The Visual System: Retinal Anatomy and Physiology

Ocular anatomy

The eye is a fluid-filled sphere enclosed by three layers of tissue. The outer layer is composed of the *sclera* and the *cornea*. The middle layer includes the *iris*, the *ciliary body*, and the *choroid*. The iris contains two sets of muscles controlling the size of the pupil. The ciliary body encircles the lens and contains a musculature that adjusts its refractive power. The choroid is a capillary bed supplying the photoreceptors. The innermost layer is the actual *retina* containing the photoreceptors.

En route to the retina, light successively travels through the cornea, the *aqueous humor* (the clear and watery liquid within the *anterior chamber* that regulates the intraocular pressure), the lens, and the *vitreous humor* (the thick gelatinous substance that accounts for the size and shape of the globe).

Retinal image formation

The formation of focused images on the photoreceptors depends on the refraction of light by the cornea and the lens. The refractive power of the former is unvarying but that of the former is adjustable. The dynamic changes in the refractive power of the lens are referred to as *accommodation*.

The ability to focus an image on the retina also depends on the *shape* of the eye globe.

Adjustments in the size of the *pupil* also contribute to the retinal image formation. Narrowing the pupil reduces both spherical and chromatic aberrations. It also increases the depth of field, i.e., the distance within which objects are seen without blurring.

Retinal organization

There are five types of neurons in the retina distributed in five layers. The *photoreceptors* are in the outer nuclear layer, the *horizontal*, *amacrine* and *bipolar* cells are in the inner nuclear layer, and the ganglion cells are in the *ganglion cell* layer. The outer plexiform layer contains the processes and cell contacts of the photoreceptors, horizontal and bipolar cells. The inner plexiform layer contains those of the bipolar, amacrine, and ganglion cells.

A direct *three-neuron chain* – from photoreceptor to bipolar to ganglion cell – is the major route of information flow from the light source to the optic nerve. The horizontal and amacrine cells are primary responsible for *lateral interactions*.

Duplex theory of vision

There are two types of photoreceptor, *rods* and *cones*, in the retina. The rods contain the visual pigment rhodopsin sensitive to blue-green light. Rods are highly sensitive photoreceptors exclusively active during *scotopic* vision. They are completely inactivated during *photopic* vision, when cones are fully active. Cones contain different visual pigments that are maximally sensitive to long (red light), medium (green light) or short (blue light) wavelengths of light. Cones of different wavelength sensitivity are the basis of our *color perception*.

Rods and cones also differ in the degree of convergence onto ganglion cells. While inputs from many rods converge to a single ganglion cell, the latter receive inputs from a single cone or from very few. *Convergence* makes the rod system a better *light detector*, but reduces its spatial resolution. The one-to-one mapping within the cone system maximizes the discrimination of fine detail, *visual acuity*.

Rods and cones are unevenly distributed. The density of rods exceeds that of the cones, except in the fovea where the cone density is highest. The central region of the fovea (foveola) is even rod-free. The high density of cones with their one-to-one relationship with bipolar and ganglion cells allow the fovea to mediate high visual acuity. The superior foveal acuity further benefits from reduced optical distortion provided by the displacement of the inner nuclear and ganglion cell layers.

Phototransduction

On the photoreceptor's disks, light strikes photosensitive molecules and triggers a molecular cascade whose objective is to control the cell's cGMP concentration to modulate the photoreceptor's release of neurotransmitter (glutamate). In the dark, high cGMP concentration keeps Na+ channels open and generates the dark current: the photoreceptor is depolarized. Light lowers cGMP concentration, which closes Na+ channel: the photoreceptor becomes hyperpolarized.

Molecular cascade:
1) A photon converts a rhodopsin molecule (11cis-retinal + opsin to all-trans-retinal + opsin)
2) This activates 100 molecules of the G-protein transducin.
3) Each of which activates a cGMP phosphodiesterase molecule.
4) Each causes the breakdown of 100's molecules of cGMP.
5) Which close several hundred Na+ channels.
6) The photoreceptor hyperpolarizes and fewer transmitters are released.

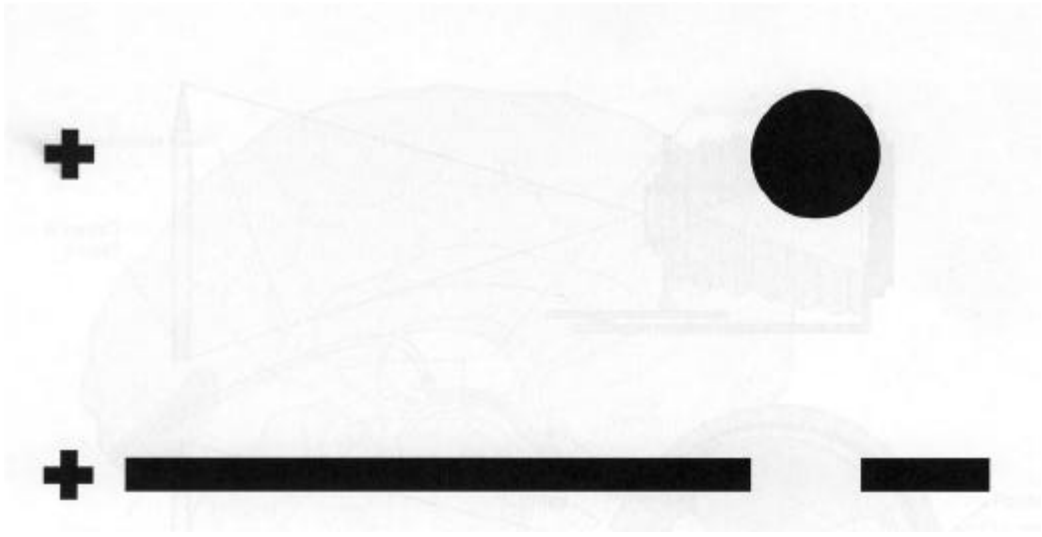
On and off channels

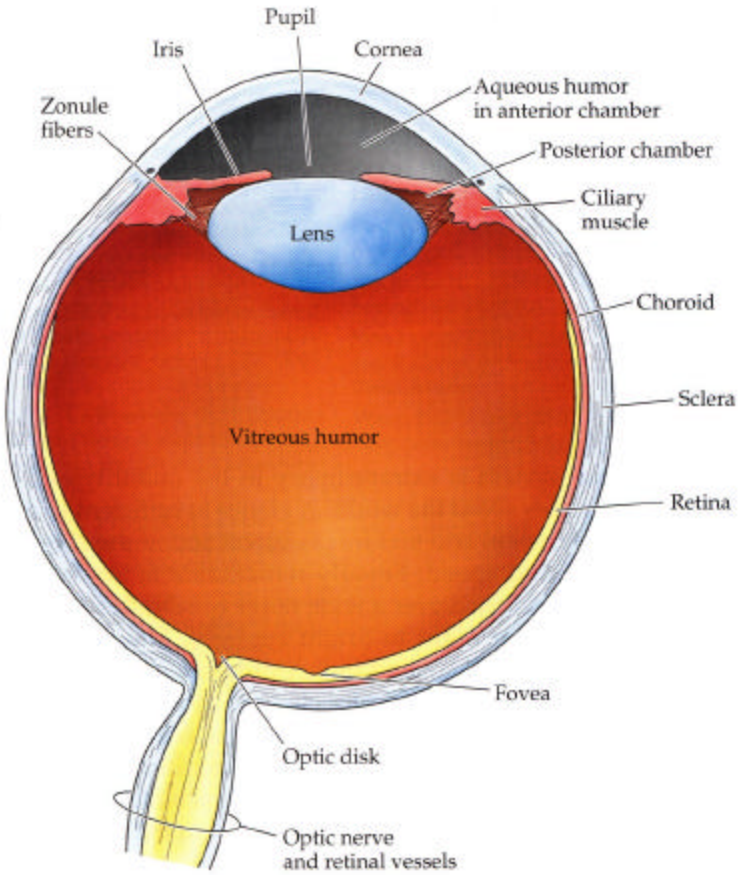
While light hyperpolarizes photoreceptors, this signal in turn triggers both hyperpolarization and depolarization within the bipolar and ganglion cells.

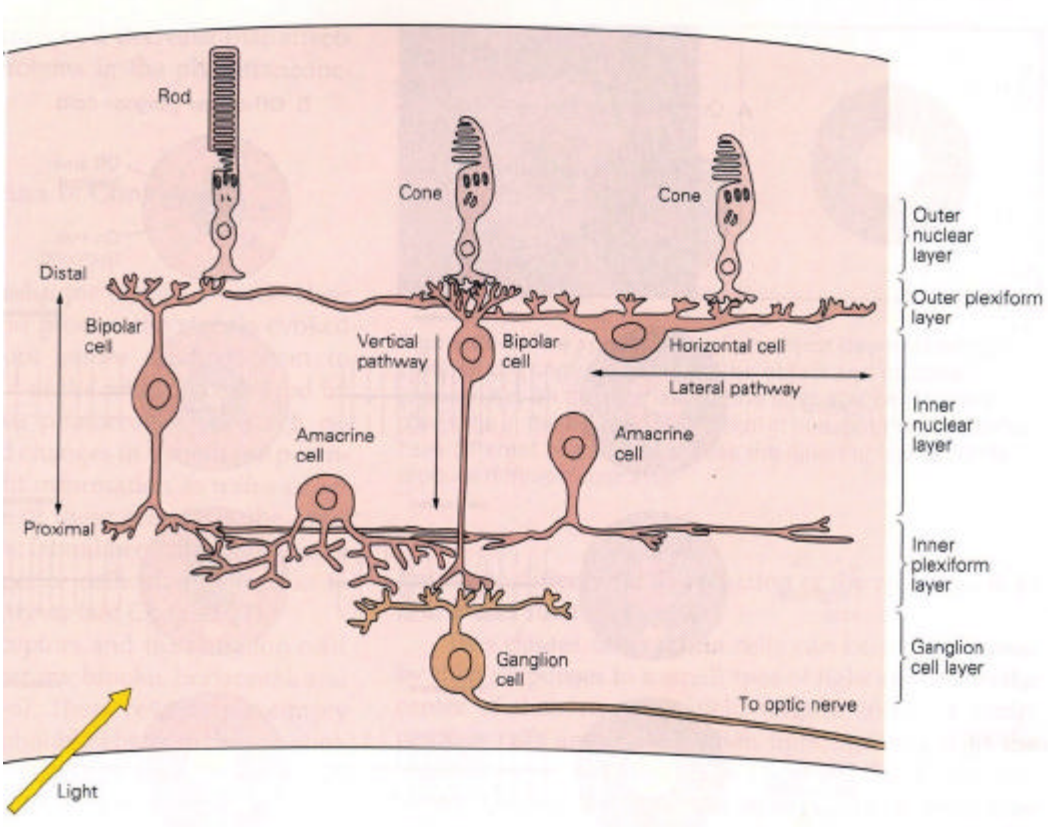
The ON and OFF bipolar cells response differently to the photoreceptor signals because they express different receptors (metabotropic and ionotropic glutamate receptors, respectively). They also make synaptic contact with ganglion cells in different strata of the inner plexiform layer. The ON and OFF bipolar and ganglion cells respectively detect increases and decreases in luminance within their receptive fields.

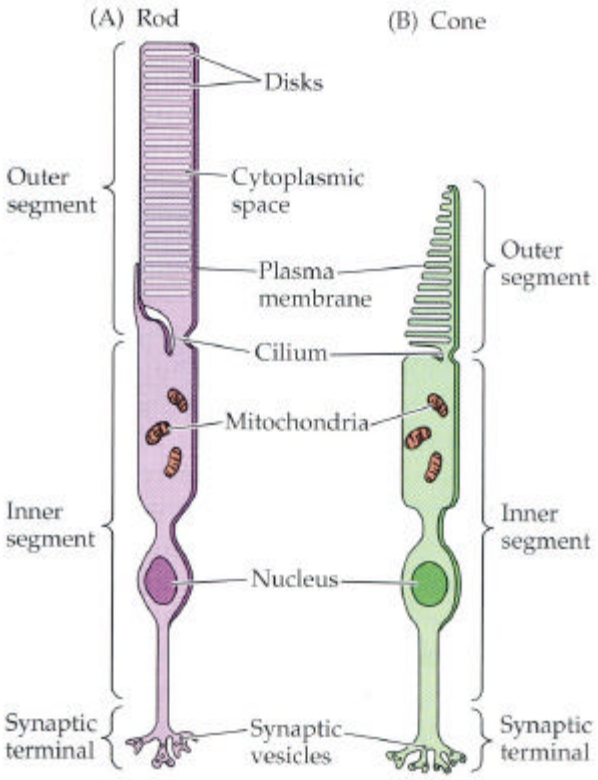
The receptive fields of ON and OFF retinal cells have a *center-surround organization*: stimulation of the region surrounding their receptive fields elicit opposite responses. The center-surround organization of ganglion cells' receptive fields is due to the *lateral inhibitory action* of horizontal cells. This lateral inhibition provides our visual system with a mean to emphasize areas of difference (*contrast*), i.e., it sharpens the boundary between objects of different luminance.

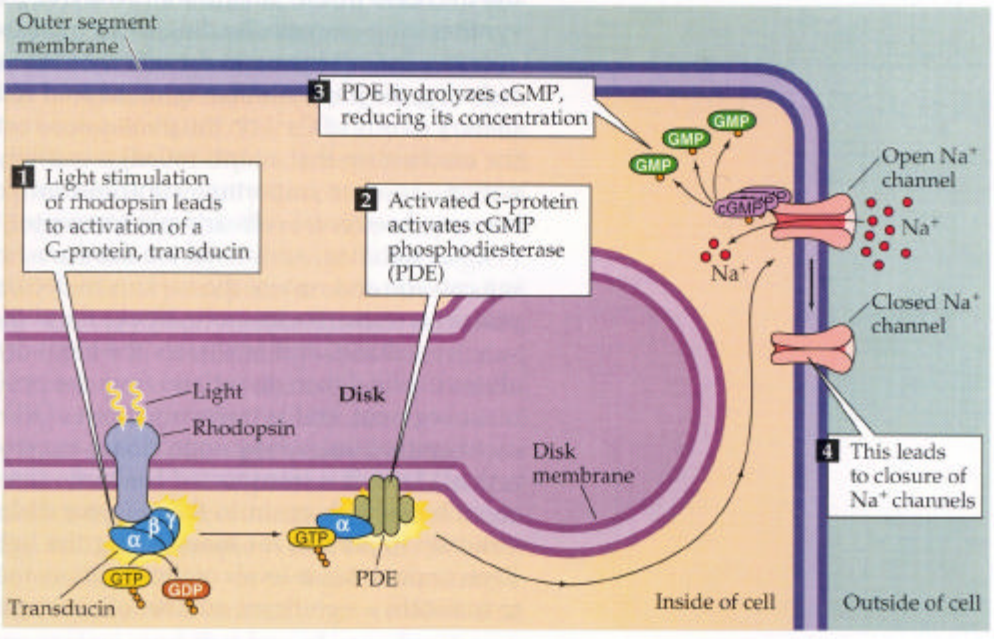
The output of the retina originates from two classes of ganglion cells, both showing the on-off center-surround patterns of activation. The *parasol* cells predominate in the peripheral retina and receive inputs mainly from rods. They have large receptive fields and sensitive to visual motion; they participate very little in color perception. The *midget* cells predominate in the central retina and receive input mainly from cones. They have small receptive fields and are sensitive to color.

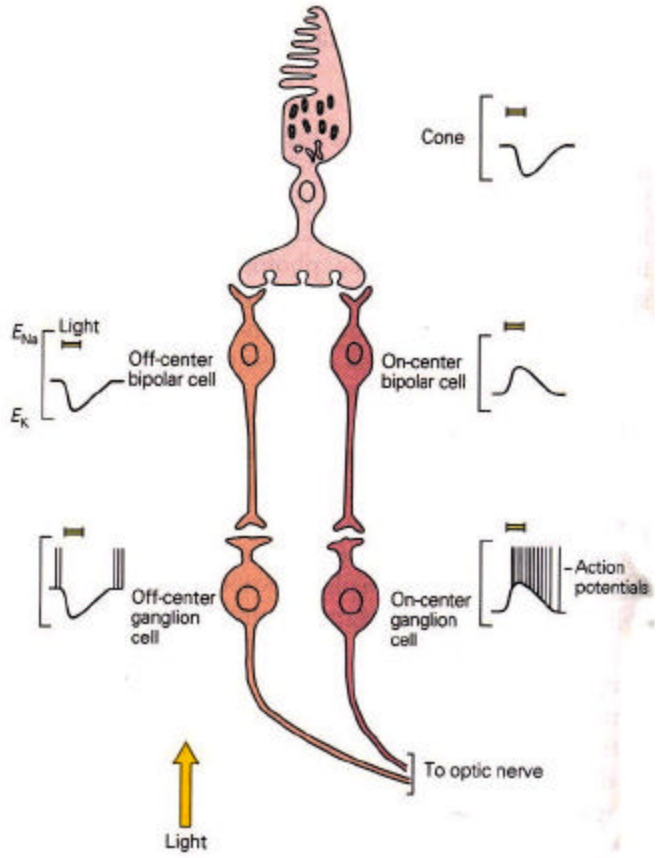


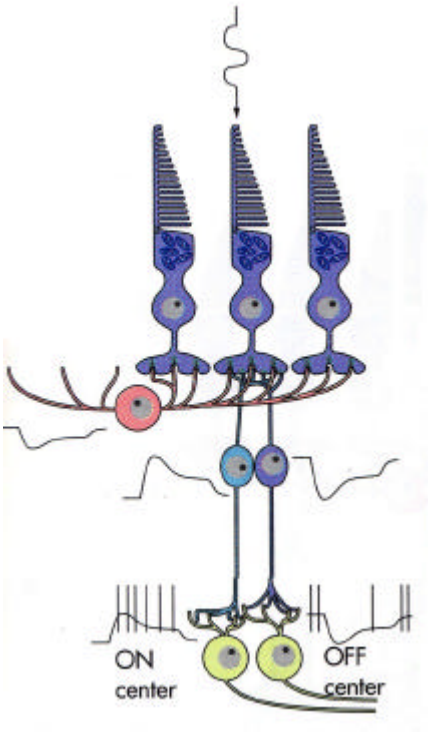

Pupil
Iris
Cornea
Zonule fibers
Aqueous humor in anterior chamber
Posterior chamber
Ciliary muscle
Lens
Choroid
Sclera
Vitreous humor
Retina
Fovea
Optic disk
Optic nerve and retinal vessels

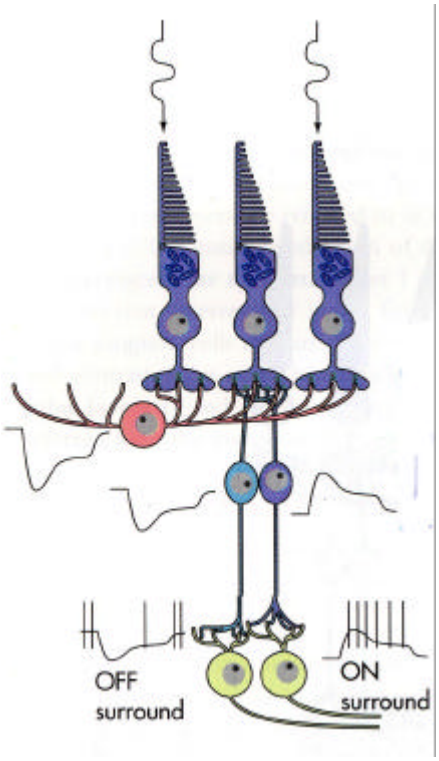

Rod
Cone
Cone
Distal
Bipolar cell
Vertical pathway
Bipolar cell
Horizontal cell
Lateral pathway
Amacrine cell
Amacrine cell
Proximal
Ganglion cell
To optic nerve
Light
Outer nuclear layer
Outer plexiform layer
Inner nuclear layer
Inner plexiform layer
Ganglion cell layer


(A) Rod
(B) Cone
Disks
Outer segment
Cytoplasmic space
Plasma membrane
Cilium
Mitochondria
Inner segment
Nucleus
Synaptic terminal
Synaptic vesicles


Outer segment membrane
3 PDE hydrolyzes cGMP, reducing its concentration
GMP
1 Light stimulation of rhodopsin leads to activation of a G-protein, transducin
2 Activated G-protein activates cGMP phosphodiesterase (PDE)
Open Na+ channel
Na+
Closed Na+ channel
Light
Rhodopsin
Disk
Disk membrane
4 This leads to closure of Na+ channels
GTP
GDP
Transducin
PDE
Inside of cell
Outside of cell


Cone
E_{Na}
Light
E_K
Off-center bipolar cell
On-center bipolar cell
Off-center ganglion cell
On-center ganglion cell
Action potentials
To optic nerve
Light


ON center
OFF center


OFF surround
ON surround