CSE511 Brain & Memory Modeling

Lect19-20: Vision – The Eye
Chapter 11 of Purves et al., 4e

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The *choroid* layer is a rich capillary bed (to nourish retinal photoreceptors) plus light absorbing melanin (to avoid reflections); a night hunter eye has a mirror “tapetum lucidum = bright tapestry”.

**Ciliary muscles** in a ring around the **lens** changes eye refractive focus. Two sets of **iris muscles** adjust pupil opening and amount of light entering the eye. The **sclera** is the tough outer layer supporting and shaping the eye. Its clear front is the **cornea**. The **aqueous** (“watery”) **humor** (fluid), nourishing the cornea and lens front, is replaced every 2 hours by the **posterior chamber**. The **vitreous humor** “glassy fluid”, filling the back 80% of an eye, contains phagocytic “cell eating) cells to remove blood and other floating debris that would block vision.
Refractive errors.

(A) In the normal eye, with ciliary muscles relaxed, an image of a distant object is focused on the retina. (B) In myopia, from too curved a cornea or too long an eyeball, light rays are focused in front of the retina. (C) In hyperopia, too weak ciliary muscles or too short an eyeball focus images at a point behind the retina.
(D) Changes in the ability of the lens to round up (accommodate) with age. The graph also shows how the near point (the closest point to the eye that can be brought into focus) changes. Accommodation, which is an optical measurement of the refractive power of the lens, is given in diopters. (After Westheimer. 1974.)
Accommodation for focusing on near objects involves the contraction of the ciliary muscle, which reduces the tension in the zonule fibers and allows the elasticity of the lens to increase its curvature.
Figure 11.3 The inner surface of the retina, viewed with an ophthalmoscope.

The optic disk (papilla “nipple”) is the region where the ganglion cell axons leave the retina to form the optic nerve; it is also characterized by the entrance and exit, respectively, of the ophthalmic arteries and veins that supply the retina. The macula lutea (“yellow spot”) can be seen as a distinct area at the center of the optical axis (the optic disk lies nasally); the macula is the region of the retina that has the highest visual acuity. The fovea (“pit”) is a depression about 1.5 mm in diameter that lies at the center of the macula.
Figure 11.4 Development of the human eye.

(A) The retina develops as an outpocketing from the neural tube, called the optic vesicle. (B) The optic vesicle invaginates to form the optic cup. (C,D) The inner wall of the optic cup becomes the neural retina, while the outer wall becomes the pigment epithelium, the dark layer between the choroid capillaries and the retinal receptors. (A-C from Hilfer and Yang, 1980; D courtesy of K. Tosney.)
Figure 11.5 Structure of the retina. (A) Section of the retina showing overall arrangement of retinal layers. (B) Diagram of the basic circuitry of the retina. A three-neuron chain—photoreceptor, bipolar cell, and ganglion cell—provides the most direct route for transmitting visual information to the brain. Horizontal cells and amacrine cells mediate lateral interactions in the outer and inner plexiform layers. The terms *inner* and *outer* refer to relative distances from the center of the eye (inner, near and outer, away from the center, toward the pigment epithelium). (C) Structural differences between rods and cones. Although generally similar in structure, rods and cones differ in their size and shape, as well as in the arrangement of the membranous disks in their outer segments.

*(See next 3 slides for larger images.)*
Figure 11.5-1 Structure of the retina.

(A) Section of retina

Photoreceptors

Horizontal cells

Bipolar cells

Amacrine cells

Ganglion cells

(A) Section of the retina showing overall arrangement of retinal layers. The photoreceptors at the back of the retina, furthest from the light, are shown at the top of the image.
A three-neuron chain—photoreceptor, bipolar cell, and ganglion cell—provides the most direct route for transmitting visual information to the brain. Horizontal cells and amacrine cells mediate lateral interactions in the outer and inner plexiform layers. The terms *inner* and *outer* refer to distances from the center of the eye (*inner*, near and *outer*, away from the center, toward the pigment epithelium).
Figure 11.5-3 Structure of the retina. (C) Structural differences between rods and cones. Although generally similar in structure, rods and cones differ in their size and shape, as well as in the arrangement of the membranous disks in their outer segments.
Figure 11.6-1 Removal of photoreceptor disks by the pigment epithelium.

(A) The tips of the outer segments of Photoreceptors are embedded in pigment epithelium. Epithelial cell processes extend down between the outer segments. (A after Oyster, 1999.)
Figure 11.6-2 Removal of photoreceptor disks by the pigment epithelium. (B) The life span of photoreceptor disks is seen in the movement of radioactively labeled amino acids injected into the inner segment and incorporated into disks. The labeled disks migrate from the inner segment to the outer portion of the outer segment over a 12-day period. (B after Young, 1971.)
Figure 11.6-3 Removal of photoreceptor disks by the pigment epithelium. (C) Expended disks are shed from the outer segment and phagocytosed. The photopigment from the disks enters the pigment epithelium, where it will be biochemically cycled back to ‘newborn’ photoreceptor disks. (C after Young, 1971.)

Besides removal of photoreceptor disks, the epithelium also regenerates photopigment molecules after they have been exposed to light.
Figure 11.7 An intracellular recording from a single cone stimulated with different amounts of light (the cone has been taken from a turtle retina, which accounts for the relatively long time course of the response). Each trace represents the response to a brief flash that was varied in intensity. At the highest light levels, the response amplitude saturates (at about -65 mV). The hyperpolarizing response is characteristic vertebrate photoreceptors; interestingly, some invertebrate photoreceptors depolarize in response to light. (After Schnapf and Baylor, 1987.)
Retinitis pigmentosa (RP) refers to a large group of hereditary eye disorders characterized by progressive vision loss caused by a gradual degeneration of photoreceptor cells, which die by apoptosis (cell 'suicide'). The figure shows the characteristic appearance of the retina in patients with RP. Note the dark clumps of pigment that are the hallmark of this disorder.

(What is the position of the nose in this image?)
Figure 11.8 Cyclic GMP-gated channels in the outer segment membrane are responsible for the light-induced changes in the electrical activity of photoreceptors. A rod is shown in this simplified diagram, but the same scheme applies to cones.

(A) In the dark, cGMP (cyclic guanosine monophosphate) levels in the outer segment are high; cGMP binds to the Na\(^+\)-permeable channels in the membrane, keeping them open and letting sodium and other cations enter, thus depolarizing the cell.

(B) Absorption of photons leads to a decrease in cGMP levels, closing the cation channels and resulting in receptor hyperpolarization.
Figure 11.9-1: Details of phototransduction in rod photoreceptors.

(A) Rhodopsin resides in the disk membrane of the photoreceptor outer segment. The seven transmembrane domains of the opsin molecule enclose the light-sensitive retinal molecule. (B) Absorption of a photon of light by retinal leads to a change in configuration from the 11-cis to the all-trans isomer.
Figure 11.9-2 Details of phototransduction in rod photoreceptors. (C) The second messenger cascade of phototransduction. The change in the retinal isomer activates transducin, which in turn activates a phosphodiesterase (PDE). The phosphodiesterase hydrolyzes cGMP, reducing its concentration in the outer segment and leading to closure of many channels in the outer segment membrane. The biochemical cascade started by one photon capture provides enormous signal amplification; each photon can close 200 channels.
Figure 11.10-1 The retinoid cycle and photoadaptation. (A) Following photoisomerization, all-trans retinal is converted into all-trans retinol and is transported by the chaperone protein IRBP into the pigment epithelium. There, in a series of steps, it is converted to 11-cis retinal and transported back to the outer segment (again via IRBP), where it recombines with opsin.

(A retinyl-FA ester is a combination of retinol with a fatty acid.)
Figure 11.10-2 (B) Photoreceptor adaptation. Calcium in the outer segment inhibits the activity of guanylate cyclase and rhodopsin kinase, and reduces the affinity of cGMP-gated channels for cGMP. Light-induced closure of channels in the outer segment membrane leads to a reduction in Ca$^{2+}$ concentration and a reduction in Ca$^{2+}$-mediated inhibition of these elements of the cascade. As a result, the photoreceptor's sensitivity to photon capture is reduced.
The range of luminance values over which the visual system operates. At the lowest levels of illumination, only rods are activated. Cones begin to contribute to perception at about the level of starlight and are the only receptors that function under relatively bright conditions. (cd are candelas)

The retinal rod system has very low spatial resolution but is extremely sensitive to light; it is specialized for sensitivity at the expense of resolution. Conversely, the cone system has very high spatial resolution but is relatively insensitive to light; it is specialized for acuity at the expense of sensitivity. The cone system also allows humans and many other animals to perceive colors.
Figure 11.12 Differential responses of human rods and cones.

(A) Suction electrode recordings of the reduction in inward current produced by flashes of successively higher light intensity. For moderate to long flashes, the rod response continues for more than 600 ms; even for the brightest flashes tested, the cone response returns to baseline (with an overshoot) in roughly 200 ms.

(B) Difference in the amount of convergence in the rod and cone pathway. Each rod bipolar cell receives synapses from 15-30 rods. Additional convergence occurs at downstream sites in the rod pathway. In contrast, in the center of the fovea, each bipolar cell receives its input from a single cone and synapses with a single ganglion cell. (A after Baylor, 1987.)
Figure 11.13-1 Distribution of photoreceptors in the human retina. (A) Cones are present at a low density throughout the retina, with a sharp peak in the center of the fovea (the foveola). Conversely, rods are present at high density throughout most of the retina, with a sharp decline in the fovea; rods are absent in the foveola. Boxes show face-on sections through the outer segments of the photoreceptors at different eccentricities. The increased density of cones in the fovea is accompanied by a striking reduction in the diameter of their outer segments. Note also the lack of receptors at the optic disk, where retinal ganglion cell axons gather to exit the retina.
Figure 11.13-2 Distribution of photoreceptors in the human retina. (B) Diagrammatic cross section through the fovea. The overlying cellular layers and blood vessels are displaced so that light is subjected to a minimum of scattering before photons strike the outer segments of the cones in the foveola.
Figure 11.14 Absorption spectra and distribution of cone opsins. (A) Light absorption spectra of the four photopigments in normal human retina. (Recall that *light* is defined as electromagnetic radiation having wavelengths between ~400 and 700 nm. *Absorbance* is defined as the log value of the intensity of incident light divided by intensity of transmitted light.) Solid curves represent the three cone opsins; the dashed curve shows rod rhodopsin for comparison.

(B) Using a technology known as adaptive optics and clever "tricks" of light adaptation, it is possible to map with great precision the distribution of different cone types within the living retina. Pseudocolor has been used to identify the short- (blue), medium- (green), and long-wavelength (red) cones. (B from Hofer et al., 2005.)
Box 11E The genesis of contrast and constancy effects by exactly the same context. The two panels demonstrate the effects on apparent color when two similarly reflective target surfaces (A) or two differently reflective target surfaces (B) are presented in the same context in which all the information provided is consistent with illumination that differs only in intensity. The appearances of the relevant target surfaces in a neutral context are shown in the insets below. (From Purves and Lotto, 2003.)
Figure 11.15  Effect of cone loss (protanopia and deuteranopia) on vision

Figure 11.15 Simulation of the image of a flower as it would appear to an observer with normal color vision (A), an observer with protanopia (loss of long wavelength sensitive cones) (B) and an observer with deuteranopia (loss of medium wavelength sensitive cones) (C). The graphs show absorption spectra of retinal cones in males with normal and defective color vision. (Photographic color simulations courtesy of vischeck.com.)
Figure 11.16 Genetics of the cone pigments (Part 1)

Figure 11.16-1 Genetics of the cone pigments. (A) In these representations of the amino acid sequences of human S-, M-, and L-cone pigments, colored dots identify amino acid differences between each photopigment and a comparison pigment.

(A) There are substantial differences in the amino acid sequences of rhodopsin and the S-cone pigment, and between the S- and M-cone pigments; however, only a few amino acid differences separate the M- and L-cone pigment sequences. (A after Nathans, 1987.)
Genetics of the cone pigments. (B,C) Many deficiencies of color vision arise from alterations in the M- or L-cone pigment genes as a result of chromosomal crossing over during meiosis. Colored squares represent the six exons of the L and M genes. (B) Unequal recombination in the intergenic region results in loss of a gene (or duplication of a gene). Loss of a gene results in dichromatic color capabilities (protanopia or deuteranopia). (B after Deeb, 2005.)
Figure 11.16-3 Genetics of the cone pigments. (B,C) Many deficiencies of color vision arise from alterations in the M- or L -cone pigment genes as a result of chromosomal crossing over during meiosis. Colored squares represent the six exons of the L and M genes. (C) Intragenic recombination results in hybrid genes that code for photopigments with abnormal absorption spectra, consistent with the color vision capabilities of anomalous trichromats. (C after Deeb, 2005.)
Box 11F(1) The Perception of Light Intensity

(A) [Image of two panels, one dark and one light, each with a central gray rectangle.]

(B) [Image of multiple horizontal bars, alternating black and gray, arranged in a pattern.]

NEUROSCIENCE, Fourth Edition, Box 11F (1)
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Box 11F(2) The Perception of Light Intensity
Figure 11.17  The responses of on-center and off-center retinal ganglion cells

(A) Light spot in center
(B) Dark spot in center
(C) Center plus surround

On-center ganglion cell
Off-center ganglion cell

Time
Figure 11.17  The responses of on-center and off-center retinal ganglion cells (Part 1)
Figure 11.17 The responses of on-center and off-center retinal ganglion cells (Part 2)
Figure 11.17  The responses of on-center and off-center retinal ganglion cells (Part 3)
Figure 11.18 Generation of receptive field center responses of retinal ganglion cells

(A) Diagram of retinal ganglion cell with surrounding layers and cone cells. glutamate neurotransmitter, mGluR6 receptor, AMPA kainate receptor, on-center bipolar cell, off-center bipolar cell, on-center ganglion cell, off-center ganglion cell.

(B) Light spot in center: On-center bipolar cell depolarized; Off-center bipolar cell hyperpolarized.

(C) Dark spot in center: On-center bipolar cell hyperpolarized; Off-center bipolar cell depolarized.

Center cone: On-center ganglion cell; Off-center ganglion cell.
Figure 11.18 Generation of receptive field center responses of retinal ganglion cells (Part 1)
Figure 11.18  Generation of receptive field center responses of retinal ganglion cell (Part 2)

(B)

On-center bipolar cell

Off-center bipolar cell

On-center ganglion cell

Off-center ganglion cell

Light spot in center

Center cone

Time
Figure 11.18  Generation of receptive field center responses of retinal ganglion cell (Part 3)

(C)

Dark spot in center

On-center bipolar cell

Off-center bipolar cell

On-center ganglion cell

Off-center ganglion cell

Center cone

Time
Figure 11.19 Responses of on-center ganglion cells to different light conditions

(A) Light

(B) Dark

Response rate (impulses/s)

<table>
<thead>
<tr>
<th>Distance (degrees) from center of receptive field</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
</tr>
<tr>
<td>100</td>
</tr>
</tbody>
</table>

Spontaneous level of activity

On-center ganglion cells

Figure 11.19 Responses of on-center ganglion cells to different light conditions (Part 1)

(A)

Light

Response rate (impulses/s)

Spontaneous level of activity

Distance (degrees) from center of receptive field
Figure 11.19 Responses of on-center ganglion cells to different light condition (Part 2)

(B)

Dark

Edge

Light

On-center ganglion cells

Response rate

Position

Spontaneous level of activity
Figure 11.20  Discharge rate of a single on-center ganglion cell depends on relative light intensity
Figure 11.21 Generation of the receptive field surround of an on-center retinal ganglion cell
Figure 11.21  Generation of the receptive field surround of an on-center retinal ganglion cell (Part 1)
Figure 11.21 Generation of the receptive field surround of an on-center retinal ganglion cell (Part 2)
Figure 11.21 Generation of the receptive field surround of an on-center retinal ganglion cell (Part 3)

Horizontal cell

On-center bipolar cell

Horizontal cell

On-center ganglion cell
Slides unused this year
Figure 11.6 Removal of photoreceptor disks by the pigment epithelium

(A) Endoplasmic reticulum
   Mitochondrion
   Pigment

(B) Pigment epithelial cell
   Outer segment
   Labeled amino acids
   Inner segment

Days after injection of radiolabel

0 3 6 9 12

(C) Disks shed and are phagocytosed

Days after injection of radiolabel

0 3 6 9 12

Disks shed and are phagocytosed

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Figure 11.9 Details of phototransduction in rod photoreceptors.
Figure 11.10  The retinoid cycle and photoadaptation
Figure 11.13 Distribution of photoreceptors in the human retina
Figure 11.14 Absorption spectra and distribution of cone opsins (Part 1)
Figure 11.14  Absorption spectra and distribution of cone opsins (Part 2)
(A) Normal (trichromat)
(B) Protanopia
Figure 11.15  Effect of cone loss (protnaopia and deuteranopia) on vision (Part 3)

(C) Deuteranopia

NEUROSCIENCE, Fourth Edition, Figure 11.15 (Part 3)
Figure 11.16  Genetics of the cone pigments

(A) S pigment  M pigment  L pigment

Rhodopsin → S  S → M  M → L

(B) L pigment  M pigment
Parental genotypes (normal trichromats)

Offspring genotypes Deuteranopia  Normal

Unequal crossing over

(C) Parental genotypes (normal trichromats)

Offspring genotypes Deuteranomalous trichromat  Protanomalous trichromat

Unequal crossing over

NEUROSCIENCE, Fourth Edition, Figure 11.16

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