Physiological optics, information processing in the retina.

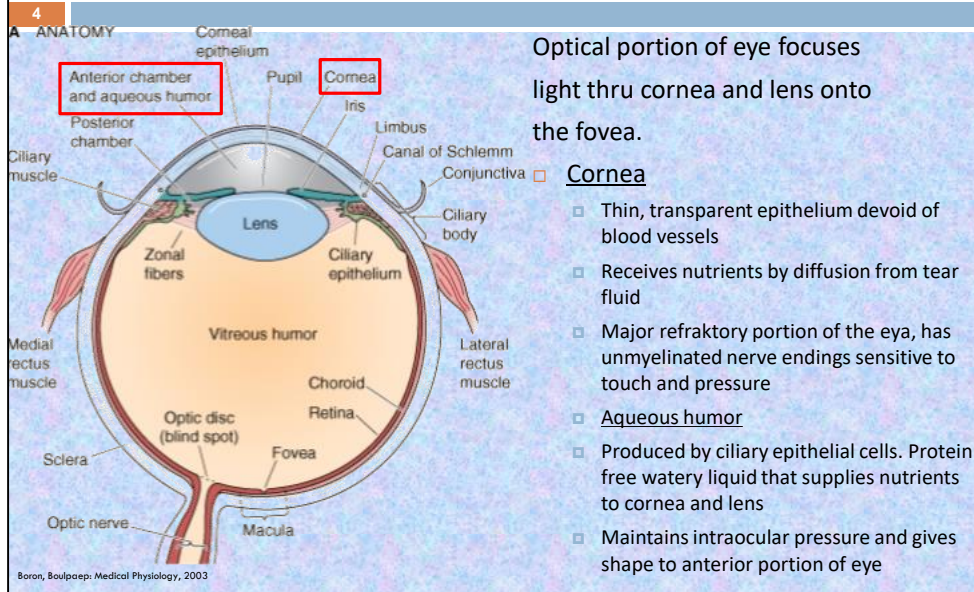## Perception of motion, depth, form and color

Readings

B&B: Chapter 13, pages 331 - 343

BLKS: Chapter 8

Physiology of vision

The auditory system is one of the engineering masterpieces of the human body. At the heart of the system is an array of miniature acoustical detectors packed into a space no larger than a pea. These detectors can faithfully transduce vibrations as small as the diameter of an atom, and they can respond a thousand times faster than visual photoreceptors. Such rapid auditory responses to acoustical cues facilitate the initial orientation of the head and body to novel stimuli, especially those that are not initially within the field of view. Although humans are highly visual creatures, much human communication is mediated by the auditory system; indeed, loss of hearing can be more socially debilitating than blindness. From a cultural perspective, the auditory system is essential not only to language, but also to music, one of the most aesthetically sophisticated forms of human expression. For these and other reasons, audition represents a fascinating and especially important aspect of sensation, and more generally of brain function.

Optical anatomy of the eye

A ANATOMY

Corneal epithelium
Anterior chamber and aqueous humor
Pupil
Cornea
Iris
Posterior chamber
Limbus
Canal of Schlemm
Conjunctiva
Ciliary muscle
Lens
Ciliary body
Zonal fibers
Ciliary epithelium
Medial rectus muscle
Vitreous humor
Lateral rectus muscle
Choroid
Retina
Optic disc (blind spot)
Sclera
Fovea
Optic nerve
Macula

Boron, Boulpaep: Medical Physiology, 2003

Optical portion of eye focuses light thru cornea and lens onto the fovea.

- Cornea
  - Thin, transparent epithelium devoid of blood vessels
  - Receives nutrients by diffusion from tear fluid
  - Major refraktory portion of the eya, has unmyelinated nerve endings sensitive to touch and pressure
  - Aqueous humor
  - Produced by ciliary epithelial cells. Protein free watery liquid that supplies nutrients to cornea and lens
  - Maintains intraocular pressure and gives shape to anterior portion of eye

Cornea: major refractory portion of the eye (fixed refractory index). Has unmyelinated nerve endings sensitive to touch and pressure. Receives nutrients thru diffusion from tear fluid. Laser eye surgery reshapes the cornea to reduce the need for corrective lenses.
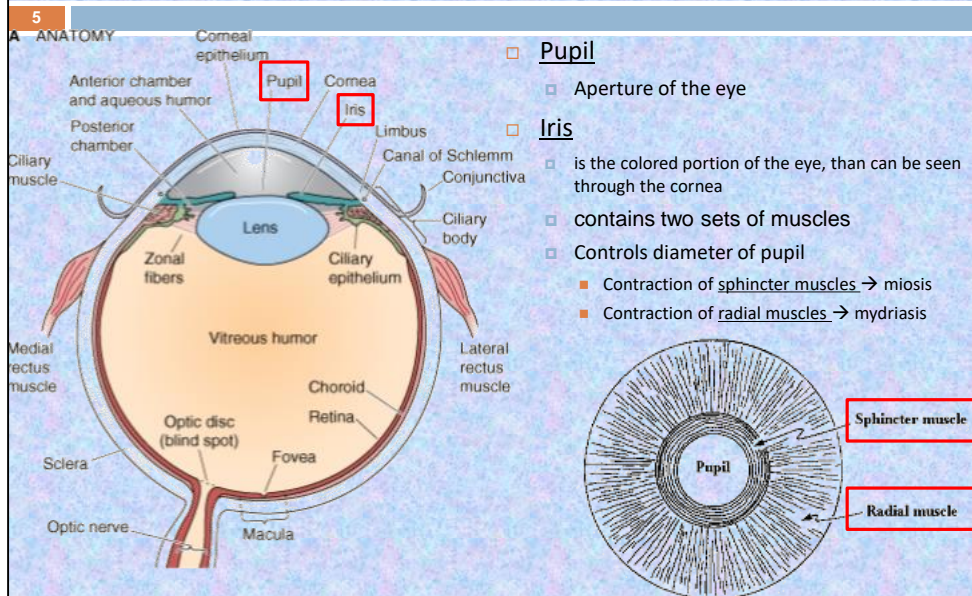
Aqueous humor: produced by ciliary epithelial cells. High rate of turnover. Gluacoma increases pressure in eye due to increased production or decreased drainage. Canals of Schlemm drain the aqeuous humor.
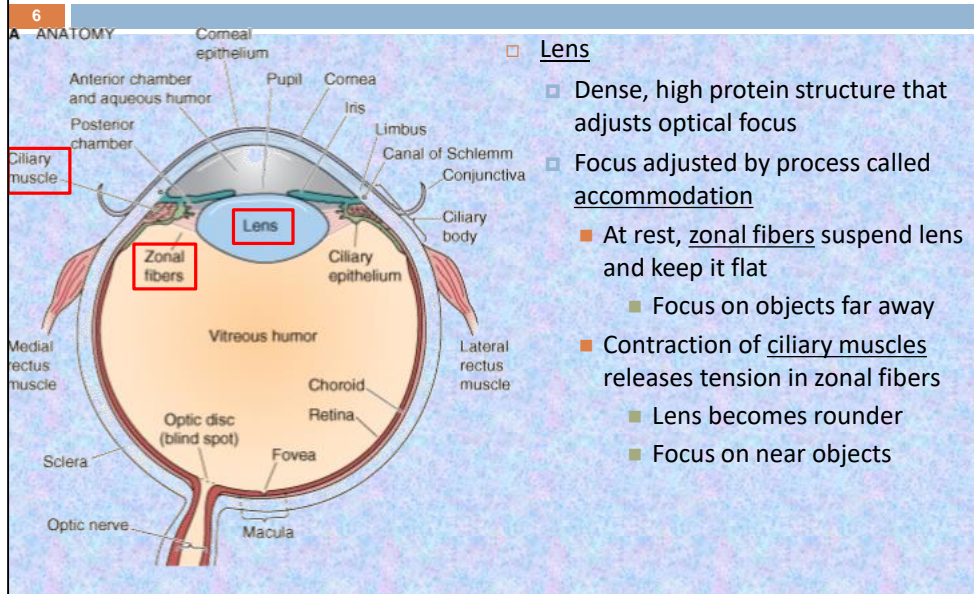
The eye is a fluid-filled sphere enclosed by three layers of tissue (Figure 11.1). Most of the outer layer is composed of a tough white fibrous tissue, the sclera. At the front of the eye, however, this opaque outer layer is transformed into the cornea, a specialized transparent tissue that permits light rays to enter the eye. The middle layer of tissue includes three distinct but continuous structures: the iris, the ciliary body, and the choroid. The iris is the colored portion of the eye that can be seen through the cornea. It contains two sets of muscles with opposing actions, which allow the size of the pupil (the opening in its center) to be adjusted under neural control. The ciliary body is a ring of tissue that encircles the lens and includes a muscular component that is important for adjusting the refractive power of the lens, and a vascular component (the so-called ciliary processes) that produces the fluid that fills the front of the eye. The **choroid** is composed of a rich capillary bed that serves as the main source of blood supply for the photoreceptors of the retina. Only the innermost layer of the eye, the retina, contains neurons that are sensitive to light and are capable of transmitting visual signals to central targets.

En route to the retina, light passes through the cornea, the lens, and two distinct fluid environments. The **anterior chamber**, the space between the lens and the cornea, is filled with **aqueous humor**, a clear, watery liquid that supplies nutrients to these structures as well as to the lens. Aqueous humor is produced by the ciliary processes in the **posterior chamber** (the region between the lens and the iris) and flows into the anterior chamber through the pupil. A specialized meshwork of cells that lies at the junction of the iris and the cornea is responsible for its uptake. Under normal conditions, the rates of aqueous humor production and uptake are in equilibrium, ensuring a constant intraocular pressure. Abnormally high levels of intraocular pressure, which occur in glaucoma, can reduce the blood supply to the eye and eventually damage retinal neurons.

The space between the back of the lens and the surface of the retina is filled with a thick, gelatinous substance called the **vitreous humor**, which accounts for about 80% of the volume of the eye. In addition to maintaining the shape of the eye, the vitreous humor contains phagocytic cells that remove blood and other debris that might otherwise interfere with light transmission. The housekeeping abilities of the vitreous humor are limited, however, as a large number of middle-aged and elderly individuals with vitreal "floaters" will attest. Floaters are collections of debris too large for phagocytic consumption that therefore remain to cast annoying shadows on the retina; they typically arise when the aging vitreous membrane pulls away from the overly long eyeball of myopic individuals.

Optical anatomy of the eye

5 A ANATOMY

□ Pupil
  □ Aperture of the eye

□ Iris
  □ is the colored portion of the eye, than can be seen through the cornea
  □ contains two sets of muscles
  □ Controls diameter of pupil
    ■ Contraction of sphincter muscles → miosis
    ■ Contraction of radial muscles → mydriasis

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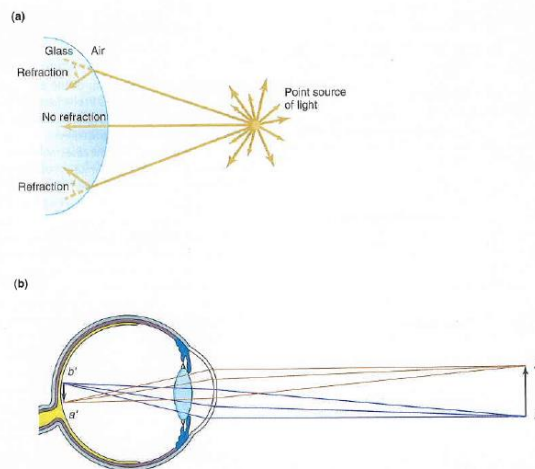
(a)

Glass Air

Refraction

No refraction

Refraction

Point source
of light

(b)

b'

a'

a

b

FIGURE 12–8 **Focusing point sources of light. (a)** When diverging light rays enter a dense medium at an angle to its convex surface, refraction bends them inward. **(b)** Refraction of light by the lens system. For simplicity, refraction is shown only at the corneal surface (site of greatest refraction) although it also occurs in the lens and elsewhere. Incoming light from *a* (above) and *b* (below) is bent in opposite directions, resulting in *b'* being above *a'* on the retina. (From Widmaier EP, Raff H, Strang KT: *Vander's Human Physiology*, 11th ed. McGraw-Hill, 2008.)
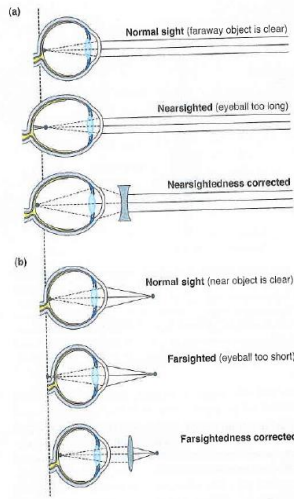
FIGURE 12–9   Common defects of the optical system of the eye. In hyperopia (farsightedness), the eyeball is too short and light rays come to a focus behind the retina. A biconvex lens corrects this by adding to the refractive power of the lens of the eye. In myopia (near-sightedness), the eyeball is too long and light rays focus in front of the retina. Placing a biconcave lens in front of the eye causes the light rays to diverge slightly before striking the eye, so that they are brought to a focus on the retina. (From Widmaier EP, Raff H, Strang KT: *Vander's Human*

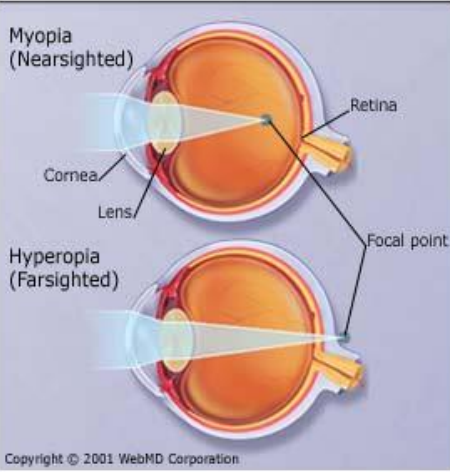# Accommodation and associated disorders
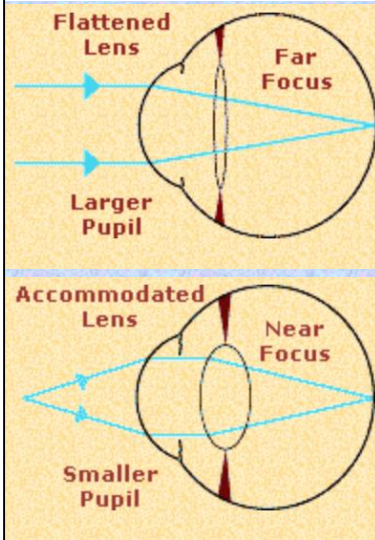
- Accommodation of the lens is limited and age dependent
  - With age, lens becomes stiffer and less compliant.
    - Age related loss of accommodation called **presbyopia**
- Accommodation accompanied by adaptive changes in size of pupil

Accommodation and associated disorders

Myopia and Hyperopia

Myopia (Nearsighted)

Cornea
Lens
Retina
Focal point

Hyperopia (Farsighted)

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- □ Myopia
  - □ Image focused in front of retina
  - □ Far away objects appear blurry
- □ Hyperopia
  - □ Image focused behind retina
  - □ Close objects appear blurry

Each can be caused by abnormal shape of the eye as well.
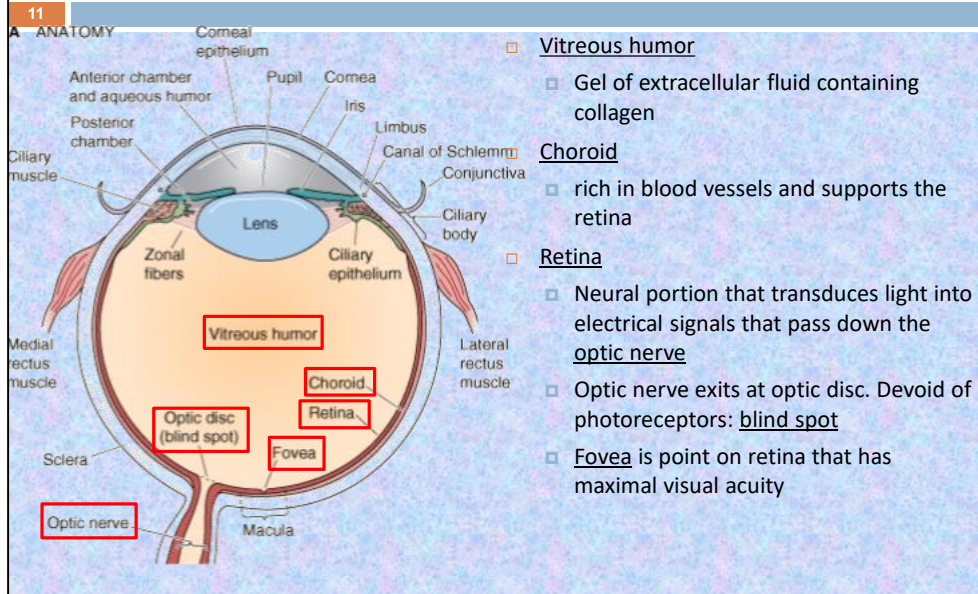
Myopia: lens is too round

Hyperopia: lens is too flat

Astigmatism is abnormal curvature of cornea, images are blurry both near and far.

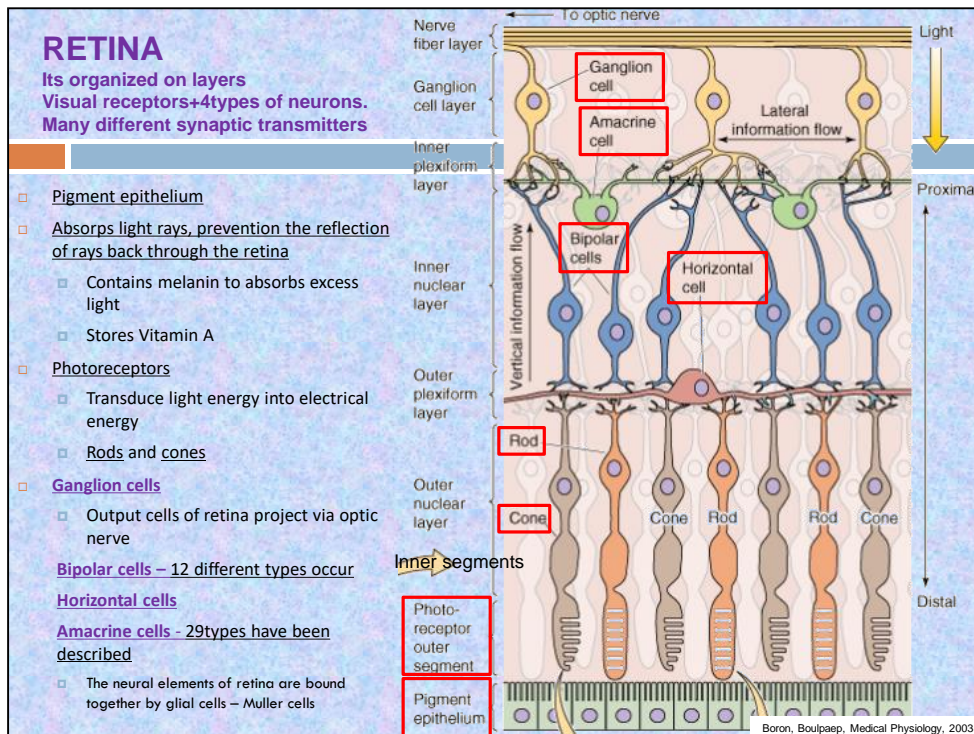Myopia and hyperopia can be caused by abnormal shape of eyeball as well.

Eye that is longer than normal results in myopia, corrected with a concave lens (focuses images at longer distance)

Optical anatomy of the eye

A ANATOMY

[Diagram of the eye with labels: Corneal epithelium, Pupil, Cornea, Iris, Anterior chamber and aqueous humor, Posterior chamber, Limbus, Canal of Schlemm, Conjunctiva, Ciliary muscle, Lens, Ciliary body, Zonal fibers, Ciliary epithelium, Vitreous humor, Medial rectus muscle, Lateral rectus muscle, Choroid, Retina, Optic disc (blind spot), Fovea, Sclera, Optic nerve, Macula]

- Vitreous humor
  - Gel of extracellular fluid containing collagen
- Choroid
  - rich in blood vessels and supports the retina
- Retina
  - Neural portion that transduces light into electrical signals that pass down the optic nerve
  - Optic nerve exits at optic disc. Devoid of photoreceptors: blind spot
  - Fovea is point on retina that has maximal visual acuity

Retina is part of the CNS derived from diencephalon

Macula is yellow region at back of eye on retina. Contains fovea is broader region responsible for central vision
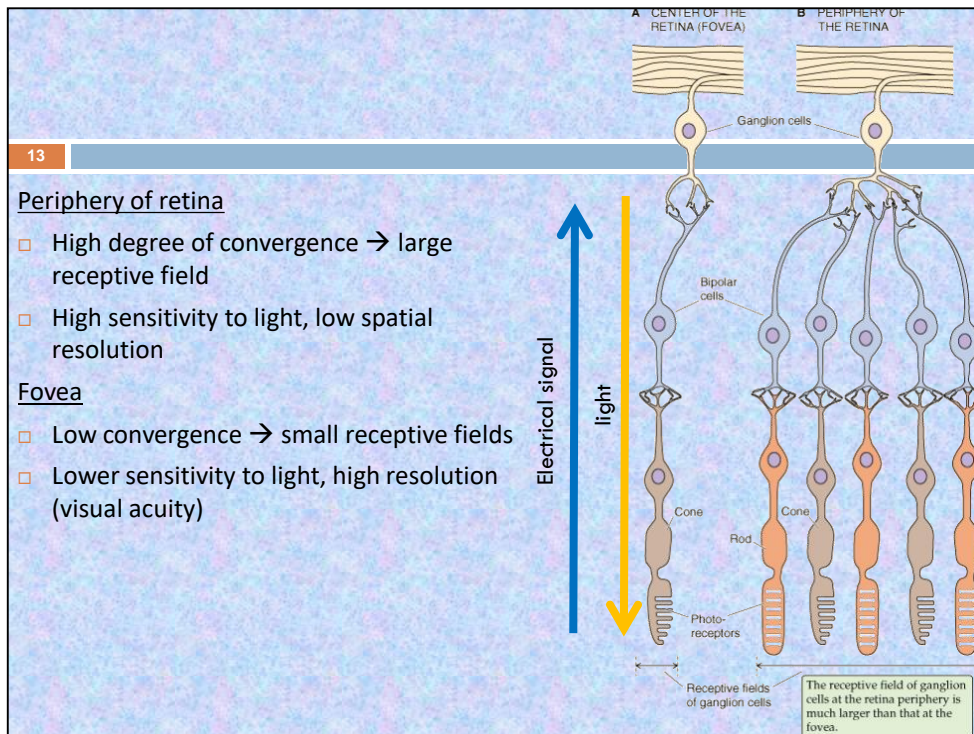
RETINA

Its organized on layers
Visual receptors+4types of neurons.
Many different synaptic transmitters

- Pigment epithelium
- Absorps light rays, prevention the reflection of rays back through the retina
  - Contains melanin to absorbs excess light
  - Stores Vitamin A
- Photoreceptors
  - Transduce light energy into electrical energy
  - Rods and cones
- Ganglion cells
  - Output cells of retina project via optic nerve
  - **Bipolar cells** – 12 different types occur
  - **Horizontal cells**
  - **Amacrine cells** - 29types have been described
    - The neural elements of retina are bound together by glial cells – Muller cells

Boron, Boulpaep, Medical Physiology, 2003

Despite its peripheral location, the retina or neural portion of the eye, is actually part of the central nervous system.

There are five types of neurons in the retina: **photoreceptors, bipolar cells, ganglion cells, horizontal cells**, and **amacrine cells**.

Absorption of light by the photopigment in the outer segment of the photoreceptors initiates a cascade of events that changes the membrane potential of the receptor, and therefore the amount of neurotransmitter released by the photoreceptor synapses onto the cells they contact.

At first glance, the spatial arrangement of retinal layers seems counterintuitive, since light rays must pass through the non-light-sensitive elements of the retina (and retinal vasculature!) before reaching the outer segments of the photoreceptors, where photons are absorbed. The reason for this curious feature of retinal organization lies in the special relationship that exists between the outer segments of the photoreceptors and the pigment epithelium. The outer segments contain membranous disks that house the light-sensitive photopigment and other proteins involved in the transduction process. These disks are formed near the inner segment of the photoreceptor and move toward the tip of the outer segment, where they are shed. The pigment epithelium plays an essential role in removing the expended receptor disks; this is no small task, since all the disks in the outer segments are replaced every 12 days. In addition, the pigment epithelium contains the biochemical machinery that is required to regenerate photopigment molecules after they have been exposed to light. It is presumably the demands of the photoreceptor disk life cycle and photopigment recycling that explain why rods and cones are found in the outermost rather than the innermost layer of the retina. Disruptions in the normal relationships between pigment epithelium and retinal photoreceptors such as those that occur in retinitis pigmentosa have severe consequences for vision

At the periphery of the retina there is convergence of synaptic input from many photoreceptors onto bipolar and ganglion cells, reducing spatial resolution because receptive fields are larger, but increasing sensitivity because more photoreceptors collect light

Outside fovea density of cones drops and density of rods rises; there are no photoreceptors at optic disc where ganglion cell axons leave retina (blind spot).

Fovea is region 300-700 μm in diameter located in center of retina and contains the highest density of cones

Over most of retina, light must travel through several layers to reach photoreceptors; at fovea layers of neurons are shifted aside, reducing distortion due to light scatter

Most photoreceptors in fovea synapse on only one bipolar cell which in turn synapses on only one ganglion cell, resulting in smallest receptive fields and greatest resolution

13
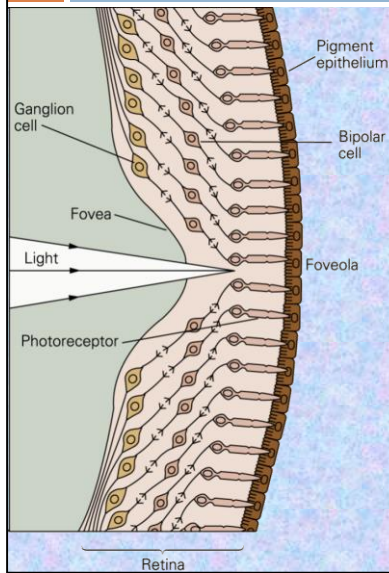
Fovea

Visual acuity of fovea enhanced by:

- One to one ratio of photoreceptor to ganglion cell
- Lateral displacement of neurons to minimize scattering of light
- High density of cones
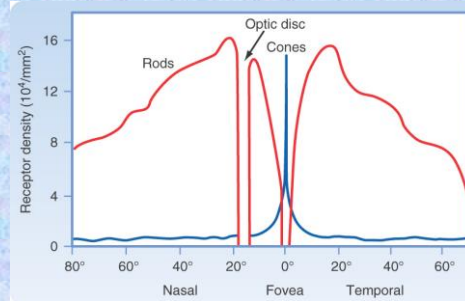
Cones are narrower and can pack more densley

Photoreceptors

Rods
- Responsible for monochromatic, dark-adapted vision
- Inner segment contains nucleus and metabolic machinery
    - Produces photopigment
- Outer segments is transduction site
    - Consists of high density of stacks of disk membranes: flattened, membrane bound organelles
        - contain the photopigment rhodopsin
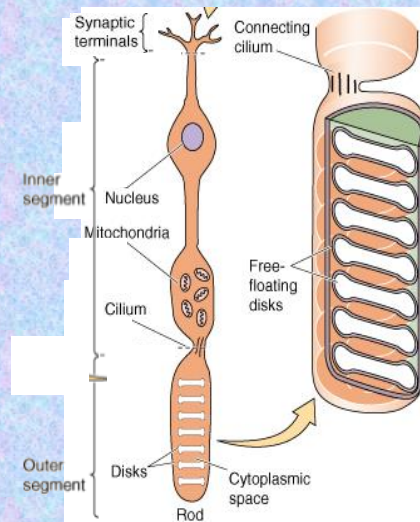
Photoreceptors consist of synaptic terminal connected by short axon to inner segment (contains nucleus and metabolic machinery) and outer segment.

Outer segments of rods consist of stacks of membrane discs rich in photopigment rhodopsin.

Inner segment synthesizes photopigments and inserts them into membrane of vesicles which move from inner to outer segment.

In rods vesicles become incorporated into new discs, which move up the stack until they reach apex where they are shed and recycled by pigment epithelium.

Photoreceptors

Cones

- 3 subtypes responsible for colour vision
- Inner segment produces photopigments similar to rhodopsin
- Outer segments is transduction site
  - consist of infolded stack membranes that are continuous with the outer membrane
    - vesicles containing pigment are inserted into the membrane folds of the outer segment

Ciliary stalk

Folding of outer cell membrane

Synaptic terminals

Inner segment

Nucleus

Mitochondria

Cilium
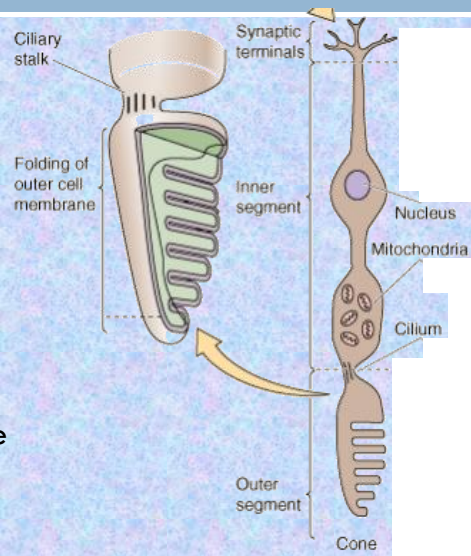
Outer segment

Cone

Photopigments contain same retinal, just different forms of opsin

Outer segments of cones consist of folded, stacked membrane containing other photopigments (opsins) but in lower concentration than rods therefore less sensitive to light.

As with rods, the inner segment synthesizes photopigments and inserts them into membrane of vesicles which move from inner to outer segment.

However, in cones the vesicles are inserted into membrane folds of outer segment

Phototransduction: Dark current

- Partially active <u>guanylyl cyclase</u> keeps cytoplasmic [cGMP] high in the dark
- Outer segment contains <u>cGMP-gated cation channels</u>
  - Influx of Na^+ and Ca^{2+}
- Inner segment contains <u>non-gated K^+ selective channels</u>
  - K^+ efflux
- Resting, or dark V_m is -40 mV
- concentration gradients maintained by Na^+/K^+ pump and NCX
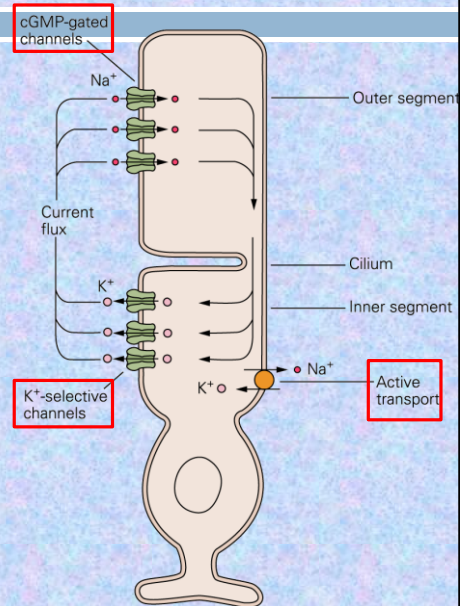
Guanylyl cyclase synthesizes cGMP from GTP

Outer segment membrane has cation channels which remain open in the dark whereas inner segment has K+ channels that are not regulated by light.

Na+ (90%) and Ca++(10%) enter through cation channels in outer segment and K+ leaves inner segment, <u>resulting in hyperpolarization </u>(resting membrane potential of rods is ~ – 40 mV) and <u>ionic current called dark current</u>.

Na-K pump removes Na+ from inner segment and Na-Ca exchanger removes Ca++ from outer segment to maintain concentration gradients.
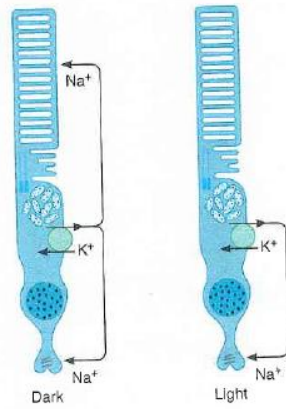
17

FIGURE 12–12 **Effect of light on current flow in visual receptors.** In the dark, Na$^+$ channels in the outer segment are held open by cGMP. Light leads to increased conversion of cGMP to 5'-GMP, and some of the channels close. This produces hyperpolarization of the synaptic terminal of the photoreceptor.

Phototransduction

Photoreceptors <u>hyperpolarize</u> in response to light and release <u>less</u> neurotransmitter

- In darkness, the V_m of -40 mV keeps CaV channels in the synaptic terminal **open**
    - photoreceptors continuously release neurotransmitter **glutamate**
- absorption of light by photopigment ⇓'s [cGMP]
    - cation channels close
    - K^+ efflux predominates, hyperpolarizes cell (-70mV)
    - CaV channels close, **decreased release** of glutamate

Depolarized state of membrane keeps voltage-gated Ca++ channels open in synaptic terminals, resulting in constant release of neurotransmitter (glutamate)

Phototransduction: mechanism

[20]

opsin   C

Disk interior

Cytosol

Retinal   Attachment site for retinal
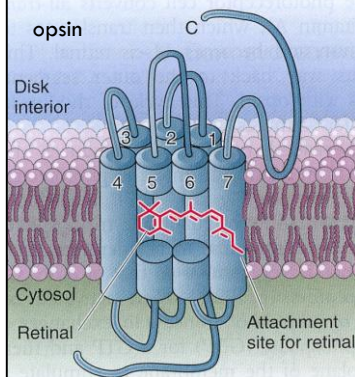
Photopigment rhodopsin is the light receptor in rods

- opsin
  - G-protein coupled membrane receptor
- Retinal= retinene1
  - Light absorbing compound
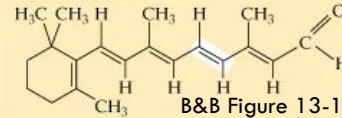 - the aldehyde form of retinol or Vitamin A

11-*cis* retinal

Light

All-*trans* retinal

B&B Figure 13-11

- retinal changes conformation from 11-cis to all-trans after absorbing a photon
- isomerization of retinal activates opsin
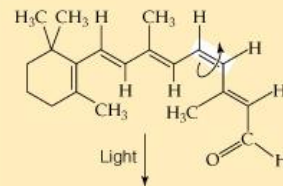
Aldehyde is r-c=o

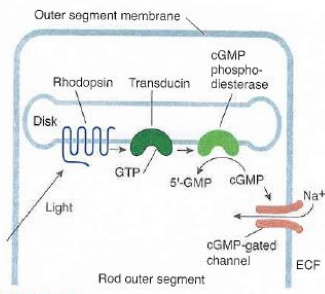Retinol contains only an C-OH

Trans form is more stable

FIGURE 12–14 Initial steps in phototransduction in rods. Light activates rhodopsin, which activates transducin to bind GTP. This activates phosphodiesterase, which catalyzes the conversion of cGMP to 5'-GMP. The resulting decrease in the cytoplasmic cGMP concentration causes cGMP-gated ion channels to close.

darkness. The amount of rhodopsin in the receptors therefore varies inversely with the incident light level.

CONE PIGMENTS

Primates have three different kinds of cones. These receptors subserve color vision and respond maximally to light at wave-
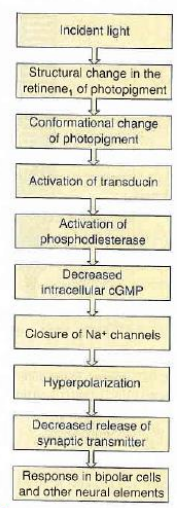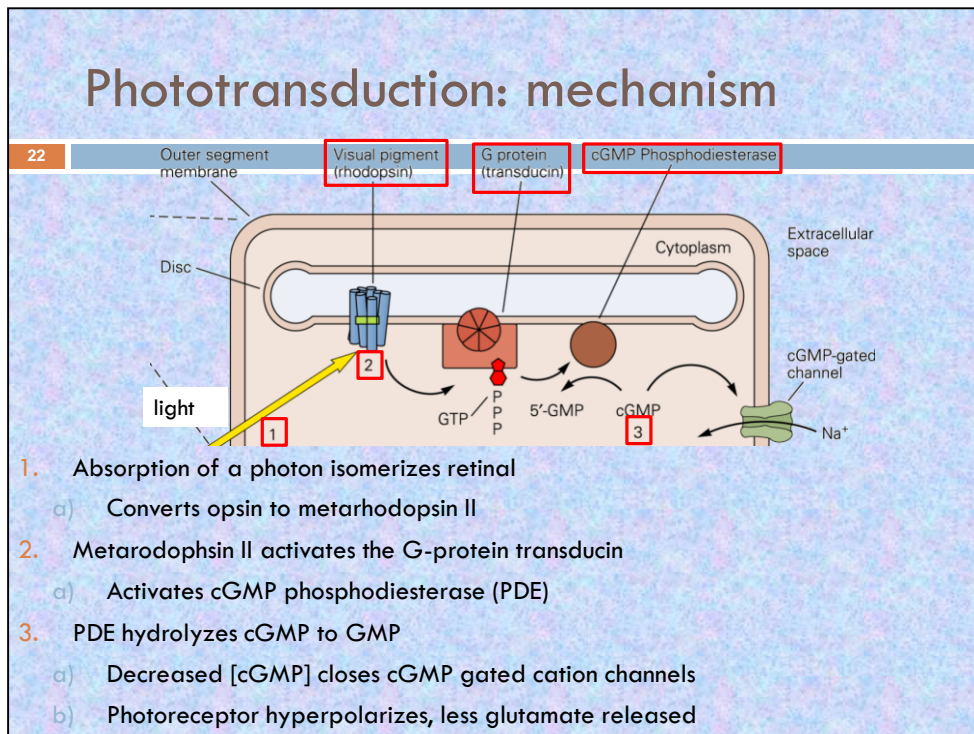

FIGURE 12–15 Sequence of events involved in phototransduction in rods and cones.

Phototransduction: mechanism

22 | Outer segment membrane | Visual pigment (rhodopsin) | G protein (transducin) | cGMP Phosphodiesterase

Disc — Cytoplasm — Extracellular space

light

GTP, P P P, 5'-GMP, cGMP, cGMP-gated channel, Na⁺

1. Absorption of a photon isomerizes retinal
   a) Converts opsin to metarhodopsin II
2. Metarodophsin II activates the G-protein transducin
   a) Activates cGMP phosphodiesterase (PDE)
3. PDE hydrolyzes cGMP to GMP
   a) Decreased [cGMP] closes cGMP gated cation channels
   b) Photoreceptor hyperpolarizes, less glutamate released

transducin exchanges GDP for GTP

activated transducin (G protein) → activates cGMP phosphodiesterase → hydrolyzes cGMP to GMP (5'-guanylate monophosphate)→ ↓ [cGMP]i → closes cGMP-gated cation channels → hyperpolarization → ↓ neurotransmitter release

all-trans retinal separates from opsin (bleaching)

converts to retinol

translocates to the pigment epithelium where it is converted back to *11-cis* retinal

returns to the outer segment and recombines with opsin

recycling process takes several minutes

Phototransduction: termination

- Activated rhodopsin is a target for phosphorylation by <u>rhodopsin kinase</u>
  - Phosphorylated rhodopsin inactivated by cytosolic protein <u>arrestin</u>
- All-trans retinal transported to the pigment epithelium where it is converted back to 11-cis retinal, and recycled back to the rod
- Activated transducin inactivates itself by hydrolyzing GTP to GDP

Ca++ entry through cation channels inhibits guanylyl cyclase, which synthesizes cGMP, and stimulates phosphodiesterase to regulate [cGMP]I

closure of cGMP-gated channels → ↓ [Ca++]i, reducing inhibition of guanylyl cyclase and inhibiting phosphodiesterase to increase [cGMP]i

Phototransduction: light adaptation

Eyes adapt to increased light intensity and remain sensitive to further changes in light

- Optic adaptation:
  - Constriction of pupils to allow in less light
- Photoreceptor adaptation:
  - The closure of cGMP gated channel reduces inward flux of Ca^{2+} → decreased $[Ca^{2+}]_i$
  - Ca^{2+} induced inhibition of guanylyl cyclase removed
    - More cGMP made → reopening of some cGMP gated channels → influx of cations → slight depolarization

Photoreceptor can once again be stimulated (hyperpolarized) by photons

Ca++ entry through cation channels inhibits guanylyl cyclase, which synthesizes cGMP, and stimulates phosphodiesterase to regulate [cGMP]I

closure of cGMP-gated channels → ↓ [Ca++]i, reducing inhibition of guanylyl cyclase and inhibiting phosphodiesterase to increase [cGMP]i

Colour Vision

25

- 3 types of cones, each contain photopigment with different absorption spectra
  - 420 nm – blue
  - 530 nm – green
  - 560 nm - red
- Colour interpreted by ratio of cone stimulation
  - Orange (580nm) light stimulates:
    - Blue cone – 0%
    - Green cone – 42%
    - Red cone – 99%
  - 0:42:99 ratio of cone stimulation interpreted by brain as orange
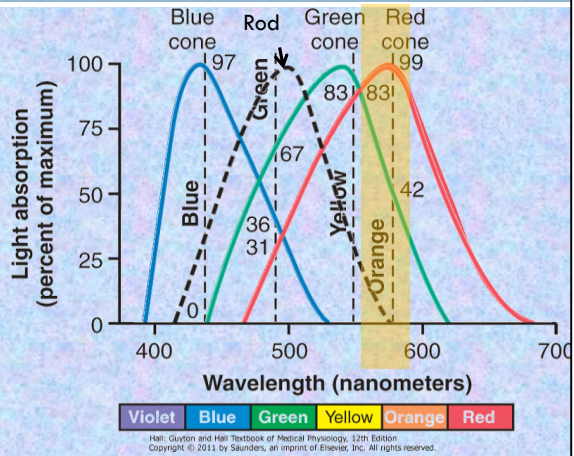
Guyton Figure 50-8

Cones actually respond to violet, yellow-green, and yellow-red but called blue green red by convention

Rod peak wavelength at 500nm

Red green colour blindness: red or green cones missing, therefore cannot distinguish red from green because the colour spectra overlap.

Colour Vision: Disorders

- □ Malfunction of one group of cones leads to colour blindness
- □ Most common form is red-green colour blindness
  - ▫ Either red or green cones are missing
  - ▫ Difficulty distinguishing red from green because the colour spectra overlap (ratio of cone stimulation is affected → impaired neural interpretation of colours)
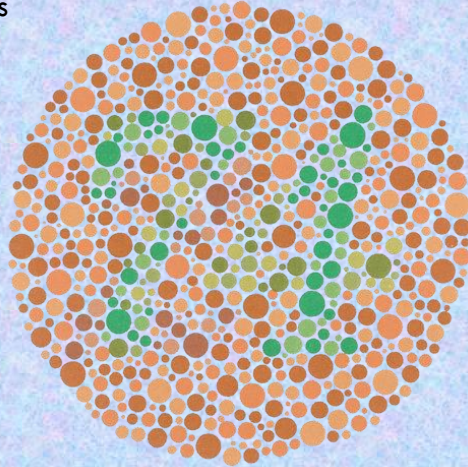
The spots are arranged so that a normal vision person sees a 74, whereas a red-green colour blind person sees a 21

Retinal circuitry: review of cell types

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- **rods and cones** synapse on <u>bipolar cells</u> and <u>horizontal cells</u>
- **horizontal cells** make lateral inhibitory synapses with surrounding <u>bipolar cells</u> or <u>photoreceptors</u>
- **bipolar cells** make synaptic connections with <u>ganglion cells</u> and <u>amacrine cells</u>
- **amacrine cells** transmit signals from <u>bipolar cells</u> to <u>ganglion cells</u> or to other <u>amacrine cells</u>
- **ganglion cells** transmit action potentials to the <u>brain</u> via the optic nerve
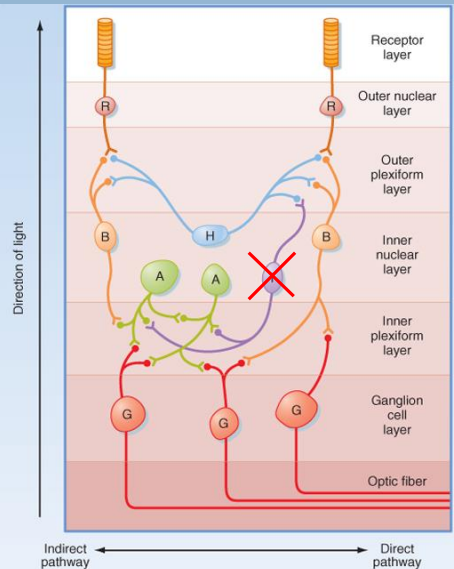
B&L Figure 8-7

Interplexiform cells: transmit signals in the retrograde manner from the inner plexiform layer to the outer plexiform layer. Signals are inhibitory and control lateral spread of visual signals by horizontal cells in the outer plexifrom layer. Role may be to help control the degree of contrast in the visual image.

Amacrine cells help analyze visual signals before they leave the retina.

There are two type of bipolar cells:
- "on type" have excitatory receptors
- "off-type" have inhibitory receptors

Amacrine cells:
- transform sustained bipolar cell output into transient responses of ganglion cells
- act as interneurons in pathway from rod bipolar cells to ganglion cells

Retinal circuitry: key features

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- 2 types of bipolar cells
    - On center: hyperpolarized by glutamate
    - Off center: depolarized by glutamate
- Bipolar and horizontal cells play a role in lateral inhibition
    - Important for increasing visual contrast
    - Set up "surround" arrangement of ganglion cell receptive fields
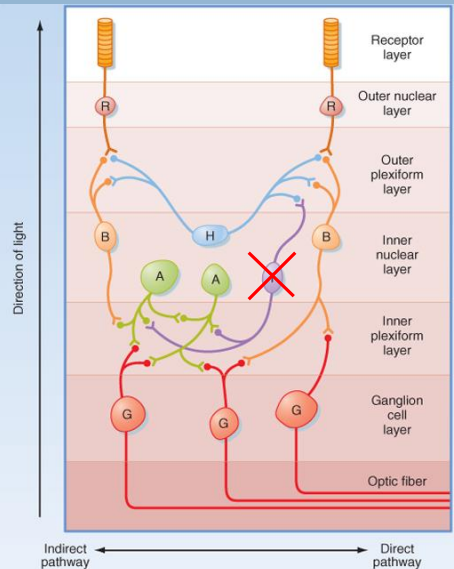
B&L Figure 8-7

Direct path:

Photoreceptor → bipolar cell → ganglion cell

Indirect path:

Photoreceptor → horizontal, amacrine, bipolar cells → ganglion cells

cones in center of ganglion cell receptive field influence ganglion cell activity by direct pathway

cones in surround of ganglion cell receptive field influence ganglion cell activity by indirect pathway

Receptive fields

- **Photoreceptor** receptive fields include retinal area that, when stimulated by light, results in hyperpolarization of individual photoreceptor
  - Small and circular
- **Ganglion cell** receptive field *size* determined by
  - ganglion cell type
  - degree of convergence of photoreceptors and bipolar cells

  and field *type* by retinal circuitry (lateral inhibition)
    - On-center/off-surround
    - Off-center/on-surround

> Where in the retina is there is there a high degree of convergence?

i.e., response in center of receptive field is opposite to response in surround, due to opposite effects of

direct and lateral pathways

depolarized by glutamate (opening of Na+ channels)

hyperpolarized by glutamate (opening of K+ channels or closing of Na+ channels)

Receptive fields

- <u>On-center/off-surround</u>
  - Light shines on center of ganglion cell receptive field → ganglion cell increases AP firing
  - Light on surround region → decreased AP firing
- <u>Off-center/on-surround</u>
  - Light on center → decreased AP firing
  - Light on surround → increased AP firing
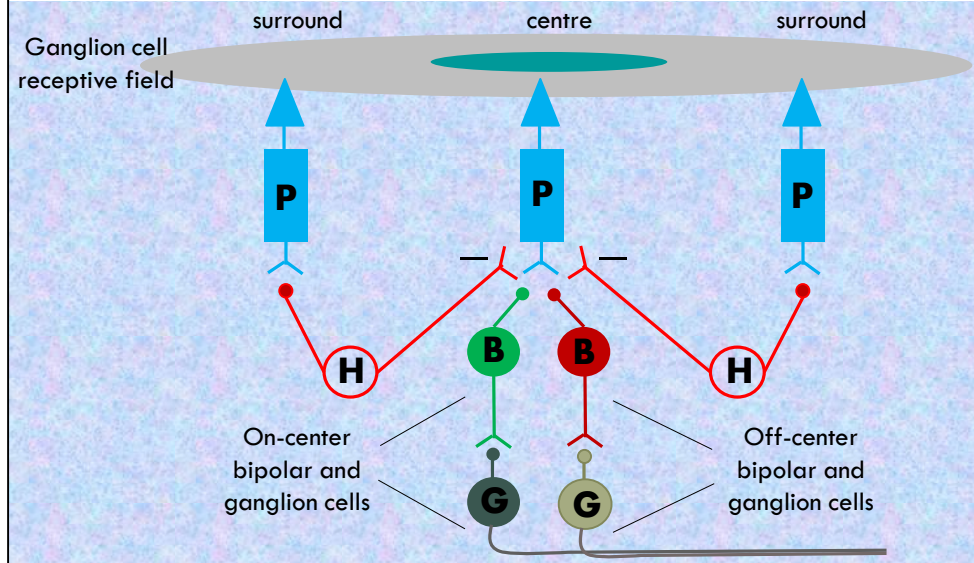
B&L Figure 8-8

Light

Central spot of light

Peripheral spot
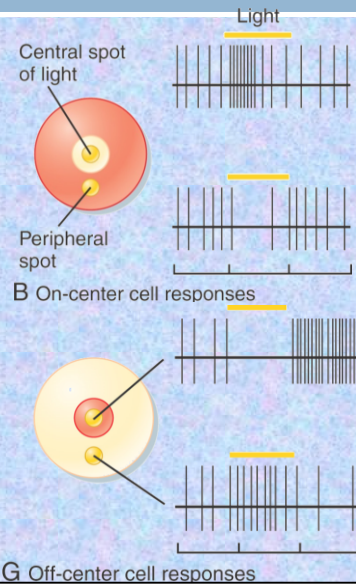
B On-center cell responses

G Off-center cell responses

Always have a tonic release of AP, but their frequency is mediated by center/surround receptive fields

Neural circuits of retinal receptive fields

On center bipolar cells hyperpolarized by glutamate

Off center bipolar cells depolarized by glutamate

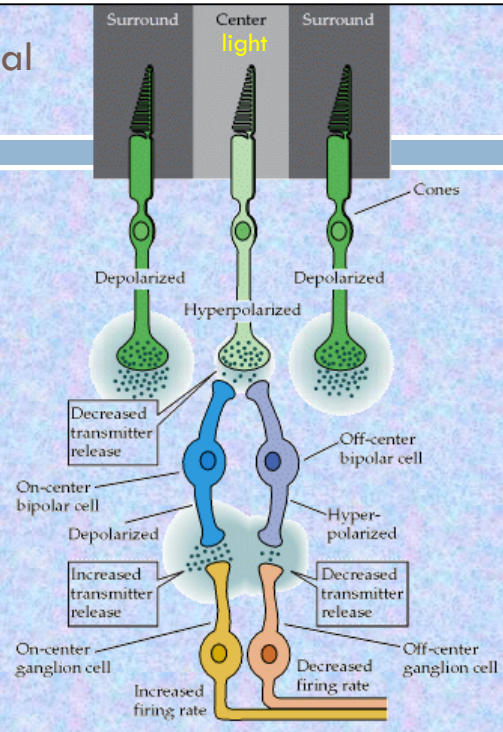Center photoreceptors always synapse onto bipolar cells of each type, on center and off center

Surround photoreceptors synapse on horizontal cells which mediate signals via lateral inhibitory connections

Neural Circuits of Retinal Receptive Fields

Light stimulus on center:

- ↓ glu release from central photoreceptor
  - ↓ inhibition of on-center bipolar cell → depolarization
    - ↑ NT release → <u>on-center ganglion cell excited</u>
  - less glu available to excite off-centre bipolar cell → hyperpolarization
    - ↓NT release→ <u>off-center ganglion cell inhibited</u>

Surround Center light Surround

Cones

Depolarized Hyperpolarized Depolarized

Decreased transmitter release

Off-center bipolar cell

On-center bipolar cell

Depolarized

Hyper-polarized

Increased transmitter release

Decreased transmitter release

On-center ganglion cell

Increased firing rate

Decreased firing rate

Off-center ganglion cell

On center bipolar cells hyperpolarized by glutamate

Neural Circuits of Retinal Receptive Fields

**Light stimulus on surround:**

- ↓ glu release from surround photoreceptor
  - ↓ excitation of horizontal cells → ↓ inhibitory NT released
    - ↓ inhibition of central photoreceptor → ↑ glu released
    - ↑ glu hyperpolarizes on-center bipolar cell and depolarizes off-center bipolar cell
    - <u>On-center ganglion cell inhibited</u>, <u>off-center ganglion cell excited</u>

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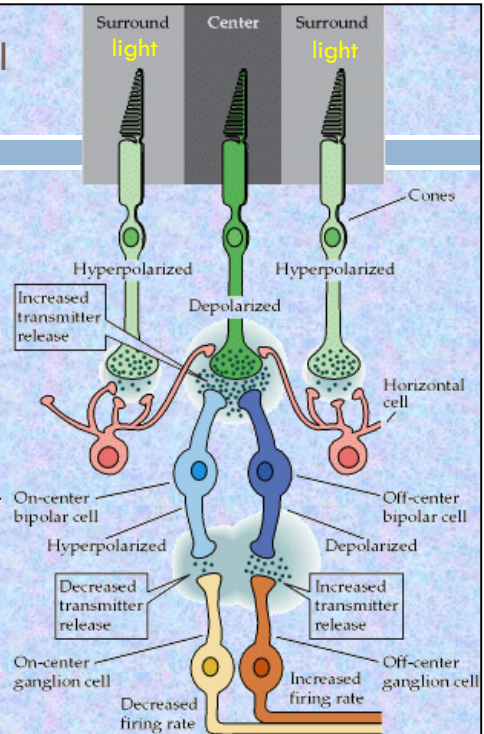
Retinal receptive fields: outcome

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- Surround arrangement and lateral inhibition allows ganglion cells to respond best to contrast borders in a visual scene
  - Ex. Reading dark letters against a white background
  - Respond only weakly to diffuse illumination

A On-center field

F Off-center field

E Diffuse illumination

J Diffuse illumination

B&L Figure 8-8
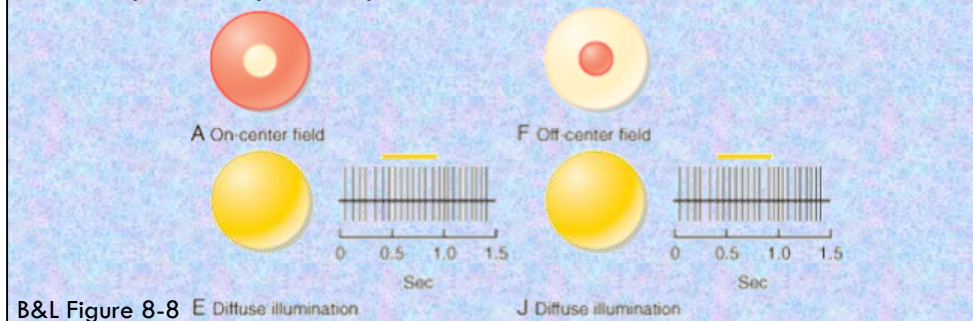
Light impinging on both center and surround of bipolar cell may result in cancellation of center and surround effects.

Responses of amacrine cells depend on pattern of convergence from on-center and off-center bipolar cells (response involves increase or decrease in firing rate).

Firing rate of ganglion cells is determined by input from bipolar and amacrine cells

•dominant input from amacrine cells can produce uniform or mixed responses across receptive field

•dominant input from bipolar cells produces center-surround responses

Ganglion cell types and projections

Lateral geniculate nucleus
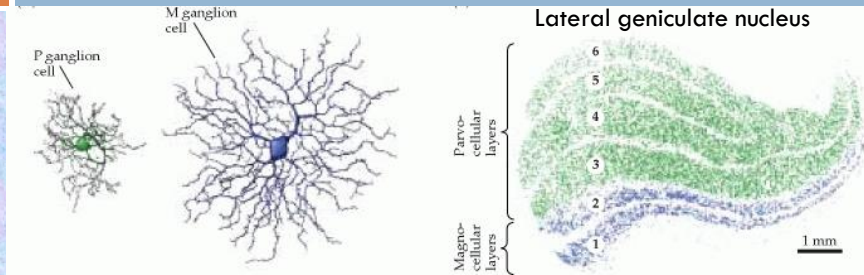
- **P cells**
  - Project to parvocellular layer of LGN
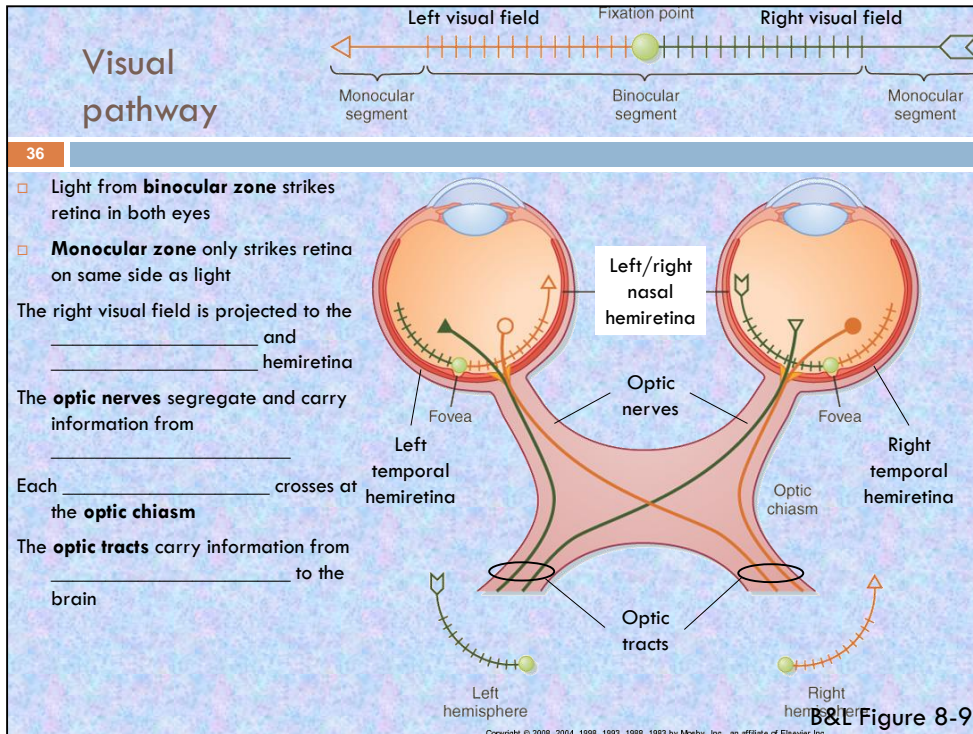 - Tonic firing, small surround receptive fields,
  - Important for colour detection, form and detail of visual image
- **M cells**
  - Project to magnocellular layer of LGN
  - Transient activity, large surround receptive fields
  - Convey information about illumination and movement
- **W cells**
  - Resemble M cells, large diffuse receptive fields
  - Function is less clear

Visual pathway

Left visual field — Fixation point — Right visual field

Monocular segment | Binocular segment | Monocular segment

- Light from **binocular zone** strikes retina in both eyes
- **Monocular zone** only strikes retina on same side as light

The right visual field is projected to the _____ and _____ hemiretina

The **optic nerves** segregate and carry information from _____

Each _____ crosses at the **optic chiasm**

The **optic tracts** carry information from _____ to the brain

Left/right nasal hemiretina

Optic nerves

Fovea

Left temporal hemiretina

Right temporal hemiretina

Optic chiasm

Optic tracts

Left hemisphere

Right hemisphere

B&L Figure 8-9

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Fibers from the nasal hemiretina of each eye cross to the opposite side at the optic chiasm, whereas fibers from the temporal hemiretina do not cross. In the illustration, light from the right half of the binocular zone falls on the left temporal hemiretina and right nasal hemiretina. Axons from these hemiretinas thus contain a complete representation of the right hemifield of vision (see Figure 27-6).
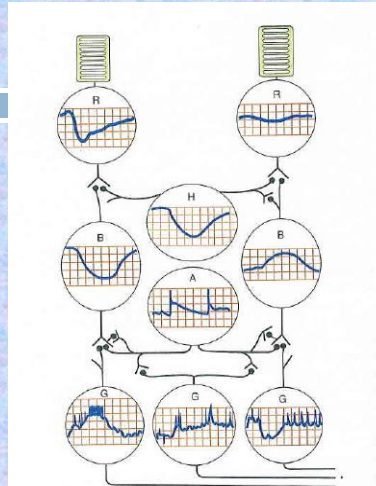
FIGURE 12–11 **Intracellularly recorded responses of cells in the retina to light.** The synaptic connections of the cells are also indicated. The eye is unique in that the receptor potentials of the photoreceptors and the electrical responses of most of the other neural elements in the retina are local, graded potentials. The rod (R) on the left is receiving a light flash, whereas the rod on the right is receiving steady, low-intensity illumination. The responses of rods and horizontal cells (H) are hyperpolarizing, responses of bipolar cells (B) are either hyperpolarizing or depolarizing, and amacrine (A) cells produce depolarizing potentials and spikes that may act as generator potentials for propagated spikes of ganglion cells (G). (Reproduced with permission from