in the fovea are responsible for photopic, light-adapted vision (i.e., high visual acuity and color vision) in the central visual field (Figure 14.21B)



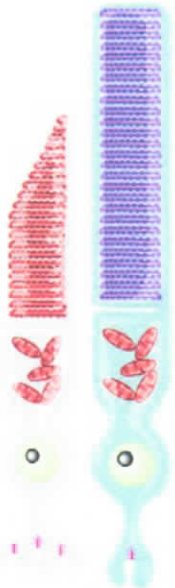


Figure 14.21
The rods, are taller, have longer outer segments and, consequently, contain more outer segment disks and more photopigment than cones. Cone receptors are concentrated in the fovea of the eye (at 0° eccentricity), whereas rod receptors are concentrated in more peripheral retina (A). Visual acuity is maximal in the central area of the visual field (at 0° eccentricity), whereas it is minimal in more peripheral areas (B). Notice that the location of the optic disc relative to the fovea corresponds to the location of the blind spot relative to the visual field center.

Biochemical processes in the photoreceptors participate in dark and light adaptation. Notice when you enter a darkened room after spending time in daylight, it takes many minutes before you are able to see objects in the dim light. This slow increase in light

sensitivity is called the dark-adaptation process and is related to the rate of regeneration of photopigments and to the intracellular concentration of calcium[3]. A contrasting, but faster, process occurs in high levels of illumination. When you are fully dark-adapted, exposure to bright light is at first blinding (massive photopigment breakdown and stimulation of photoreceptors) and is followed rapidly by a return of sight. This phenomenon, light adaptation, allows the cone response to dominate over rod responses at high illumination.

14.5 Visual Processing in the Retina

The photoreceptors exhibit a fairly high basal release of glutamate. When light strikes the photoreceptor cell, it initiates a biochemical process in the cell that *reduces* the release of glutamate from its axon terminal. The **glutamate**, in turn, affects the activity of the bipolar and horizontal cells, which synapse with the photoreceptor. The bipolar cells, in turn, synapse with amacrine and retinal ganglion cells. It is the axons of the retinal ganglion cells that exit the eye as the optic nerve and terminate in the brain. Notice that the direct pathway for the transmission of visual information from the eye to the brain includes only the receptor cell, bipolar cell and ganglion cell. The horizontal cells modulate the synaptic activity of receptor cells and, thereby, indirectly affect the transmission of visual information by bipolar cells. Similarly the amacrine cells modulate the synaptic activity of the retinal bipolar and ganglion cells, thereby affecting the transmission of visual information by the ganglion cells.

Bipolar Cells

Within the outer plexiform layer of the retina, approximately 125 million photoreceptor cells synapse with approximately 10 million **bipolar cells**. A smaller number of horizontal cells also synapse with the photoreceptor cells within the outer plexiform layer of the retina. The bipolar and horizontal cells respond to the glutamate released by the photoreceptor cells[4].

- Bipolar cells
  - do not generate action potentials.
  - respond to the release of glutamate from photoreceptors with graded potentials (i.e., by hyperpolarizing or depolarizing).

Bipolar cells differ based on their responses to photoreceptor stimulation.

- There are at least two types of bipolar cells based on their responses to glutamate.
  - The *off* bipolar cells are depolarized by glutamate.
  - The *on* bipolar cells are *hyperpolarized* by glutamate.
- The two bipolar cell types have different functional properties.
  - The *off* bipolar cells function to detect dark objects in a lighter background.
  - The *on* bipolar cells function to detect light objects in a darker background.

The stimulus condition that produces a depolarizing response from a bipolar cell is used to name the bipolar cell type.

- An *off* bipolar cell depolarizes when the photoreceptors that synapse with it are in the dark (i.e., when the light is off, Figure 14.22).
- An *on* bipolar cell depolarizes when the photoreceptors that synapse with are in the light (i.e., when the light is on, Figure 14.22). Note that the depolarization of the *on* bipolar cell does not result from excitation of the presynaptic cell but rather from a reduction of the inhibitory action of glutamate produced by the light-induced decreased release of glutamate from the photoreceptor.

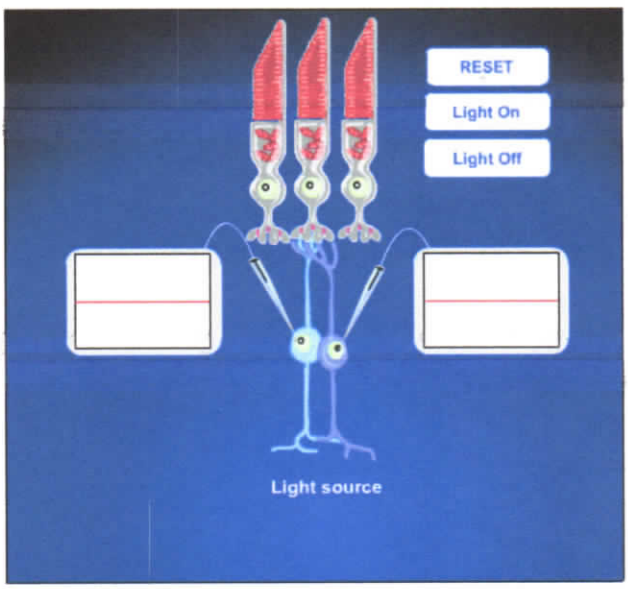


Figure 14.22
When the receptor cells with which an off bipolar cell synapses are in the dark, the off bipolar cell is depolarized and the on bipolar cell is hyperpolarized. In contrast, when the receptor cells with which an off bipolar cell synapses are in the light, the off bipolar cell is hyperpolarized and the on bipolar cell is depolarized.

Bipolar Cell Receptive Field: The receptive field of a bipolar cell is defined anatomically by the location and distribution of receptor cells with which it makes synaptic contact.

- Each **cone-bipolar cell** makes direct synaptic contact with a circumscribed patch of cone receptors, which may be as few as one foveal cone. Consequently, the receptive fields of bipolar cells synapsing with cones in the fovea are extremely small and are color sensitive. The cone-bipolars may be hyperpolarized or depolarized by glutamate and, consequently, may be on-type or off-type bipolar cells.
- Each **rod-bipolar cell** may make synaptic contact with a few to fifty or more of rod receptor cells. Consequently, the rod-bipolar cell receptive field is relatively large and color insensitive. All rod-bipolar cells are hyperpolarized by glutamate and, consequently, are on-type bipolar cells exclusively.

The bipolar cell receptive field is also defined *physiologically* as the retinal area which when exposed to light produces a response (i.e., depolarization or hyperpolarization) in the bipolar cell.

Bipolar cells have concentric receptive fields. Light directed on the photoreceptor(s) that synapse with a bipolar cell produces a response from the bipolar cell called the *center* response (Figure 14.23). In contrast, light directed on immediately surrounding receptors produce the opposite response (Figure 14.24).

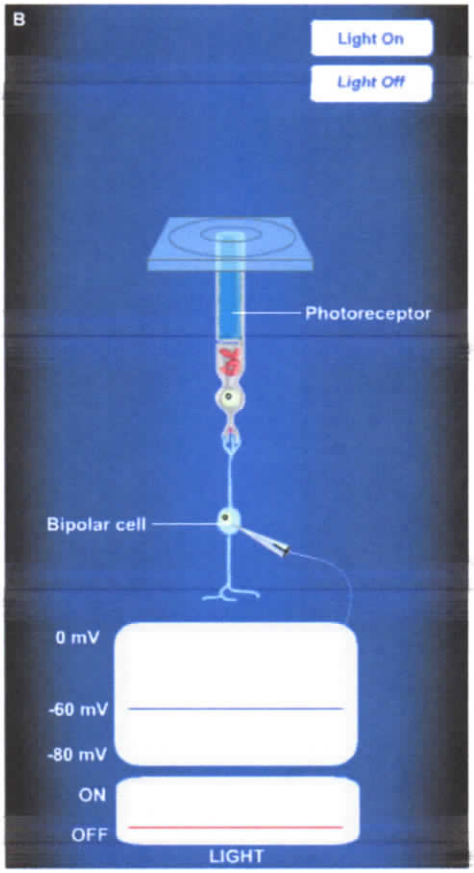


Figure 14.23
Bipolar cells have concentric receptive fields. The on bipolar cell depolarizes when the receptor cells with which it synapses are illuminated ("Light On"). These center receptors (i.e., the ones making direct synaptic contact with the bipolar cell) produce the bipolar cell center response.

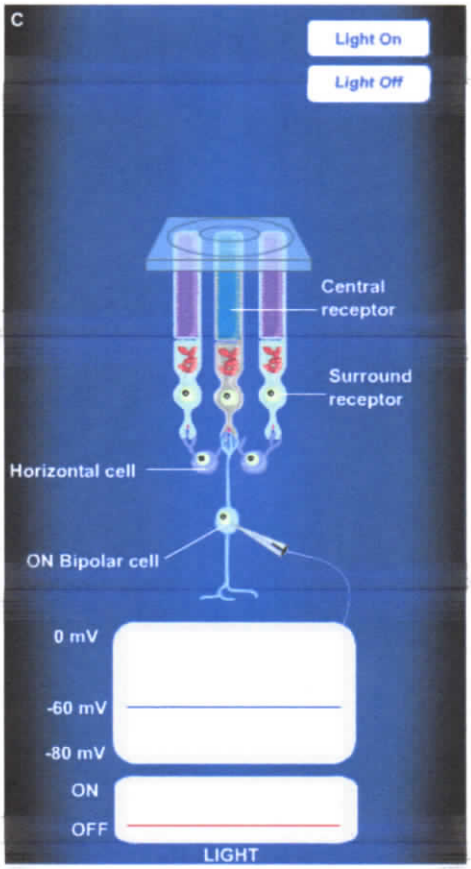
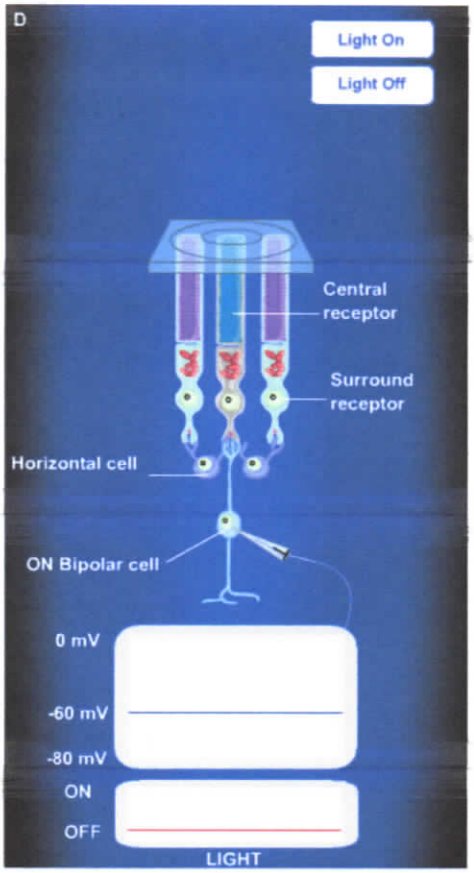


Figure 14.24
Bipolar cells have concentric receptive fields. When the receptors surrounding the center receptors of the on bipolar receptive field are illuminated ("Light On") and the center receptors kept in the dark, the on bipolar cell is hyperpolarized.

When both the center and surrounding receptor cells are illuminated with light, the *on* bipolar cell response to stimulation of the center receptors is reduced by stimulation of the surround receptors (Figure 14.25).

Figure 14.25

Bipolar cells have concentric receptive fields. When both the center and surrounding receptors of the on bipolar cell receptive field are illuminated, the on bipolar cell depolarizes. However, the magnitude of the depolarization is reduced to less than the depolarization to illumination of only the center receptors.



Consequently, the strongest *on* bipolar cell response is produced when the stimulus is a light spot encircled by a dark ring. For the *off* bipolar cell, a dark spot encircled by a light ring produces maximal depolarization.

Horizontal Cells

Within the outer plexiform layer, the photoreceptor cells make both presynaptic and postsynaptic contact with **horizontal cells**.

- The horizontal cells have large receptive fields involving
  - presynaptic (axonal) contact with a small group of photoreceptors and
  - postsynaptic (dendritic) contact with a larger group of surrounding photoreceptor cells.

By controlling the responses of their "center" photoreceptors (based on the responses of the surrounding photoreceptors), the horizontal cells indirectly produce the bipolar cell receptive field *surround* effect. The surround effect produced by the horizontal cell is weaker than the center effect.

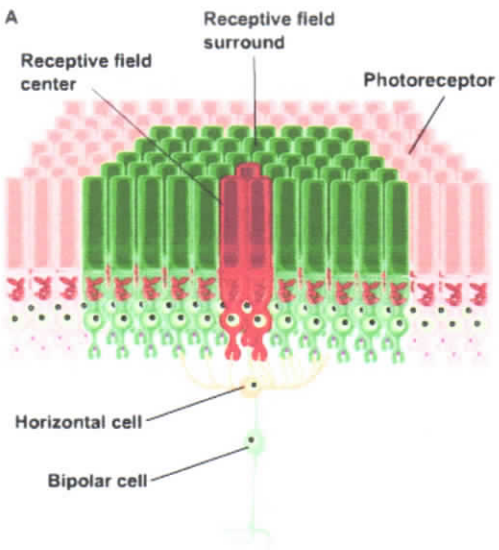


Figure 14.26
The horizontal cells make presynaptic and postsynaptic contact with photoreceptor cells. The axon terminals of a horizontal cell receives synaptic contact from one group of photoreceptors (colored red) and its processes make synaptic contact with surrounding photoreceptor cells (colored green).

The surround effect, produced by the horizontal cells, enhances brightness contrasts to produce sharper images, to make an object appear brighter or darker depending on the background and to maintain these contrasts under different illumination levels.

Retinal Ganglion Cells

Within the inner plexiform layer, the axon terminals of bipolar cells (the 2° visual afferents) synapse on the dendritic processes of **amacrine cells** and **ganglion cells**. As in most neurons, depolarization results in neurotransmitter release by the bipolar cell at its axon terminals. Most *bipolar cells release glutamate*, which is excitatory to most ganglion cells (i.e., depolarizes ganglion cells). The amacrine cells may synapse with bipolar cells, other amacrine cells or ganglion cells. It is the axons of the retinal ganglion cells (the 3° visual afferents) that exit the eye to form the optic nerve and deliver visual information to the lateral geniculate nucleus of the thalamus and to other diencephalic and midbrain structures.

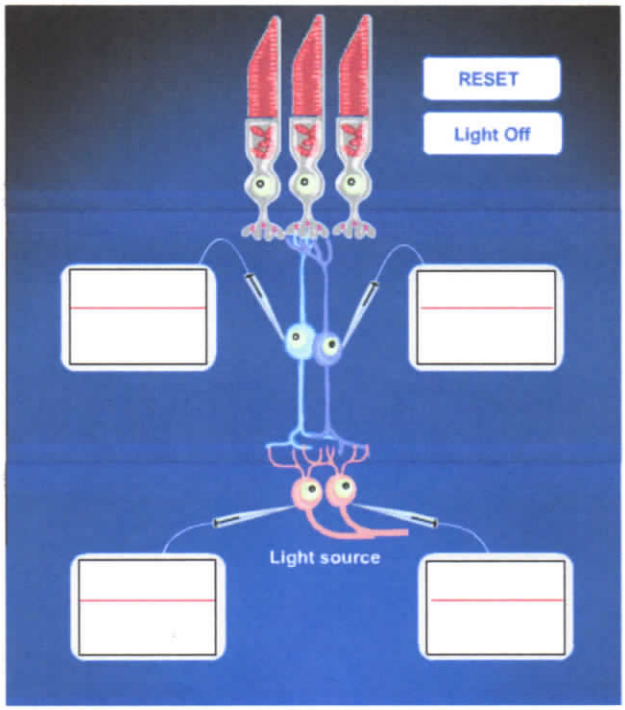


Figure 14.27
An off ganglion cell synapses with an off bipolar cell and produces action potentials (i.e., is excited) when the off bipolar cell is depolarized (i.e., when the light is off). In contrast, an on ganglion cell that synapses with an on bipolar cell reduces the rate at which it produces action potentials (i.e., is inhibited) when the on bipolar cell is hyperpolarized (when the light is off).

Ganglion Cell Response Properties. The retinal ganglion cells are the final retinal elements in the direct pathway from the eye to the brain. Because they must carry visual information some distance from the eye, *they posses voltage-gated sodium channels in their axonal membranes and generate action potentials* when they are depolarized by the glutamate released by the bipolar cells.

The *off* bipolar cell (Figure 14.27, Right) will depolarize when it is dark on its center cones and will therefore release glutamate when it is dark on the center of its receptive field. This will result in the depolarization of the retinal ganglion cells with which the off bipolar synapses and in the production of action potentials (i.e., discharges) by these ganglion cells (Figure 14.27, Right). Consequently, the retinal ganglion cells that synapse with *off* bipolar cells will have *off-center/on-surround* receptive fields and are called *off* ganglion cells.

The *on* bipolar cell (Figure 14.28, Left) will depolarize when there is light on its center cones and will therefore release glutamate when it is light on the center of its receptive field. This will result in the depolarization of the retinal ganglion cells with which the on bipolar synapses and in the production of action potentials (i.e., discharges) by these ganglion cells (Figure 14.28, Left). Consequently, the retinal ganglion cells that synapse with on bipolar cells will have *on-center/off-surround* receptive fields and are called *on* ganglion cells.

In short, the receptive fields of the bipolar cells with which the retinal ganglion cell synapses determine the receptive field configuration of a retinal ganglion cell.

The retinal ganglion cells provide information important for detecting the shape and movement of objects.

In the primate eye, there are two major types of retinal ganglion cells, Type M and Type P cells, that process information about different stimulus properties.

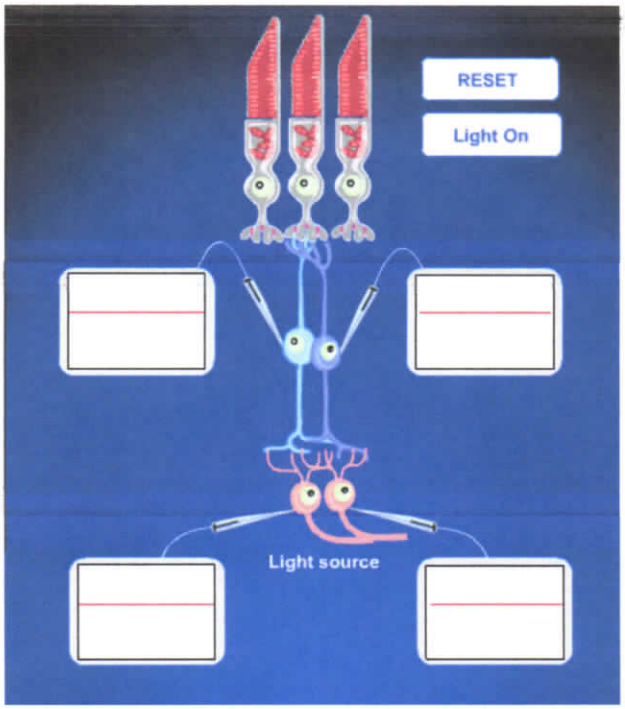


Figure 14.28
Left: The on ganglion cell synapses with an on bipolar cell and produces action potentials (i.e., is excited) when the on bipolar cell is depolarized (i.e., when the light is on). Right: In contrast, an off ganglion cell that synapses with an off bipolar cell reduces the rate at which it produces action potentials (i.e., is inhibited) when the off bipolar cell is hyperpolarized (when the light is on).

Type P retinal ganglion cells are color-sensitive object detectors.

The P ganglion cell(s)

- outnumber the M-ganglion cells, by approximately 100 to 1 in the primate retina
- makes synaptic contact with one to a few cone bipolars that are innervated by cone receptors in the macula fovea
- *is color sensitive*
- *has a small concentric receptive field*
- produces a sustained, *slowly adapting response* that lasts as long as a stimulus is centered on its receptive field.
- produces weak responses to stimuli that move across its receptive field.

The slowly adapting response of the Type P retinal ganglion cell is best suited for signaling the presence, color and duration of a visual stimulus and is poor for signaling stimulus movement.

Type M retinal ganglion cells are color-insensitive motion detectors.

The M ganglion cell

- is much larger than P ganglion cells
- synapses with many bipolar cells
- *is color insensitive*
- *has a large concentric receptive field*
- *is more sensitive to small center-surround brightness differences*
- responds with a transient, *rapidly adapting response* to a maintained stimulus.
- responds maximally, with high discharge rates, to stimuli moving across its receptive field.

The rapidly adapting responses of Type M ganglion cells are best suited for signaling temporal variations in, and the movement of, a stimulus.

The axons of the M and P retinal ganglion cells travel in the retina optic nerve fiber layer to the optic disc where they exit the eye. Most of the axons travel to and terminate in the lateral geniculate nucleus of the thalamus.

Amacrine Cells

Amacrine cells synapse with bipolar cells and ganglion cells and are similar to horizontal cells in providing lateral connections between similar types of neurons (e.g., they may connect bipolar cells to other bipolar cells)[5]. They differ from horizontal cells, however, in also providing "vertical" links between bipolar and ganglion cells.

Amacrine cell types. There are 20 or more types of amacrine cells based on their morphology and neurochemistry. The roles of three types have been identified. One type

- is responsible for producing the movement sensitive (rapidly adapting) response of the Type M ganglion cells.
- enhances the center-surround effect in ganglion cell receptive fields.
- connects rod bipolar cells to cone bipolar cells, thus allowing ganglion cells to respond to the entire range of light levels, from

scotopic to photopic.

Convergence of Inputs and Visual Acuity

Low convergence of cones to cone bipolar cells and low convergence of cone bipolar cells to P-retinal ganglion cells produce high visual acuity in the central visual field.

Recall that

- visual acuity and color vision are greatest in the central visual field.
- the image of the central visual field is projected onto the fovea.
- the cones are concentrated in the fovea, whereas the rods predominate in the peripheral retina.
- there is low convergence of foveal cones onto macular bipolar cells, as low as one cone receptor to one bipolar cell.

In addition, the cones in the fovea are of smaller diameter than those in the periphery of the retina, which allows for a greater packing density of foveal cones. The high packing density of cones and the low convergence of cones onto bipolar cells in the macula support higher visual acuity in the central visual field. Consequently, the foveal cones, macular bipolar cells and the P-retinal ganglion cells are responsible for photopic, light-adapted vision in the central visual field. In contrast, the higher convergence of the rods onto peripherally located bipolar cells and of peripheral bipolar cells onto amacrine cells forms the basis for the poor visual acuity but high light sensitivity of scotopic vision.

14.5 Clinical Manifestations of Retinal Dysfunction

The chemical and physical integrity of the retina is essential for normal visual function. Abnormalities in the blood supply and retinal pigment epithelium result in retinal dysfunctions.

Vitamin A deficiency can cause permanent blindness. An adequate supply of photopigments is necessary to sustain photoreceptors. The supply of all-*trans* retinal as a photopigment breakdown product is insufficient to maintain adequate photopigment production. Vitamin A can be oxidized into all-*trans* retinal, and is, therefore, critical in the synthesis of photopigment. In the eye, it is the retinal pigment epithelium that stores vitamin A. The retinal pigment epithelium is also the site of the oxidization of vitamin A into all-*trans* retinal and conversion of all-*trans* retinal into 11-*cis*-retinal. Vitamin A cannot be synthesized by the body and must be ingested. It is found in blood and stored in the liver and retinal pigment epithelium. Vitamin A deficiency, which can result from liver damage (e.g., from alcoholism or hepatitis), produces degeneration of photoreceptors with visual symptoms first presenting as "night blindness" (i.e., extremely poor vision under low illumination).

Retinitis pigmentosa is an inherited disorder in which there is a gradual and progressive failure to maintain the receptor cells. One form involves the production of defective opsin that normally combines with 11-cis retinal to form rhodopsin. Consequently, the rods do not contain sufficient rhodopsin and do not function as the low illumination receptors. A symptom of this condition is "night blindness" and loss of peripheral vision. In this form of retinitis pigmentosa, the cones receptors function normally and central vision remains intact. Other forms of retinitis pigmentosa that affect the cones may progress to destroy central vision.

Macular Degeneration. The leading cause of blindness in the elderly is age-related macular degeneration. The *dry form* of macular degeneration involves intraocular proliferation of cells in the macular area (i.e., in the fovea and the immediately surrounding retinal areas). In the *wet form* of macular degeneration, the capillaries of the choroid coat invade the macular area and destroy receptor cells and neurons. In both forms, the visual loss is in the central visual field and the patient will complain of blurred vision and difficulty reading. Laser surgery is the most common treatment for the wet form but has the disadvantage of destroying normal retinal cells. It also may not be effective in preventing cell proliferation following treatment.

Retinal detachment. When the neural retina is torn away from the retinal pigment epithelium (e.g., by a blow to the eye), there is a loss of vision in the area of detachment. The loss of vision results because the neural retina is dependent on the retinal pigment epithelium for 11-cis retinal, nutrients and photoreceptor integrity. *The retinal pigment epithelium supplies glucose and essential ions to the neural retina, helps support the photoreceptor cell outer segment, removes outer segment disks shed by the receptor cells, and converts retinol and stores vitamin A for photopigment resynthesis*. Lasers may be used to weld the detachment to prevent it from increasing in size. However, the detached and welded areas are functionally blind.

Diabetic retinopathy. The pathological process in diabetic retinopathy involves microaneurysms and punctate hemorrhages in the retina. The tiny swollen blood vessels and/or bleeding in the underlying choroid coat damage the receptor cells and retinal neurons and result in blindness in the regions affected. Lasers may be used to seal swollen and/or leaking blood vessels.

14.6 Summary

This chapter described the stimulus (light) properties that are important for the visual perception of our external environment, such as color, brightness, color and brightness contrasts (for form perception and visual acuity), visual field representation, binocular fusion and depth perception. Remember that there are regional differences in visual perception: the central visual field is color-sensitive, has high acuity vision and operates at high levels of illumination (i.e., operates with the photopic, light-adapted subsystem). In contrast, the visual field periphery is more sensitive at low levels of illumination, is relatively color insensitive and has poor visual acuity (i.e., operates with the scotopic, dark-adapted, subsystem). The chapter also described how the lens system of the eye produces an image on the retina of light emitted by or reflected off objects in space. The image is a smaller, inverted, and reversed picture of the object. Keep in mind that the image projected onto the retina is, in fact, projected onto a flattened sheet of receptor cells that line the inner surface of the eye. The following chapter will describe the function of the visual receptors and other retinal neurons in converting the visual image into an array of neural activity.

The chapter also reviewed the retinal neurons and the laminar structure of the retina. The image projected onto the retina is distributed over a mosaic of photoreceptors. Light energy projected onto each photoreceptor is converted into receptor membrane potential changes by a process that involves photosensitive pigments and cyclic nucleotide-gated ion channels in the photoreceptor outer segment. The phototransduction process converts light energy into photoreceptor membrane potential changes that produce a chemical signal (the release of glutamate), which results in membrane potential changes in the postsynaptic bipolar and horizontal cells. The receptor substrate for scotopic and photopic vision lies in differences between the rod and cone receptors.

In the primate eye, the information gathered by 125 million receptor cells converges on 10 million bipolar cells, which, in turn,

converge on 1 million retinal ganglion cells. The degree of convergence from receptors to bipolar cell and bipolar cells to ganglion cell differs regionally within the retina. In the peripheral retina, the convergence can be fifty or more rod receptors to one bipolar cell, which increases the sensitivity to dim lights but decreases the spatial acuity of the peripheral bipolar cell. In addition, these peripheral bipolar cells are color insensitive. The M-ganglion cells receive input from many peripheral bipolar cells, have large receptive fields, are sensitive to small brightness contrasts and are color insensitive. They also generate transient responses and are uniquely sensitive to changes in illumination levels and movement. In contrast, the bipolar cells in the macula synapse with few foveal-cone receptors, which maintain the spatial resolution of the densely packed cones. Such macular bipolar cells have small receptive field centers, are color sensitive but must operate at high illumination levels. Each P-ganglion cell synapses with few macular bipolar cells and is color sensitive, but less sensitive to dim "white" light and to small brightness contrasts. The P ganglion cells have smaller receptive fields than the M ganglion cells and respond with sustained discharges to maintained stimuli. As the M ganglion cells and P ganglion cells respond to different aspects of the visual stimulus, they are described to be encoding and carrying independent, parallel, streams (M-stream and P-stream) of information about stimulus size, color, and movement.

Test Your Knowledge

Question 1 | A | B | C | D | E

All of the following is characteristic of the cornea of the eye EXCEPT:

A. Cataracts are formed when it is damaged.

B. It is devoid of blood vessels.

C. It receives oxygen from the tear film

D. Nutrients are provided by the aqueous humor

E. Its refractive power is fixed for distance vision

Question 2 | A | B | C | D

Which of the following account for the ability of rod bipolar cells to detect and signal light at lower illumination levels than cone bipolar cells?

A. Rods are more concentrated in the fovea than the cones.

B. The rod-biplar cells projections are denser than the cone-bipolar cells projections.

C. Rods have thicker outer segments than the cones.

D. Photopigments in rods are broken down by the narrowest bandwidth of light.

BACK NEXT