

Sensory transmission from receptors to cerebral cortex: Special Senses

The Chemical Senses:

- The receptors for smell (olfaction) and taste (gustation) respond to chemicals in an aqueous solution (chemoreceptors)
- Smell receptors – respond to substances dissolved in fluids of the nasal membranes
- Taste receptors – respond to substances dissolved in saliva

Smell:

Olfactory organ

- The organ of smell is called the olfactory epithelium located in the roof of the nasal cavity

Olfactory epithelium

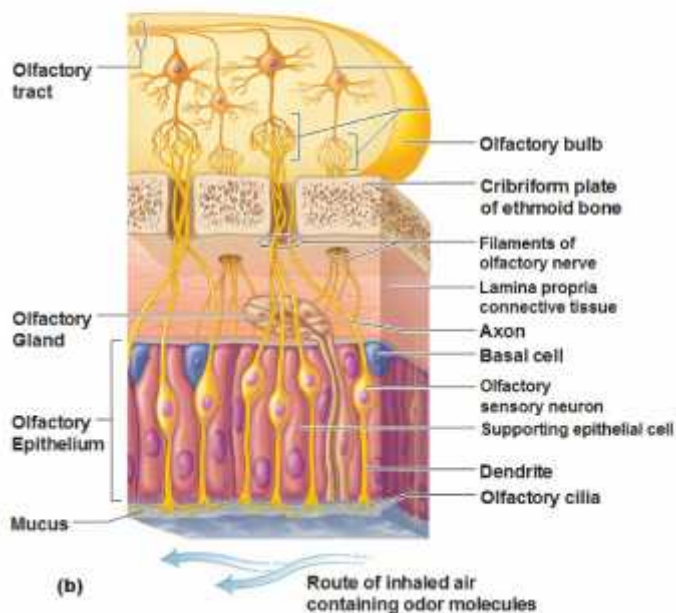
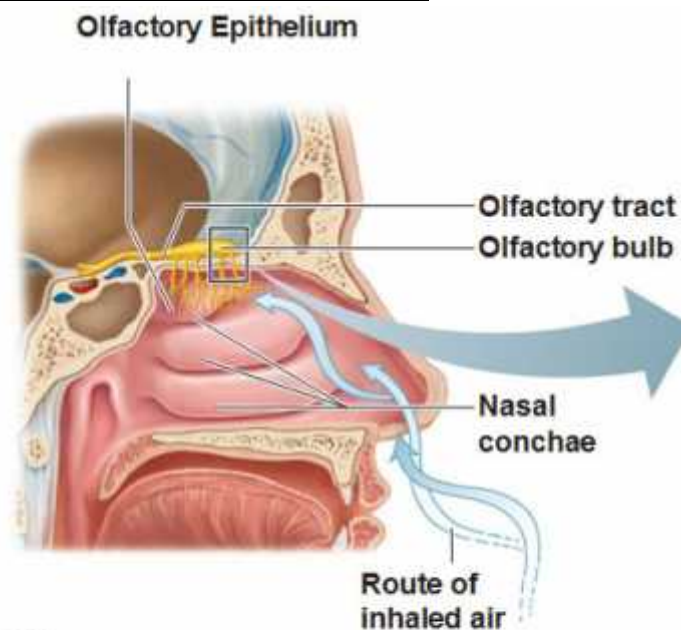
- The receptor area of the olfactory system is made of an epithelium which contains 3 kinds of cells:
 - (1) olfactory cells with olfactory cilia that detect odors
 - (2) supporting cells
 - (3) basal cells that regenerate the other cells (olfactory cells are among the few types of neurons that can be regenerated and it occurs about every 60 days)

Olfactory neurons

- One of the few types of neurons that undergo noticeable turnover throughout adult life
- Location puts them at risk for damage
- Typical life span is 30-60 days
- Olfactory stem cells in the olfactory epithelium differentiate to replace them

Specificity of olfactory receptors

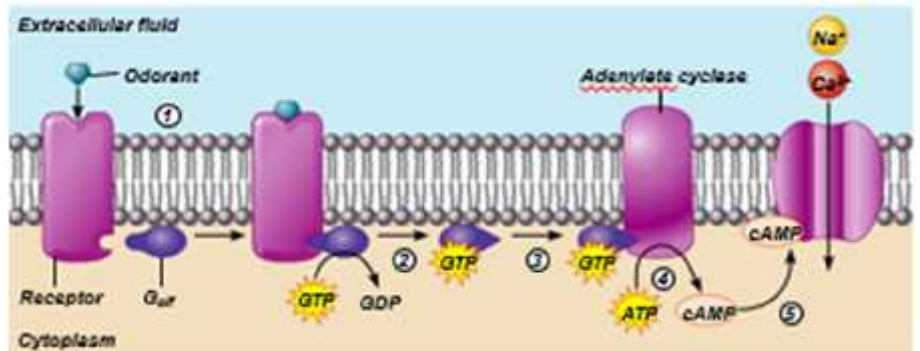
- Humans can distinguish 10,000 different odors
- There are 400 different olfactory receptor proteins which respond to odor-causing chemicals
 - Each protein responds to one or more odors and each odor binds to several receptor types



- Each receptor cell has only one type of receptor protein
- Olfactory neurons are very sensitive – just a few molecules are needed to activate them
- many olfactory receptors and their mechanisms of transduction are incompletely known
- the general mechanism: an odor molecule activates a metabotropic receptor which ultimately causes opening of a sodium channel (or closing of a potassium channel) to depolarize the cell
- Each cell would have 1 type of receptor specialized for detection of 1 type of odor and the information from each cell would be transmitted to the cortex

Smell Transduction

- G_{olf} indicates G protein first recognized in the olfactory system
- cAMP acts directly on cAMP gated ion channels that open to let Na^+ and Ca^{++} in and depolarize the receptor cell



- The influx of Na^+ produces a graded potential that leads to an action potential in the axon of the olfactory receptor neuron that travels to the olfactory bulb. The influx of Ca^{++} contributes to adaptation of this sensation.
- Recall from lecture 2: Receptors responding to pressure, touch, and smell adapt quickly (phasic)

Olfactory pathway

- Olfactory nerves synapse with the mitral cells (second order neurons) in complex structures called glomeruli
 - Axons from neurons bearing the same kind of receptor converge on a given type of glomerulus
 - Mitral cells activated, impulses flow from the olfactory bulbs via the olfactory tracts to the piriform lobe of the olfactory cortex
 - From there, two major pathways take information to various parts of the brain
- (1) Information goes to the frontal lobes just above the orbit, where smells are interpreted and identified
 - (2) Information flows to the hypothalamus, amygdala, other regions of the limbic system and the uncus -emotional responses to odors
 - *Cerebral activations with two odorants. Main clusters are seen bilaterally in the amygdala and neighboring cortex as well as in the right insula.*



Taste:

The physiology of taste

- In order to be tasted, a chemical:
 - must be dissolved in saliva
 - must contact gustatory hairs

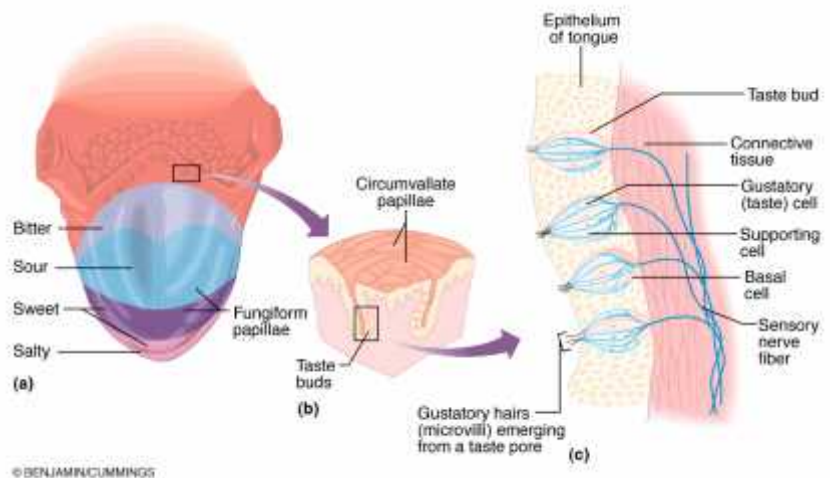
Taste organ

- 10000 or so taste buds (sensory organs for taste) are located mostly in papillae on the surface of the tongue
- Each taste bud is composed of >50 epithelial cells consisting of two types: gustatory epithelial cells (sensory taste cells) and basal epithelial cells (stem cells)
- The surface of the tongue has structures called papillae which gives it a rough texture. There are 2 kinds of papillae:

- (1) fungiform papillae which is on the soft palate, internal cheeks, pharynx, epiglottis, and predominantly on the end and sides of the tongue where there are 10000 of them
- (2) circumvallate papillae which forms a series of 7-12 towards the back of the tongue. The papillae contain taste buds each consisting of 40-60 epithelial cells forming a taste pore
 - There are 3 types of epithelial cells:

- (1) supporting cells
 - (2) gustatory cell which is the chemoreceptor containing microvilli which adapts to stimuli in 1-5 minutes (they do not produce an action potential)
 - (3) basal cells which renew the supporting and gustatory cells every 7-10 days
- The receptors for the different fundamental flavors are partially mixed on the tongue but we can generally say that as we move from the tip to the back of the tongue there is a change in the chemical sensitivity from salty, to sweet, to sour (acid), and to bitter flavors

- By drinking wine we perceive some flavors from the receptors on the tip of the tongue but then there is a bitter after taste because the wine flows slowly towards the back of the tongue and stimulates the receptors for bitter flavors
- Umami is a meaty flavor triggered by glutamate as in monosodium-glutamate (MSG) and its receptors are distributed all over the tongue



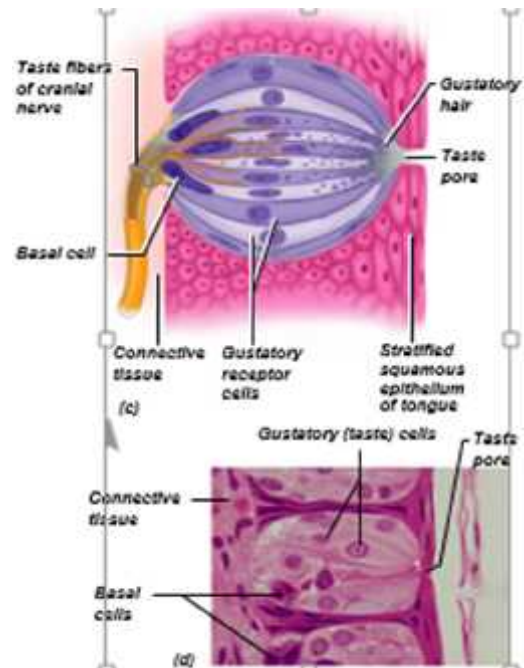
Epithelial cells

- Gustatory epithelial cells are the *receptor cells for taste* and are replaced every 7 days

- Gustatory hairs (receptor membranes) project from the tips of all gustatory epithelial cells and extend through a taste pore bathed in saliva
- Three types of gustatory epithelial cells
 - (1) Forms traditional synapses with sensory dendrites and releases serotonin
 - (2) And (3) Lack synaptic vesicles but one releases ATP as a neurotransmitter

Taste Sensations

- There are five basic taste modalities
- Sweet – sugars, saccharin, alcohol, some amino acids
- Salt – metal ions (sodium chloride)
- Sour – produced by acids (hydrogen ions)
- Bitter – alkaloids such as quinine and nicotine
- Umami – elicited by the amino acids glutamate and aspartate – savoriness of meats, cheese and other protein-heavy foods
- Contrast this to the 1000 basic smell sensations



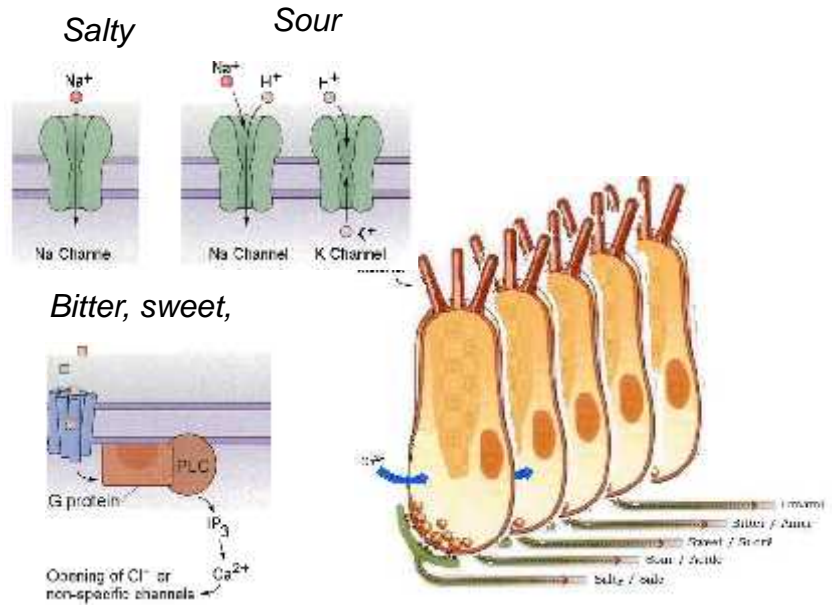
Taste Transduction

- Food chemicals bind – causes neurotransmitter release – produces generator potential in sensory dendrites
- The stimulus energy of taste is converted into a nerve impulse depending on modality:
 - Salty - Na^+ influx through sodium channels directly depolarizes gustatory epithelial cells
 - Sour - H^+ directly enters the cell and allows cation channels to open
 - Bitter, sweet and umami – Coupled to a metabotropic (G protein coupled receptor) called gustducin

Taste Receptors

- 5 types of gustatory cells
- Each cell type has receptors specific for the stimulus to which it responds
- mechanisms of transduction are as follows

- salty flavors, sodium in food crosses a sodium channel to produce depolarization, calcium entry and release of neurotransmitter
- sour flavors, hydrogen ions in food can enter by a type of sodium channel (the degree of permeability to sodium is too low in the absence of hydrogen ions to generate a depolarization) producing a depolarization, calcium entry and the release of neurotransmitter
- sweet, bitter and umami flavors, molecules bind to the receptor which activates a G protein that stimulates the increase in IP₃ which then causes the release of intracellular Ca stores to trigger neurotransmitter release



Taste Pathway

- Afferent fibers are found primarily in two cranial nerve pairs
 1. Facial nerve (VII) – carries information from the anterior 2/3 of the tongue
 2. Glossopharyngeal nerve (IX) – carries information from the posterior 1/3
- Also impulses from the epiglottis and lower pharynx are conducted primarily by the vagus nerve (X)
- All of these cranial nerves project to the solitary nucleus in the medulla
- Projections from the solitary nucleus cross the midline, innervate the thalamus and then thalamic neurons project to the gustatory cortex in the insula
- Also projections to hypothalamus and limbic system for appreciation of taste
- Substances in solution stimulate the chemoreceptors of gustatory cells which then release neurotransmitters to activate neurons of the facial (VII), glossopharyngeal (IX), or vagus (X) nerves
- These cranial nerves project to the solitary nucleus in the medulla
- The neurons of the solitary nucleus project to the thalamus which then projects to the insular cortex for perception of taste

Influence of Other Sensations on Taste

- Taste as it is interpreted in the gustatory cortex is 80% smell
- Thermoreceptors, mechanoreceptors, nociceptors also influence tastes
- Temperature and texture of food enhances or detracts from taste

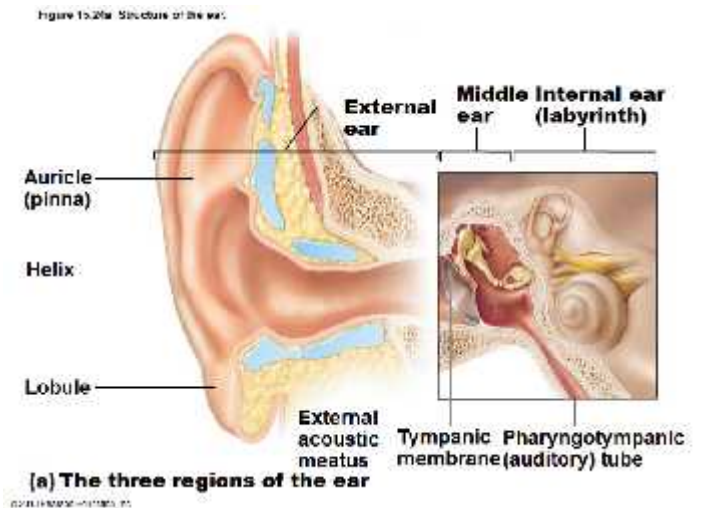
Penguins Cannot Taste Fish Meat

- A new study published in the journal Current Biology reveals that although the Arctic waters are teeming with plenty of fish, the penguins' taste palettes are "comparatively crippled." The team of scientists from the University of Michigan in Ann Arbor, Michigan, stated that penguins are missing three of the five taste buds.
- These flightless birds lack the capacity to taste anything that is sweet or bitter or umami. They lack the umami receptor genes that are responsible for allowing animals to taste meat. The study reveals that every species of penguin lack this ability to discern certain flavors.

Hearing:

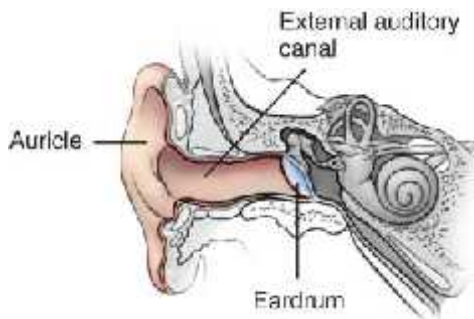
Structure of ear

- structures for hearing and balance are together
- ear includes 3 parts:
 - (1) outer ear
 - (2) middle ear
 - (3) inner ear also named the labyrinth
- outer ear starts at the pinna (the helix forms the thicker cartilaginous edge and the lobule forms the soft part without cartilage), passes along the external auditory canal and ends at the tympanic membrane (it is thin and translucent formed of fibrous conjunctive tissue)
- external auditory canal contains glands that secrete cerumen, a brownish-yellow wax that repels insects
- middle ear forms the tympanic cavity which contains ossicles (malleus, incus, and stapes) for transmitting movements of the tympanic membrane to the oval window
- tympanic cavity open into the pharyngotympanic tube that leads to the nasopharynx
- inner ear contains the sensory receptors



Structure of the external ear

- The external (outer) ear collects sound waves and passes them inwards

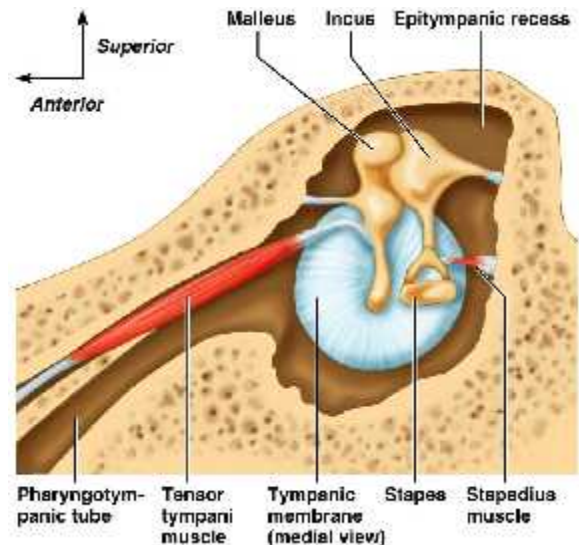


- Consists of:
 - **Auricle (pinna)** – the shell shaped projection of cartilage covered with skin, functions to funnel sound waves
 - **External acoustic meatus (auditory canal)** – short curved tube that extends from the auricle to the ear drum
 - **Tympanic membrane (ear drum)** – boundary between outer and middle ear – connective tissue covered by skin on the external side and mucosa internally

- The auricles of many animals are large and can be oriented in different directions
- Entire canal is lined with modified sweat glands which secrete cerumen (earwax) – a sticky trap for foreign bodies, also repels insects
- Sound waves make the eardrum vibrate – transfers sound energy to the tiny bones of the middle ear to set them vibrating

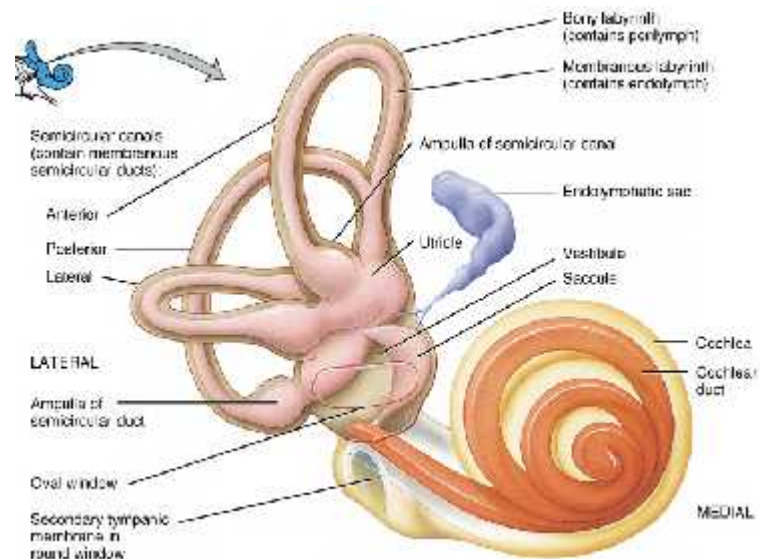
Structure of the middle ear (tympanic cavity)

- Small, air filled, mucosa-lined cavity
- Contains 3 small bones (auditory ossicles) – malleus, incus, stapes
- Two tiny skeletal muscles are associated with the ossicles
 - tensor tympani
 - stapedius
- Oval and round windows are covered connections to the inner ear
- Loud sounds are dampened by these muscles to reduce damage



Structure of the inner ear (labyrinth)

- Internal ear has two major divisions
 - **bony labyrinth** – twisting channels worming through the bone, perilymph
 - **membranous labyrinth** – series of membranous sacs and ducts contained within the bony labyrinth, endolymph
- is in the temporal bone and is formed of an bony labyrinth covered with endostium
- The cochlea, vestibule, and semicircular canals are different parts of this bony labyrinth
- The bony labyrinth itself contains a membranous labyrinth
- The cochlear duct is the membranous labyrinth in the cochlea which transduces sound
- the utricle and saccule are the membranous labyrinth in the vestibule which transduce head posture
- the semicircular ducts are the membranous labyrinth in the semicircular canals which transduce head movement



Structures of the bony labyrinth – vestibule:

- Central egg shaped cavity
- Suspended in its perilymph are two sacs
 - **saccul**e and the **utricle** – house equilibrium receptors called maculae and respond to gravity and changes in position of the head

Structures of the bony labyrinth – semicircular canals:

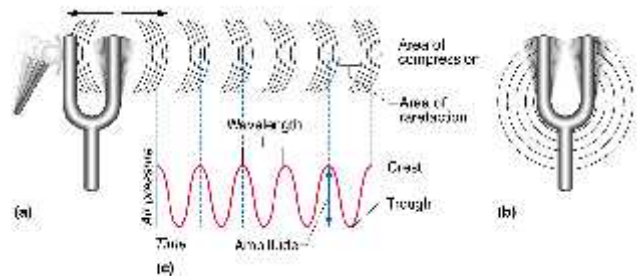
- Each define two-thirds of a circle and lie in 3 planes of space
- Membranous semicircular ducts line each canal
- Each of these ducts has an enlarged swelling at one end called an ampulla – houses an equilibrium receptor region called crista ampullaris – these receptors respond to rotational of the head

Structures of the bony labyrinth – cochlea:

- A spiral, conical, bony chamber that coils around a bony pillar called the modiolus
- It contains the cochlear duct and the spiral organ – the receptor organ of hearing
- Cochlea is divided into three chambers
 - **Scala vestibuli** – filled with perilymph
 - **Scala media** – filled with endolymph
 - **Scala tympani** – filled with perilymph

Properties of sound

- Sound is:
 - caused by changes in air pressure
 - A pressure disturbance (alternating areas of high and low pressure) originating from a vibrating object
 - Composed of areas of rarefaction (low pressure) and compression (high pressure)
 - Represented by a sine wave showing wavelength, frequency, and amplitude



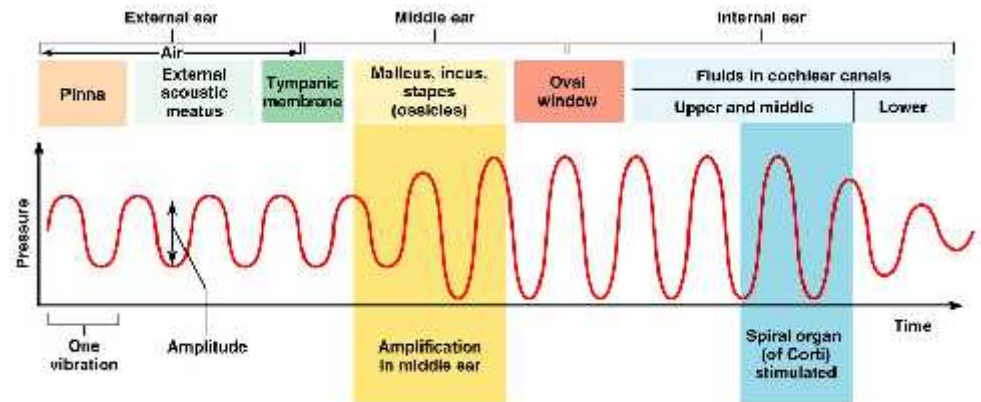
Frequency and Amplitude:

- Frequency – number of waves that pass a given point in a given time
 - Frequency range of human hearing is from 20-20,000 Hz (waves per second)
- Amplitude – height of the sound wave reveals the sound's intensity
 - Measured in decibels (dB)
- large amplitude wave corresponds to a loud sound of high intensity while a small amplitude wave corresponds to a soft sound of low intensity
- intensity is measured in decibels (0 dB = threshold of hearing, 50 dB = normal conversation, 90 dB = rock concert, 130 dB = pain)
- short duration wave corresponds to a high frequency sound (high pitch) while a long duration wave corresponds to a low frequency sound (low pitch).

Transmission of sound to the inner ear:

- Sound vibrations entering the external acoustic meatus beat against the eardrum (tympanic membrane) and set it vibrating
- Movements of this membrane are transmitted to the malleus, incus, and stapes which strikes the oval window
- Movement of this elastic window induces waves in the perilymph that can propagate through the scala vestibuli, around the helicotrema, and thence the scala tympani ending on the round window where the energy of the waves are absorbed by bulging of its membrane
- These waves induce oscillations of the cochlear duct and its sensory structure called the spiral organ of Corti which is specialized to detect sound waves

- The basilar membrane extends from the base of the cochlear membrane (near the tympanic cavity) to the apex or helicotrema. The highest frequency sounds vibrate the base of the basilar membrane while lowest frequency

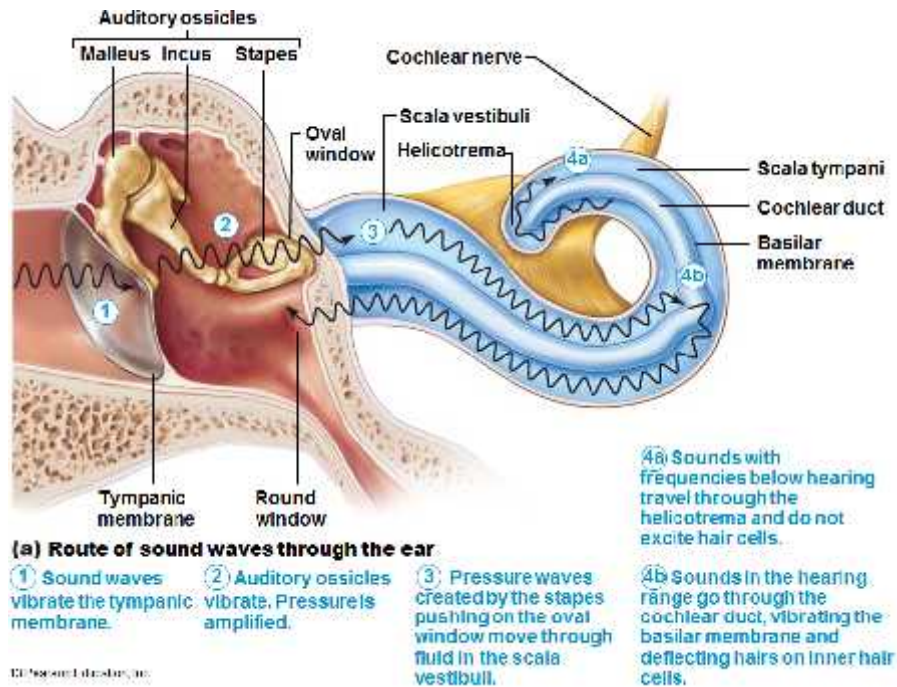


sounds vibrate its apex. Therefore, dendritic branches of the cochlear nerve at the base of the basilar membrane will transmit information from high frequency waves while dendritic branches at the apex will transmit information from low frequency waves

- The stronger the sound the greater will be the amplitude of the basilar membrane vibrations and consequently the greater the number of sensory hair cells and cochlear nerve fibers that will be stimulated-leads to the perception of a higher intensity sound
- muscles on the first and last ossicle (malleous and stapes) which are recruited 40 ms after the beginning of a strong sound to reduce the amplitude of the waves

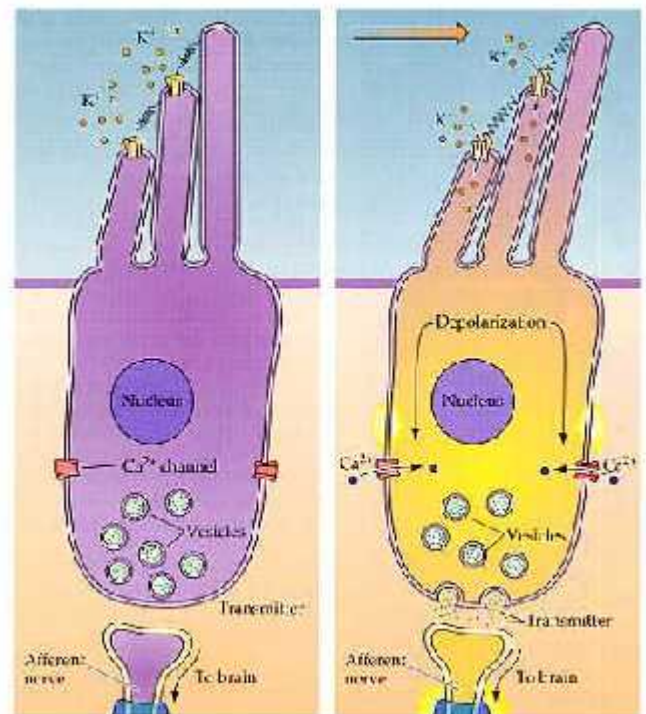
Resonance of the basilar membrane

- Stapes vibrates against oval window – sets the perilymph in the scala vestibuli into a similar motion
- Pressure wave travels through the perilymph from the basal end toward the helicotrema
- Sound waves of low frequency (inaudible):
 - Travel around the helicotrema
 - Do not excite hair cells
- Sounds with high frequency (audible):
 - are transmitted through the cochlear duct
 - vibrates the basilar membrane
- Different areas of the basilar membrane are tuned to particular frequencies



Excitation of the spiral organ:

- The spiral organ rests on top of the basilar membrane
- Composed of supporting cells and outer and inner hair cells
- Afferent fibers of the cochlear nerve (a division of CN VIII) attach to the base of the hair cells
- The hair cells have:
 - numerous stereocilia (long microvilli)
 - Single kinocilium (true cilium)
 - Are linked together by tip links
- Movement of the basilar membrane causes:
 - Bending of the cilia of inner hair cells puts tension on the tip links
 - This opens mechanically gated ion channels (K⁺)
 - Causes a graded depolarization
 - Causes release of a neurotransmitter (glutamate)
- Movement of the stereocilia cause depolarization of the inner hair cells
- Bending of the stereocilia in one direction leads to opening of potassium channels and depolarization while bending in the opposite direction leads to closing of these channels and repolarization (n.b. sensory hair cells are bathed in endolymph which is higher in

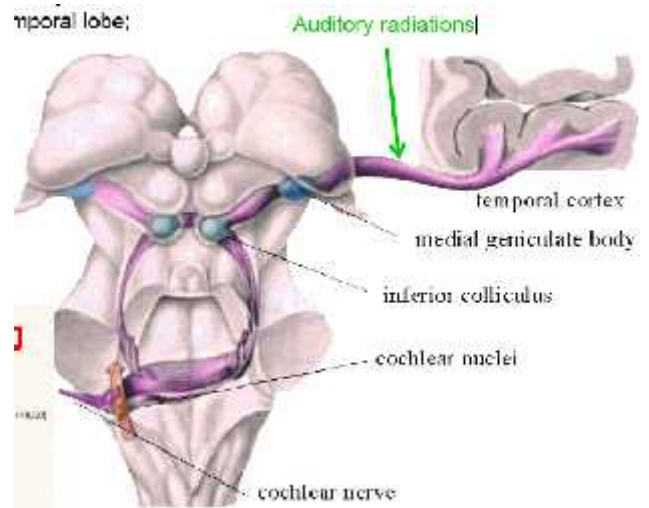
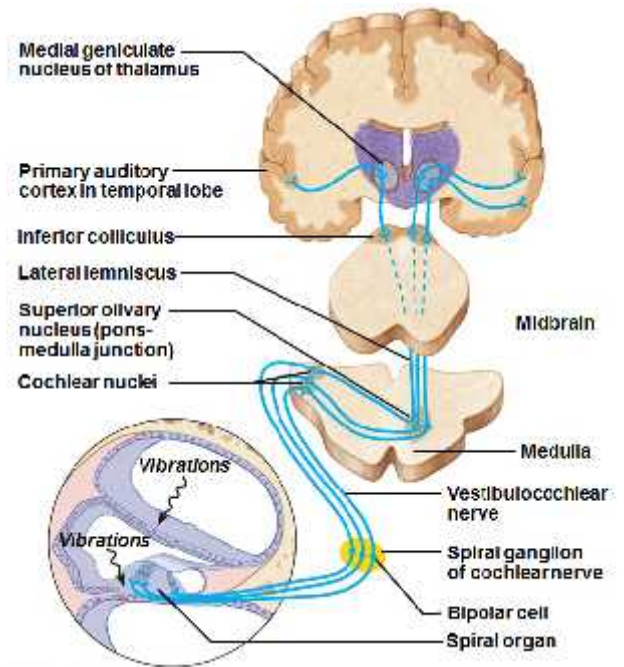


potassium than the intracellular fluid of these cells thus opening of potassium channels lead to depolarization)

- Depolarization of hair cells causes neurotransmitter release which excites dendrites of the cochlear nerve (n.b. part of the VIII cranial nerve also called vestibulocochlear nerve)
- The neurotransmitter causes cochlear fibers to transmit impulses to the brain, where sound is perceived
- Outer hair cells:
 - Contract and stretch due to messages received from the brain via the cochlear nerve
 - Increases responsiveness of the inner hair cells
 - May help protect inner hair cells from damage

The auditory pathway to the brain:

- Impulses from the cochlea pass through the spiral ganglion (auditory cell bodies are here)
- From here information is sent to:
 - Superior olivary nucleus
 - Axons ascend in the lateral lemniscus
 - Goes to the inferior colliculus (auditory reflex center)
 - Impulses then project to the medial geniculate nucleus of the thalamus
 - Thalamic axons then project to the primary auditory cortex
- Auditory pathways decussate so that both cortices receive input from both ears
- Fibers of the cochlear nerve join the vestibulocochlear nerve and then branch off to reach neurons of the cochlear nucleus
- These relay information to the contralateral superior olive which relays in the inferior colliculus and the thalamus which then relays to the auditory cortex in the temporal lobe
- There are 2 kinds of deafness:
 - a problem with the mechanical transmission of sound waves produces conduction deafness
 - a problem with the transmission of electrical activity produces sensorineural deafness (n.b. loud sounds destroy sensory hair cells)
- If a patient can only hear the sound from a tuning fork placed on the temporal bone (vibrations of the tuning fork are transmitted to the hair cells) then one can conclude that there is conduction deafness and not sensorineural deafness



Pitch, Loudness and Localization:

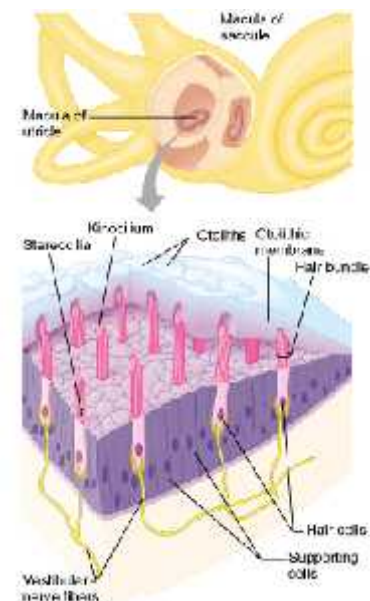
- Pitch is perceived by the primary auditory cortex
- Loudness is perceived by varying thresholds of cochlear cells and the number of cells stimulated
- Localization is perceived by the superior olivary nuclei that determine relative sound volume in the two ears
- temporal cortex has a tonotopic organization where there is an orderly numerical organization of sound frequencies reaching neighboring areas
- Low frequencies are anterior in primary auditory cortex of the temporal lobe
- Sound is localized by
 - (1) the temporal difference between the arrival of sound in the two ears
 - (2) the difference in intensity of sound which enters each ear

Equilibrium and orientation:

- Depends on head movements, inputs from internal ear, vision and info from stretch receptors of muscles and tendons
- Equilibrium receptors are in the semicircular canals and vestibule – collectively called the vestibular apparatus
- Receptors can be divided into two functional arms
 - Vestibule – monitors linear acceleration and the position of the head with respect to gravity (static equilibrium)
 - Semicircular canals – monitor changes in head rotation (dynamic equilibrium)

Anatomy of the Maculae:

- Maculae (flat epithelial patches) are the sensory receptors for static equilibrium
 - Contain supporting cells and hair cells
 - Each hair cell has stereocilia and kinocilium embedded in the otolithic membrane
- Otolithic membrane – jellylike mass studded with tiny CaCO_3 stones called otoliths
- Utricular hairs respond to horizontal movement
- Saccular hairs respond to vertical movement
- macula contains an epithelial membrane, containing supporting and sensory hair cells, onto which rests the otolithic membrane
- otolithic membrane contains crystals called otoliths whose weight on the otolithic membrane causes displacements of the stereocilia and kinocilium according to the orientation of the head



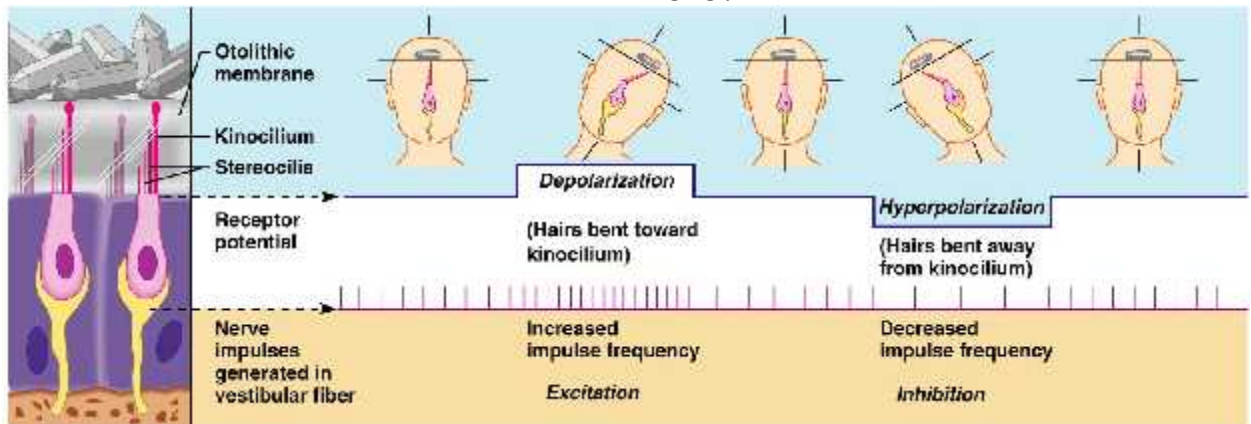
Activating macula receptors

- Hair cells synapse with fibers of the vestibular nerve
- Cell bodies of this nerve are located in the superior and inferior vestibular ganglia

- force of gravity is the stimulus; transduces the stimulus into neuronal impulses
- Bending of the stereocilia towards the kinocilium produces depolarization
- The position information provided by the macula is of the head since this structure is fixed to the head
- Tilting the head towards the kinocilia will cause depolarization of the sensory receptors
- depolarization of these sensory hair cells causes the release of neurotransmitter on the vestibular fibers of the vestibulocochlear nerve which branches off to the vestibular nuclei

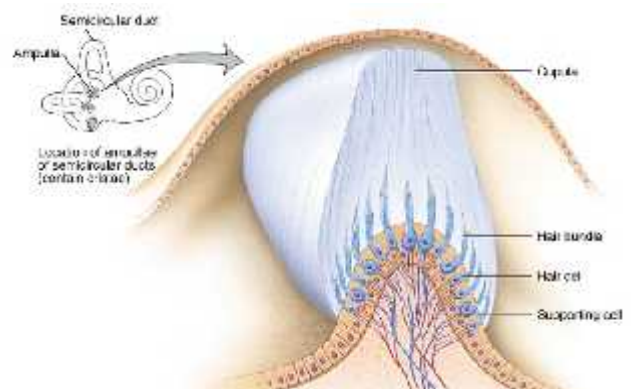
Effect of gravity on utricular receptor cells

- Otolithic movement in the direction of the kinocilia:
- Depolarizes vestibular nerve fibers
- Increases the number of action potentials generated
- Movement in the opposite direction:
- Hyperpolarizes vestibular nerve fibers
- Reduces the rate of impulse propagation
- From this information, the brain is informed of the changing position of the head



Crista ampullaris:

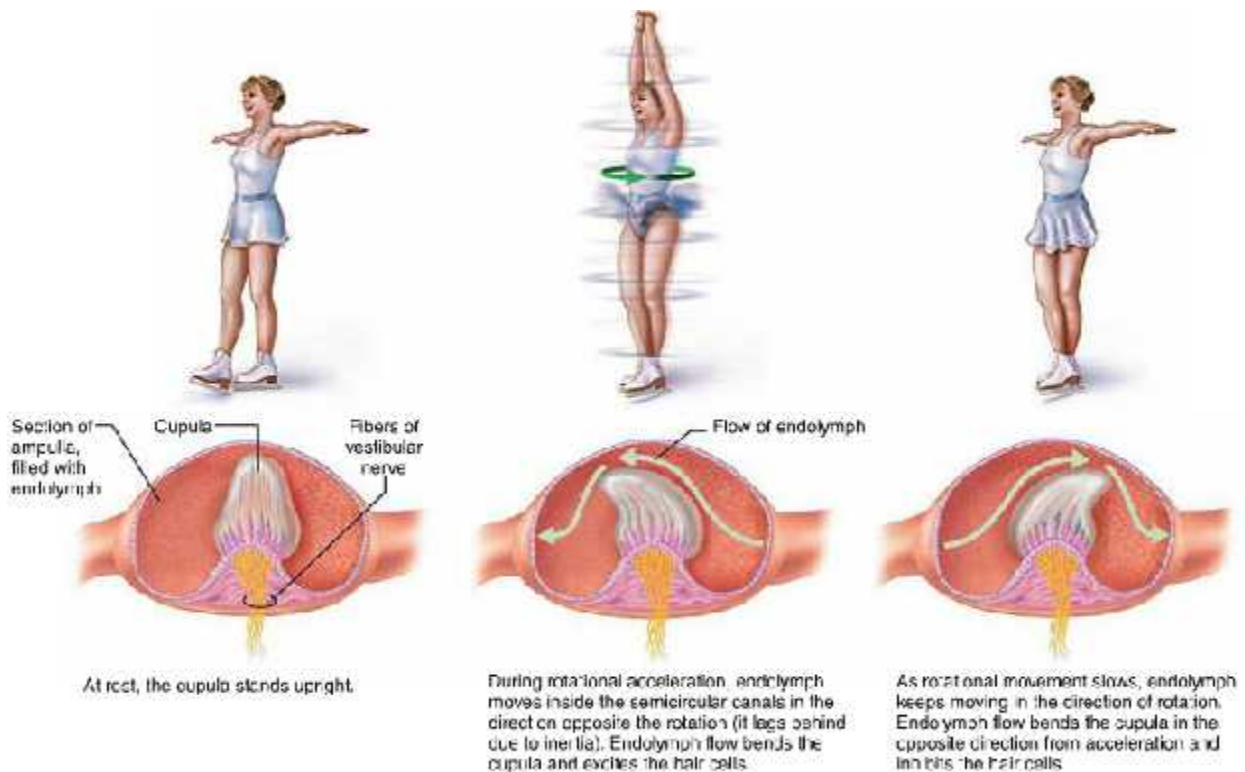
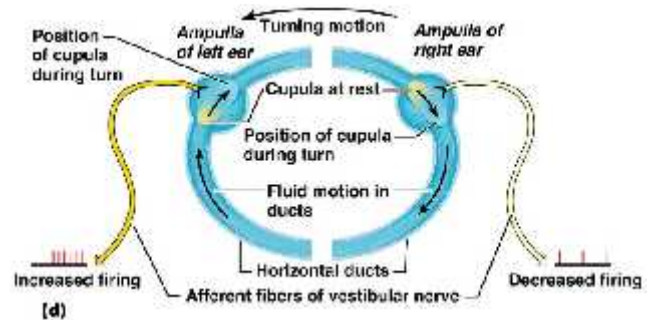
- The crista ampullaris (or crista):
 - Is the receptor for dynamic equilibrium
 - Is located in the ampulla of each semicircular canal
 - Responds to rotational (angular) movements
- 3 semicircular canals each directed to detect movement of the head in one of the 3 spatial dimensions.
- Each crista has support cells and hair cells that extend into a gel-like mass called the cupula
- Dendrites (actually sensory nerve endings) of vestibular nerve fibers encircle the base of the hair cells
- transduces acceleration of the head into neuronal impulses



- Each contains an epithelial membrane, formed of supporting and sensory hair cells, on which lies the cupula (a gelatinous mass)

Activating crista ampullaris receptors

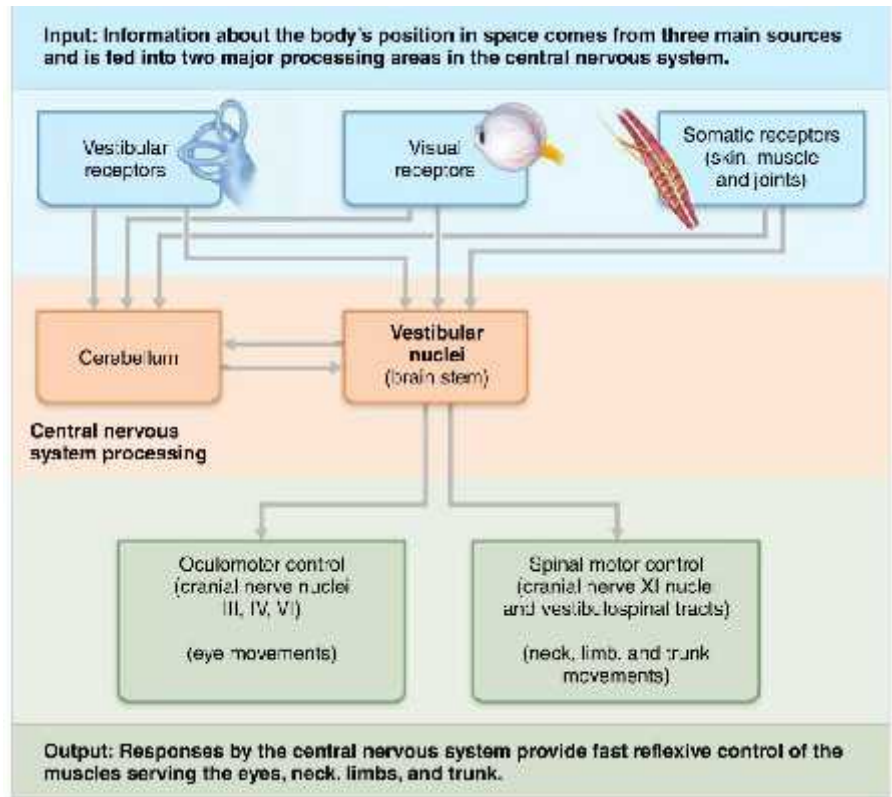
- Cristae respond to changes in velocity of rotatory movements of the head
- Directional bending of hair cells in the cristae causes:
 - Depolarization - rapid impulses reach the brain at a faster rate
 - Hyperpolarization - fewer impulses reach the brain
- Movement of the head causes movement of the crista ampullaris through the endolymph in the semicircular ducts
- cupula bends under the force of movement through the endolymph in the semicircular ducts which causes bending of the stereocilia and kinocilia and evokes depolarization and transmitter release onto vestibular fibers of the vestibulocochlear nerve



Balance and Orientation Pathways:

- There are three modes of input for balance and orientation
 - Vestibular receptors
 - Visual receptors
 - Somatic receptors

- These receptors allow our body to respond reflexively
- Fibers of the vestibular nerve join the vestibulocochlear nerve which then branch off to synapse onto cells of the lateral and superior vestibular nuclei
- latter has some projections to the brainstem to participate in reflexes (e.g. eye movements) and other bilateral projections to the ventral posterior thalamus which thence projects to the vestibular cortex in the parietal lobe



Hearing and balance summary:

- Mechanical transduction of stimuli into electrical activity by the spiral organ, the maculae, and the crista ampullaris are similar:
 - membrane with specialized supporting cells
 - sensory hair cells which are depolarized by displacement of the cilia
 - release of neurotransmitter onto the neurofibers
- The differences relate to the structure of the specialized membrane:
 - Spiral organ - tectorial membrane
 - Maculae - otolithic membrane
 - Crista ampullaris - cupula

Vision:

The eye and vision

- Vision is our dominant sense
- 70% of all sensory receptors in the body are in the eyes
- Eye has a diameter of about 2.5 cm but only the anterior 1/6 is visible
- Rest of eye is protected by the walls of the bony orbit

Accessory structures

Eye brows:

- Short coarse hairs that grow over the supraorbital margins

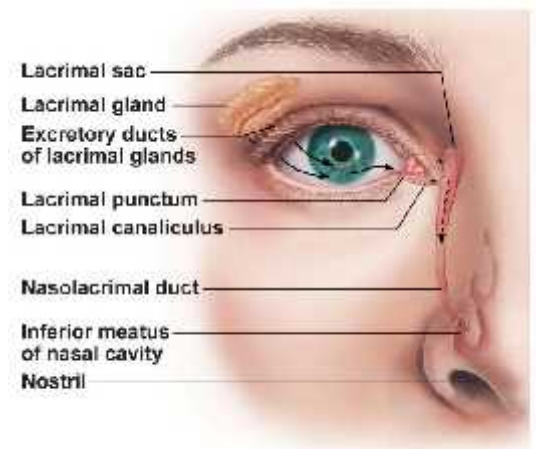
- Shade eye from sunlight
- Prevent perspiration from reaching the eye

Eyelids (palpebrae):

- Protect the eye anteriorly
- Separated by the palpebrae fissure
- Supported internally by connective tissue called the tarsal plates
- Levator palpebrae superioris – gives the upper eyelid mobility

Lacrimal sac:

- Consists of the lacrimal gland and ducts that drain lacrimal secretions into the nasal cavity
- Secretes tears (lacrimal secretions)
 - enters the eye via the excretory ducts
 - blinking spreads tears toward and into the lacrimal canaliculi
 - drain into the lacrimal sac and then into the nasolacrimal duct
- tears contain mucous, antibodies and lysozyme
- eye is lubricated by the lacrimal apparatus which includes a lacrimal gland producing a lacrimal secretion which leaves by excretory ducts of the lacrimal gland
- Blinking spreads the fluid evenly over the eye
- The excess fluid normally reaches the lacrimal punctum in the nasal corner of the eye leading to the lacrimal canal and nasolacrimal duct which pours in the inferior meatus of the nose.
- An excessive secretion overflows and run on the face as tears



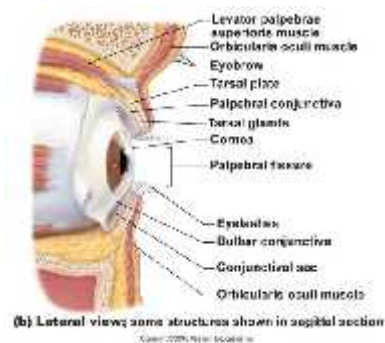
© 2012 McGraw-Hill Education, Pearson Education

Conjunctiva:

- Transparent membrane
- Lines the eyelids as the palpebral conjunctiva
- Covers the whites of the eyes as the bulbar conjunctiva

Extrinsic eye muscles:

- Six strap-like eye muscles control movement of each eyeball
- Enable us to follow movement and maintain structure of the eyeball
- Four rectus muscles originate from the common tendinous ring
- Two oblique muscles move the eye in the vertical plane
- eyes move in order that the object of interest falls onto the fovea of the retina where sensitivity is greatest
- Eye movements are produced by 3 pairs of extrinsic muscles:
 - (1) superior and inferior rectus muscles which allow looking up and down



(b) Lateral view; some structures shown in sagittal section
© 2012 McGraw-Hill Education, Pearson Education

- Thickened ring of tissue that encircles the lens – controls lens shape
- made of smooth muscles for changing the shape of the lens to which it is attached via suspensory ligaments

Iris:

- Visible colored part of the eye
- acts as a reflexively activated diaphragm to vary pupil size

Retina:

- Contains millions of photoreceptors that transduce light energy, other neurons involved in processing light and glial cells

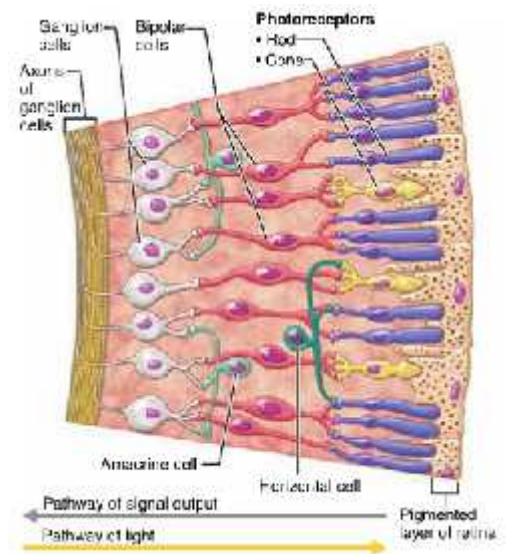
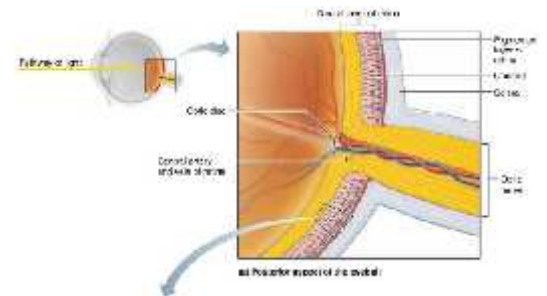
- Two layers – pigmented layer (absorbs light), neural layer

- Neural layer:

- Signals spread from photoreceptors to the bipolar cells and then to the innermost ganglion cells where action potentials are generated
- Rods – dim-light and peripheral vision receptors, more numerous, do not provide sharp images or color vision
- Cones – vision receptors for bright light and provide high-resolution color vision

- Optic disc:

- Where optic nerve exits the eye
- Lacks photoreceptors (blind spot)
- Do not see this as our brain fills in the absence of input
- Lateral to the blind spot at the eye's posterior pole is the macula lutea and in it's center is the fovea centralis – contains only cones
- Macula contains mostly cones then toward the retinal periphery cone density decreases
- Retina periphery contains mostly rods
- blood vessels of the optic nerve irrigate the posterior 2/3 of the retina (the anterior 1/3 is irrigated by the vessels of the choroid)



Lens:

- Biconvex, transparent, flexible structure
- Can change shape to precisely focus light on the retina
- Lens epithelium – anterior cells that differentiate into lens fibers
- Lens fibers – cells filled with the transparent protein crystallin
- With age the lens becomes more compact and dense and loses its elasticity

Light and optics

Pathway of Light:

- Light passes through the following structures to reach the photoreceptors: the cornea, anterior chamber, pupil, posterior chamber, lens, posterior segment and the retina (ganglion cells, bipolar cells, and finally photoreceptors)
- white surface of the eyeball and the inner surfaces of the eyelids contain a delicate mucous membrane called the conjunctiva
- The eye itself is formed of 3 layers or tunics: fibrous, vascular and sensory (retina)
 - The fibrous tunic has a part named cornea which is transparent (can be transplanted without rejection because it does not have any blood vessels to carry immune response cells) and another part named sclera which forms the white of the eyeball
 - The sclera is used as anchoring for the ocular muscles and joins the dura mater at the back which forms the envelope of the optic nerve
 - The vascular tunic (also named uvea) includes the iris and the ciliary body anteriorly and the choroid posteriorly (the junction between the ciliary body and the choroid is called ora serrata)
 - pupil is the opening of the iris which lets light pass into the eye
 - sensory tunic is commonly named the retina. It includes a pigmented layer and a neural layer
 - pigmented layer covers the choroid, ciliary body, and the posterior surface of the iris in order to absorb light so that it does not reflect on the interior walls of the eyeball
 - neural layer covers only the choroid. By looking into the eye one can see a yellow spot or macula lutea which contains at its center the fovea centralis which is the size of a pin-head
- photoreceptors synapse onto bipolar cells which in turn synapse with ganglion cells whose axons form the optic nerves
- lens divides the eyeball into a posterior segment (containing the vitreous humor which is a gelatinous substance) and an anterior segment (containing aqueous humor)
 - anterior segment is divided by the iris into the anterior chamber and the posterior chamber
 - aqueous humor is formed by filtration through the capillaries at the ciliary process
 - Evacuation of the aqueous humor is done by the scleral venous sinus (canal of Schlemm)
 - Blockage of these sinuses leads to increased intraocular pressure and glaucoma
 - Aqueous humour- fluid fills the eye; eye just empty sac
- Cornea → aqueous humour → lens → vitreous humor → neuronal layer to receptors and back

Wavelength:

- Electromagnetic radiation – includes all energy waves, from short gamma rays to long radio waves
- Light is made up of small particles called photons
- Our eyes respond to a small portion of this spectrum called the visible spectrum – band of colors
- Different cone receptor cells in the retina respond to different wavelengths of the visible spectrum
- visible spectrum includes electromagnetic wavelengths from 400 nm (blue) - 700 nm (red). A prism shows that white light is a mixture of all colors.

- Black = all light absorbed; white= light all reflected; red apple- reflecting red portion of spectrum, but absorbing everything
- Rainbow= light through a prism of rain drop and light separated
- 2 types of receptors: cone and rods (3)

Refraction:

- Light travels in straight lines and is blocked by nontransparent objects
- When light travels in a given medium its speed is constant
- When it passes from one medium into another its speed changes
- Causes bending or refraction of light rays

Lenses:

- If a lens surface is convex light rays converge at a single point - focal point (all light focused)
- Image formed (real image) is inverted

Reflection:

- ability of light to be reflected on a surface
- color of an object indicates the color reflected by the object, for example we see a ball as blue because all the wavelengths of the white light striking the ball was absorbed except for the blue light which was reflected towards our eyes.

Focus and inversion:

- The process of focusing involves the convergence of point sources through refraction of light by a lens
- Note that an object is formed of many point sources and each of these point sources reflect light in all directions so the light coming from a single point source must be combined otherwise the image would be blurred
- lens of the eye not only focuses light but causes the image to be inverted on the retina
- Inversion of the visual image on the retina is kept inverted along the path to the primary visual cortex
- Remember that the light gets absorbed by the pigmented layer of the retina so that it doesn't get reflected to other photoreceptors.
- Light passes through more mediums so the amount of reflected light under the water is different from the amount of light above water= refraction of light due to change in speed
- Have a convex lens therefore inverted image; concave lens will cause divergence of light

Focusing light on the retina

- Pathway of light entering the eye: cornea, aqueous humor, lens, vitreous humor, and the entire neural layer of the retina to excite photoreceptors
- During this passage light is refracted:
 - Entering the cornea
 - Entering the lens
 - Leaving the lens

- The lens curvature and shape allow for fine focusing of an image; refracts light onto retina either on fovea (bright) or rods (dark)

Focusing for distant vision:

- Light from a distance needs little adjustment for proper focusing
- Far point of vision – the distance beyond which the lens does not need to change shape to focus (20 ft.)
- Lens is flat and thin and ciliary muscles are relaxed
- Happiest at focusing far- less work
- Ciliary muscle help stretch or compress lens

Focusing for close vision:

- Accommodation – changing the lens shape by contraction of ciliary muscles to increase refractory power (parasympathetic stimulation)
- Constriction – the pupillary reflex constricts the pupils to prevent divergent light rays from entering the eye
- Convergence – medial rotation of the eyeballs toward the object being viewed
- accommodation reflex bends the light rays towards the focal point of the retina so that the visual field is in focus when we are looking at an object that is close or far away
- Relaxation of the ciliary body which forms a ring around the eyeball will allow the intraocular pressure to increase tension on the suspensory ligaments and stretch the lens to permit far vision while contraction of the ciliary body decreases tension of the suspensory ligaments and allows the lens to bulge from its elastic properties and permit near vision
- An object that is closer than the punctum proximum (typically to 25 cm) cannot be seen clearly because accommodation of the lens (bulging of the lens produced by contraction of the ciliary muscles) is at a maximum
- An object at the puntum remotum (typically 2-6 meters) or further does not require accommodation of the lens to be seen clearly because the light entering the eye is parallel
- accommodation of the lens is used to clearly see objects that are at a distance between the punctum proximum and remotum
- 99% of refractive problems are due to eyeball shape – too short or too long

Vision Problems

- Normal vision (emmetropia) is 20/20 (i.e. numerator is the distance in feet that you must be in order to clearly see an object and the denominator is the distance a normal subject must be in order to see the same object)
- myopia, the subject has poor far vision because the image forms in front of the retina thus the correction requires concave lenses (it's not a defect of the lens but rather that the eye is 4 mm too deep).
- hyperopia the subject has poor near vision because the image forms behind the retina thus the correction requires convex lenses (it's not a defect of the lens but rather that the eye is 4 mm too shallow)

- Astigmatism is due to unequal curvatures of the lens or cornea which requires a combination of both concave and convex lenses to correct vision

Myopia:

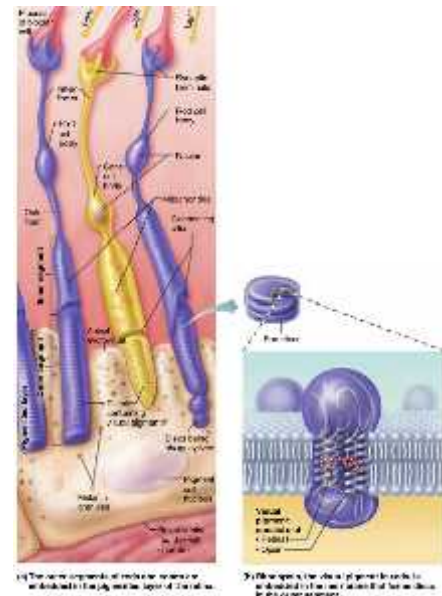
- Distant objects focus in front of the retina rather than on it
- Can see close objects but distant ones are blurred
- Results from eyeball being too long

Hyperopia:

- Light rays from nearby objects focus so far behind the retina that the lens cannot bring the focal point onto the retina
- Close objects are blurry but can see objects at a distance

Anatomy of the photoreceptors

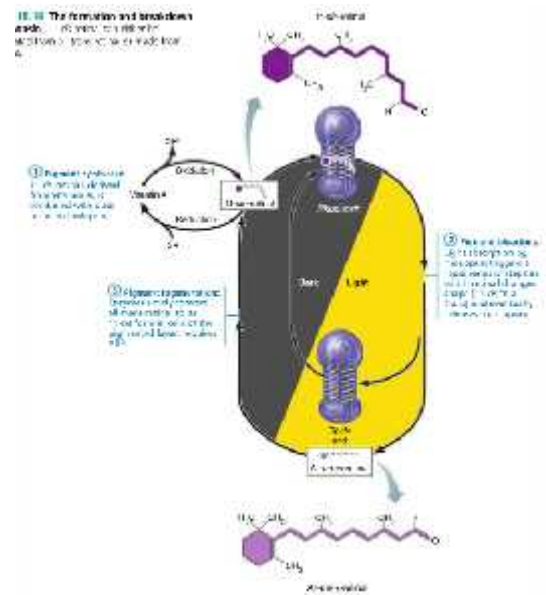
- Have inner and outer segments
- Inner segments connect to the cell body
- Outer segments have visual pigments (photopigments) that change shape as they absorb light
- Plasma membrane folds into discs to increase surface area to allow more reception of light
- detect light
- photoreceptors are made of an outer segment (light receiving area) linked by a connecting stalk to an inner segment (metabolic area). The outer segment contains visual pigment (molecules) for photoreception
- Really sensitive to bright light
- Damage rod or cone → replaced; regenerated
- The more visual pigments → more sensitivity to light and initiate action potential



Chemistry of visual pigments

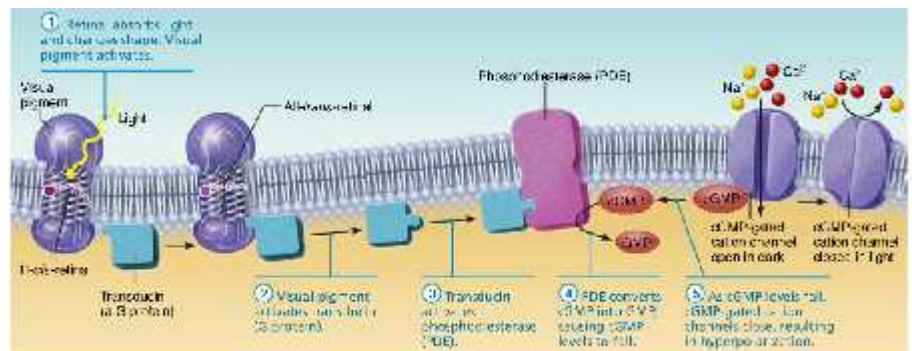
- Photoreceptors have a light-absorbing molecule called retinal that combines with proteins called opsins to form 4 types of visual pigments
- 3 visual pigments for cones – blue, green and red
- 1 visual pigment in rods (cones not activated)
- Retinal is chemically related to vitamin A – made from it (hence eat more carrots)
- Retinal can assume distinct 3D shapes called isomers
 - Bound to opsin, has bent shape – called 11-cis-retinol → *does not activate*
 - When the pigment is struck by light – called all-trans-retinol (coils and springs up → *activates*)
- Visual pigment of rods is a deep purple pigment called rhodopsin
- Rhodopsin forms and accumulates in the dark

- visual pigment is made of 2 molecules: retinal + opsin (specifically scotopsin in the rods and 3 kinds of photopsins in the cones to detect the colors blue, green, and red)
- retinal that is photosensitive: in the dark the retinal binds to the opsins to form the visual pigment while in the light the retinal dissociates with the opsin (the color absorbed by the retinal depends on the opsin to which it binds)
- visual cycle for rhodopsin which is the visual pigment of the rods: Light + Rhodopsin = Scotopsin + all-trans retinal, Dark + all-trans retinal + isomerase + ATP = 11-cis retinal, and Dark + 11-cis retinal + Scotopsin = Rhodopsin
- Vitamin A loses 2 hydrogens to form an external source of 11-cis retinal
- Light reduces the quantity of visual pigment which reduces the sensitivity to light while darkness allows the regeneration of the visual pigment to increase light sensitivity
- Adaptation to dark is slower because ATP and 2 metabolic steps are required to regenerate sufficient quantity of visual pigment
- Photoreceptors are not always active in daylight because, as we glance at different objects in our environment, some photoreceptors would receive the black parts of the object which do not reflect light
- Different opsin different visual pigments
- Rhodopsin – rod pigment- purple → in broad visual areas
- Made and stored in the dark; used up in the light; causes receptors to become bleached or inactivated (reason why blinded by light when you wake up- trying to adjust to sudden bright light)

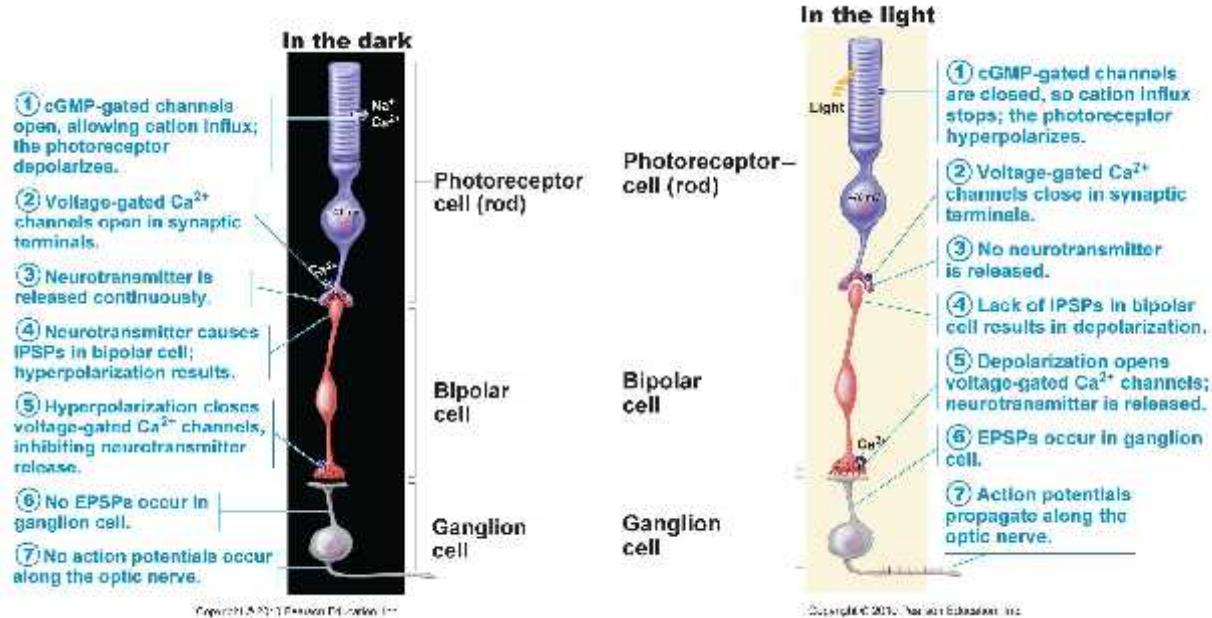


Phototransduction

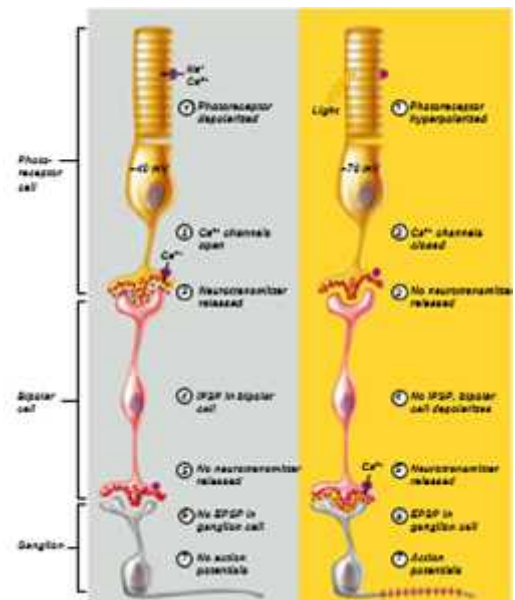
- Light-activated rhodopsin activates a G protein called transducin
- Transducin catalyzes activation of phosphodiesterase (PDE)
- PDE hydrolyzes cGMP to GMP and releases it from sodium channels
- Without bound cGMP, sodium channels close, the membrane hyperpolarizes, and neurotransmitter cannot be released
- Similar to cones
- In the dark; cGMP channels open → action potentials in the dark; Na⁺ and Ca²⁺ coming in



- In the light, closes, no more ions rushing in no more action potentials



- dark, there is plenty of cyclic-GMP which stimulates opening of the sodium channels and depolarization of the cells, but in the light there is a reduction in cyclic-GMP which leads to closing of the sodium channels and repolarization to inactivate the photoreceptor.
- Building up rhodopsin;
- Neurotransmitter released is inhibitory- glutamate- inhibits bipolar cell from AP; due to inhibition Ca²⁺ channels closed, no neurotransmitter released
- Light, Glutamate inhibited
- Bipolar cells can become depolarized and opens Ca²⁺ channels; release of excitatory neurotransmitter that acts on ganglion cell
- If comparing channels: light = cGMP bound; channels closed, not ions in; dark = cGMP not bound; channels open; ions move



Adaptation

- Adaptation to bright light (going from dark to light) involves:
 - Dramatic decreases in retinal sensitivity – rod function is turned off
 - Switching from the rod to the cone system – visual acuity is gained
- Adaptation to dark is the reverse
 - Cones stop functioning in low light

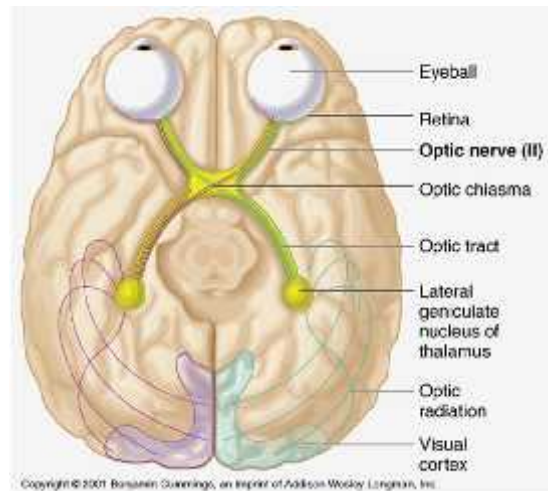
- Rhodopsin accumulates in the dark and retinal sensitivity is restored; takes time to accumulate hence not seen right away

Visual pathway to the brain

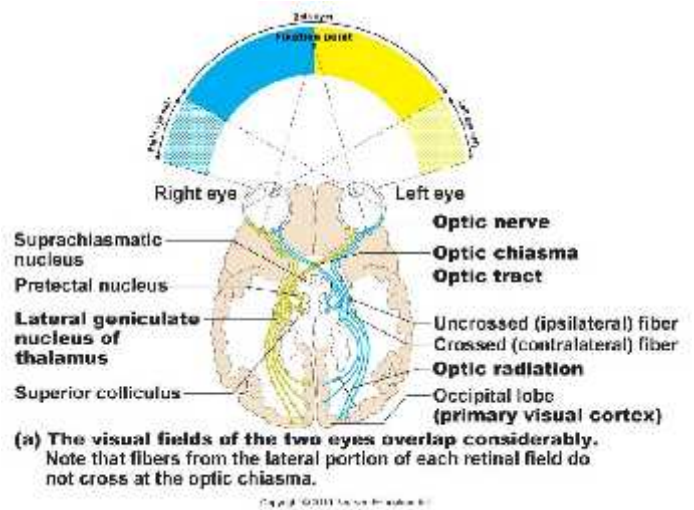
- Axons of retinal ganglion cells form the optic nerves
- Medial fibers of the optic nerve decussate at the optic chiasm and continue via the optic tracts
- Optic tract contains:
Fibers from the lateral aspect of the eye on the same side and fibers from the medial aspect of the opposite eye

Carries all the information from the same half of the visual field

- ganglion cells project to the lateral geniculate cells of the thalamus whose axons form the optic radiation terminating on cells of the primary visual cortex in the occipital lobe
- Information coming from the rods and the blue, green and red cones follow separate pathways to the primary visual cortex without mixing so that one can perceive the different colors
- A visual cortex receives information only from the contralateral visual field
- A single eye receives light from both visual fields thus the information must be directed to the correct cortex
- Visual stimuli from the ipsilateral visual field strike the nasal retina which have ganglion cells that project through the optic chiasm to reach the contralateral lateral geniculate nucleus of the thalamus whereas visual stimuli from the contralateral visual field strike the temporal retina which have ganglion cells that project to the ipsilateral lateral geniculate nucleus of the thalamus
- ganglion cell axons between the eye and the optic chiasm is called the optic nerve while the part of the ganglion cell axons between the optic chiasm and the thalamus is called the optic tract
- The thalamus projects to the ipsilateral cortex



- Other optic tract fibers end in superior colliculi (initiating visual reflexes) and pretectal nuclei (involved with pupillary reflexes)
- A small subset of visual fibers contain melanopsin (circadian pigment) which:
 - Projects to the suprachiasmatic nucleus - sets daily biorhythms
- ganglion cells have other projections towards:
 - the suprachiasmatic nucleus (SCN) of the hypothalamus which takes part in the biorhythms from the light and dark cycles
 - the superior colliculi which participates in fast movements (saccades) of the eyes towards a visual stimulus and (3) the pre-tectal nuclei which participates in the pupillary light reflex where light in one eye produces pupillary constriction in both eyes



Depth perception

- Achieved by both eyes viewing the same image from slightly different angles
- Three-dimensional vision results from cortical fusion of the slightly different images
- If only one eye is used, depth perception is lost and the observer must rely on learned clues to determine depth