Chapter 9 – Special Senses: Vision and Hearing

Objectives

Given the synopsis in this chapter, competence in each objective will be demonstrated by responding to multiple choice, matching, put-in-order, or fill-in questions, at the level of 85% or greater proficiency for each student.

A. To describe the anatomical organization of the eye and the mechanisms responsible for accommodation.
B. To explain the organization of the retina and the mechanisms responsible for the detection of light by the photoreceptors.
C. To explain the processing of visual information by the retina.
D. To explain the circuitry for processing of visual information by the central nervous system.
E. To explain the organization of the ear.
F. To explain the organization of the cochlea and the mechanisms responsible for the detection of sound by the hair cells.
G. To explain the circuitry for processing of auditory information by the central nervous system.

Eye and Vision

Organization of the eye

The eye is composed of three major layers, as shown in Figure 9.1. Sometimes these layers are called the fibrous tunic, the vascular tunic, and the neural tunic.

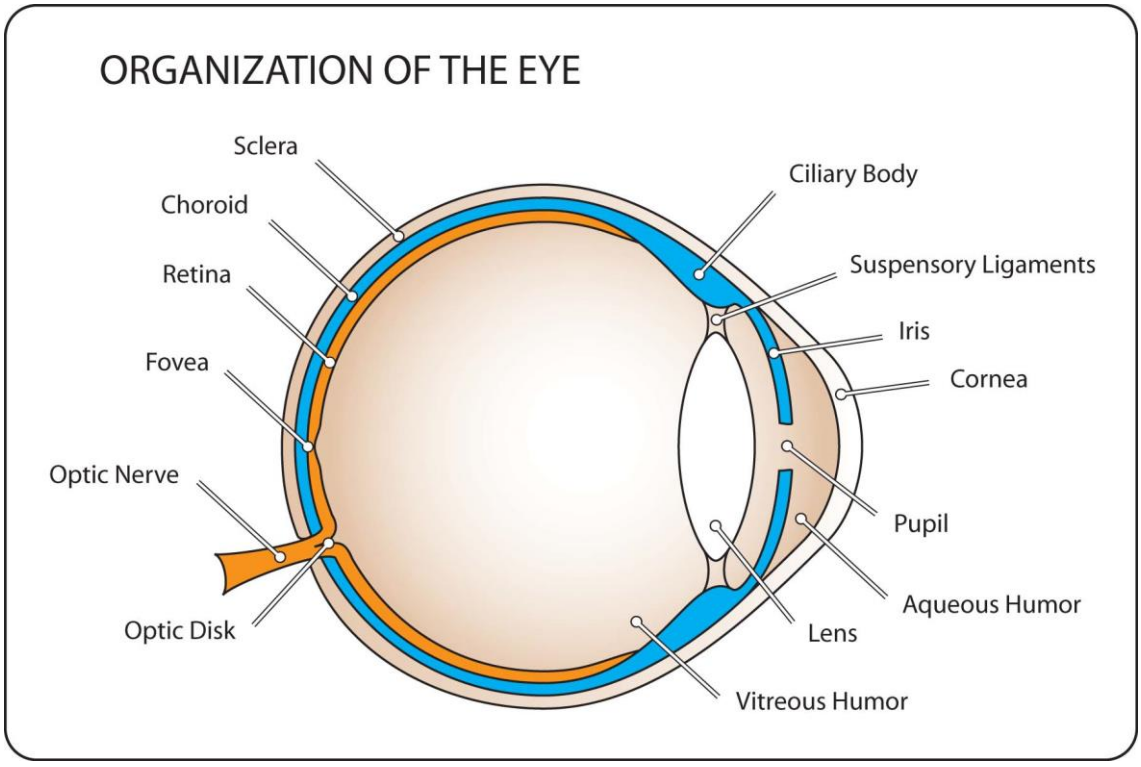

Figure 9.1 © 2010 David G. Ward, Ph.D.

The fibrous tunic includes the sclera and the cornea. The sclera is opaque and makes up the "white" of the eye. The cornea is in the front of the eye and is transparent.

- The cornea is composed of transparent layered connective tissue and provides for most of the refraction of light.

The vascular tunic includes the choroid, ciliary body, and iris. The choroid is a vascular layer under the sclera. The ciliary body and iris extend anteriorly from the choroid. The **lens** (also named **eye lens** or **crystalline lens**) is suspended by ligaments from the ciliary body. The iris continues behind the cornea. The **pupil** is the opening of the iris.

- The crystalline lens is composed of transparent layered connective tissue that is covered by fibrous and elastic tissue that force the lens to take a spherical shape.
- The ciliary body contains ciliary muscle to change the shape of the lens.
- The iris contains circular and radial muscle to change the size of the pupil.

The neural tunic includes the **retina** and associated structures. The retina is generally under the choroid, and is separated from the choroid by a pigment layer.

- Axons from the retina merge together at the optic disk to form the optic nerve.
- The highest density of photoreceptors is found in the fovea.

The fluid in front of the lens is watery and is called the **aqueous humor**. The fluid behind the lens is gelatinous and is called the **vitreous humor**.

Role of Eye Length and Shape of the Lens in Focusing

In order to see images in focus at different distances, either the lens of the eye has to change shape or the eye has to change length. Most commonly the lens changes shape. The term **lens accommodation** is often used to refer to changes in the curvature of the lens that occur when we look at objects at different distances.

- Positive Accommodation – the lens becomes more convex (higher + diopter)
- Negative Accommodation – the lens becomes less convex (lower + diopter)

With an **emmetropic** eye (the eye is normal length), the lens must be made more convex (higher + diopter) (positive accommodation), in order to focus the image of a near object on the retina. In contrast, the lens must be made less convex (lower + diopter) (negative accommodation), in order to focus the image of a distant object on the retina. With an emmetropic eye corrective eyeglasses are usually not required. See Figure 9.2a.

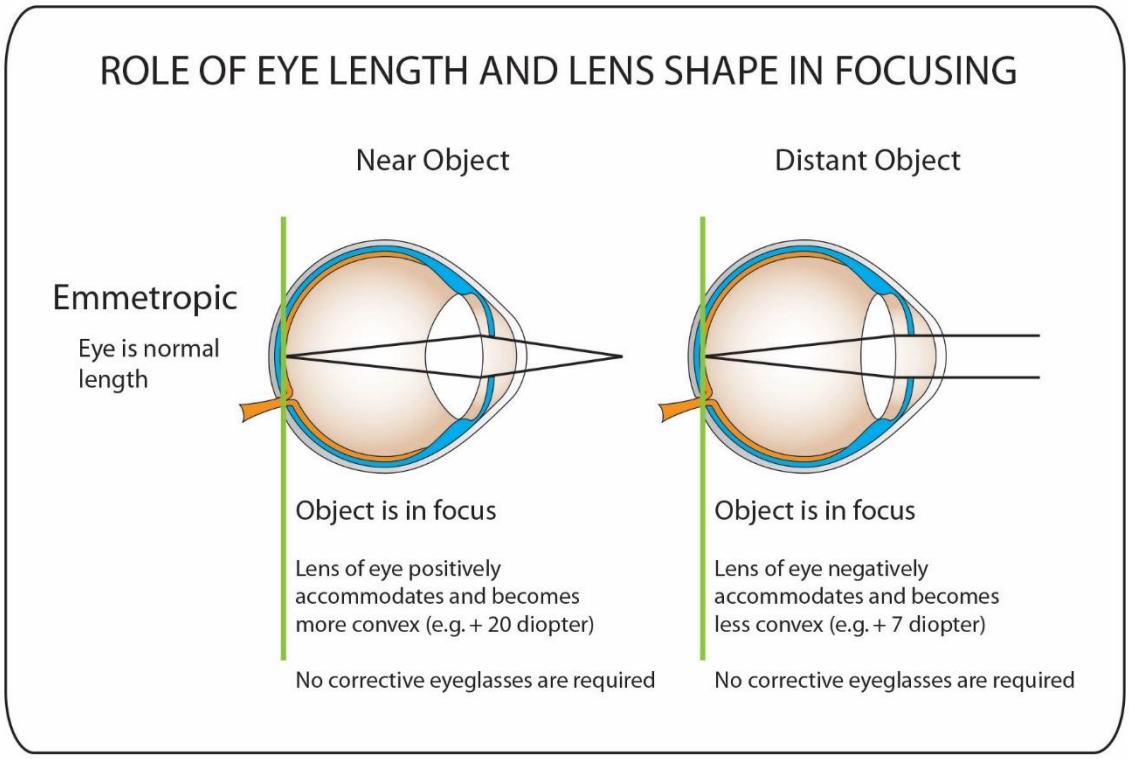

Figure 9.2a © 2016 David G. Ward, Ph.D.

With a **hyperopic** eye (the eye is shorter than normal), the lens must be made more convex than is typically possible, in order to focus the image of a near object on the retina. Without corrective eyeglasses, the image will be brought to a focus point behind the retina. In contrast, the lens can be made suitably convex to focus the image of a distant object on the retina. Thus, a person with hyperopia is said to be "farsighted" and needs + diopter corrective eyeglasses for near vision. See Figure 9.2b.

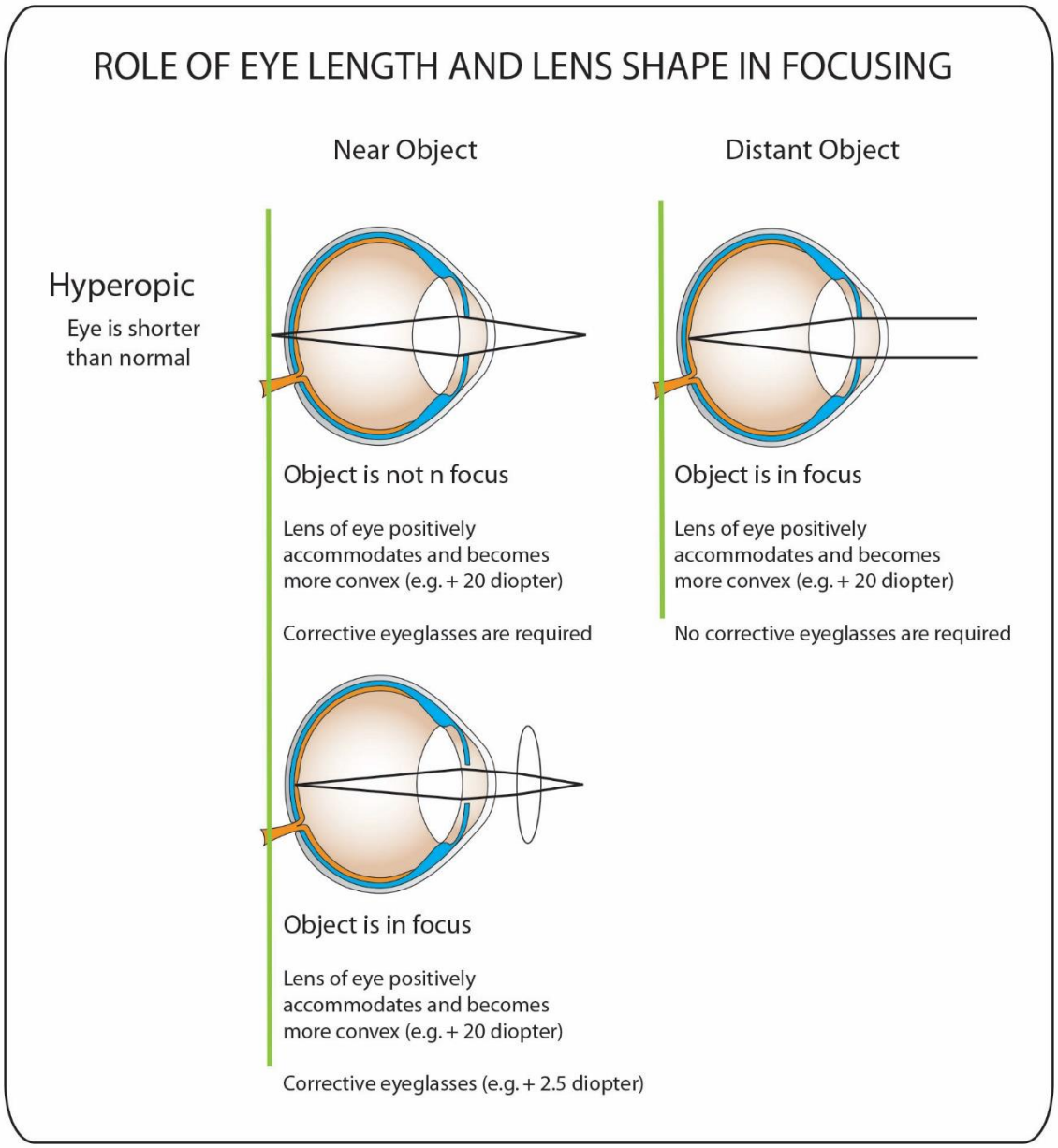

Figure 9.2b © 2016 David G. Ward, Ph.D.

With a **myopic** eye (the eye is longer than normal), the lens can be made suitably convex to focus the image of a near object on the retina. In contrast, the lens must be made less convex than is typically possible, in order to focus the image of a far object on the retina. Without corrective eyeglasses, the image will be brought to a focus point in front of the retina. Therefore, a person with myopia is said to be "nearsighted" and needs - diopter corrective eyeglasses for far vision. See Figure 9.2c.

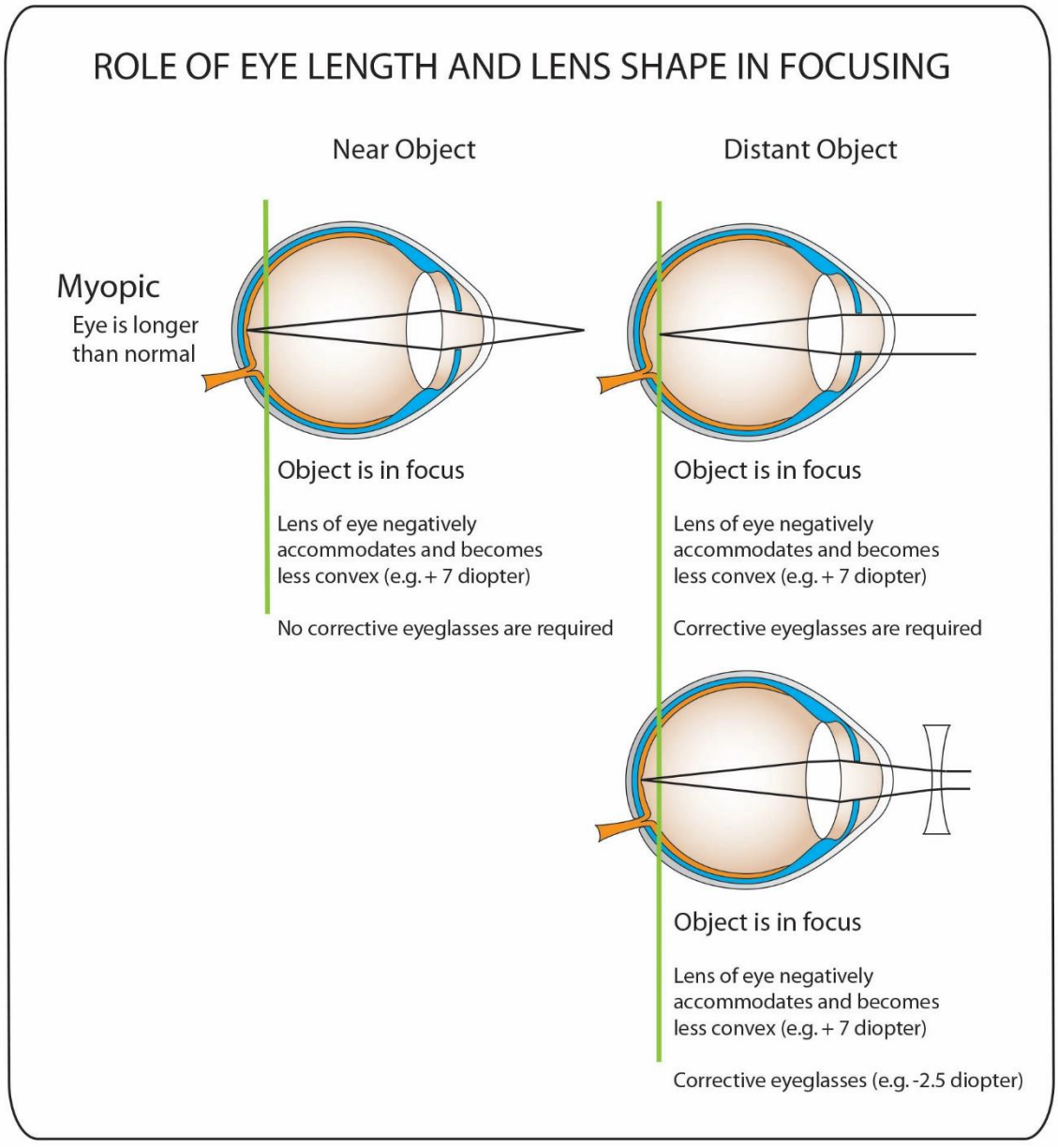

Figure 9.2c © 2016 David G. Ward, Ph.D.

Control of Lens accommodation

Accommodation for close vision normally requires that the lens of the eye is made more convex (positive accommodation). As described above, the lens is covered by fibrous and elastic tissues that force the lens to take a spherical shape. As shown in Figure 9.3, contraction of ciliary muscles decreases the pull on the lens and allows the elastic connective tissue to recoil and round the lens, making it more convex. Contraction of the ciliary muscle is controlled predominantly by the parasympathetic nervous system and can cause "eye fatigue."

In contrast, accommodation for distant vision requires that the lens is made less convex (negative accommodation). As shown in Figure 9.3, relaxation of the ciliary muscle increases the pull on the lens and flattens the lens making it less convex

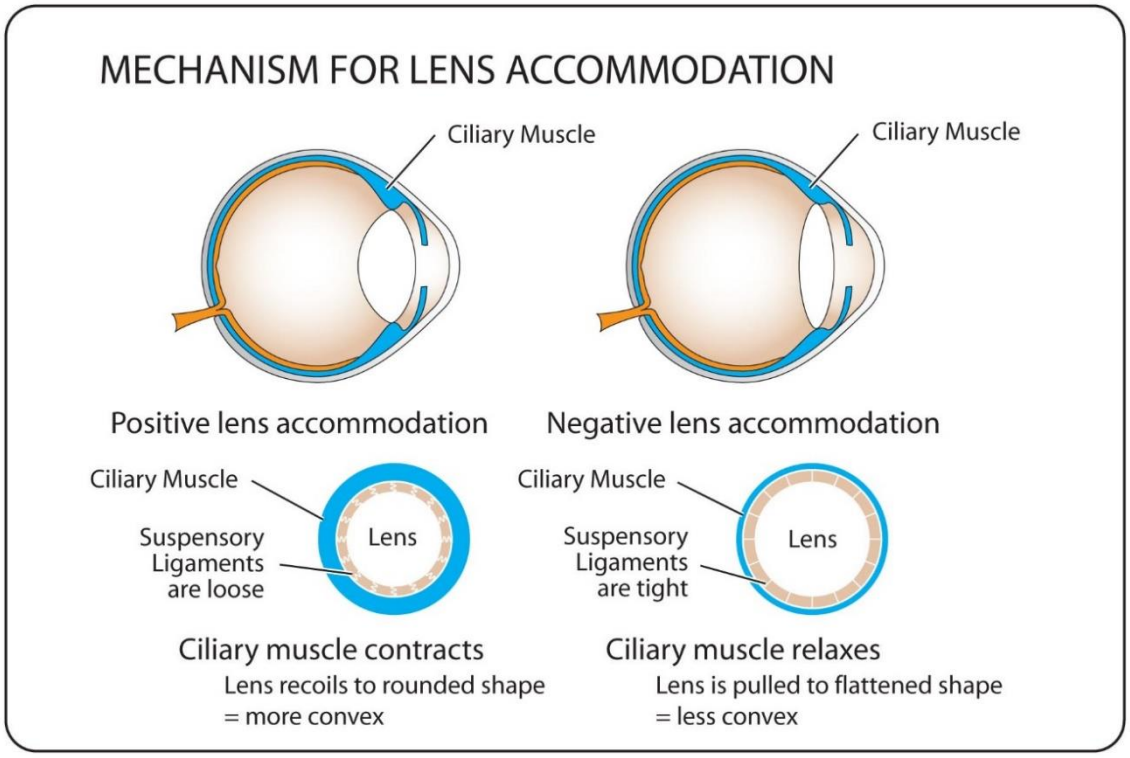

Figure 9.3 © 2014 David G. Ward, Ph.D.

- Contraction of the ciliary muscle, which allows close vision, is controlled predominantly by the parasympathetic nervous system.

Control of pupil size

Changes in the size of the pupil serve two functions: to control the amount of light striking the retina, and to influence the depth of focus. Constriction of the pupils decreases the circle of light striking the retina and increases the depth of focus, at the expense of a decrease in sharpness. Depth of focus refers to the range of distance that is in focus at any given level of accommodation.

- Contraction of the circular muscle of the pupil constricts the pupil and is controlled largely by the parasympathetic nervous system.
- Contraction of radial muscle of the pupil dilates the pupil and is controlled largely by the sympathetic nervous system.

Exposure of the eye to bright light will cause a pupil constriction reflex. Conversely, removal of bright light will cause a pupil dilation reflex.

Visual abnormalities

There are several common visual abnormalities that include:

- Myopia which is nearsightedness and may be caused by an eye that is too long or a lens that is too rounded (too convex) - corrected with concave lens.
- Hyperopia which is farsightedness and may be caused by an eye that is too short or a lens that is too flattened (not convex enough) – corrected with convex lens.
- Astigmatism which uneven focus is caused by irregular curvatures of the lens.
- Presbyopia which is limited focusing caused by loss in elasticity of the lens.
- Cataract which is cloudy vision caused by loss of transparency of the lens.
- Glaucoma which is loss of retinal functioning caused by abnormally high pressure of the intraocular fluids.

Retinal organization

The retina is generally under the choroid, and is separated from the choroid by a pigment layer. The retina consists of several layers of neurons, as shown in the photomicrograph in Figure 9.4 and in the illustration in Figure 9.5.

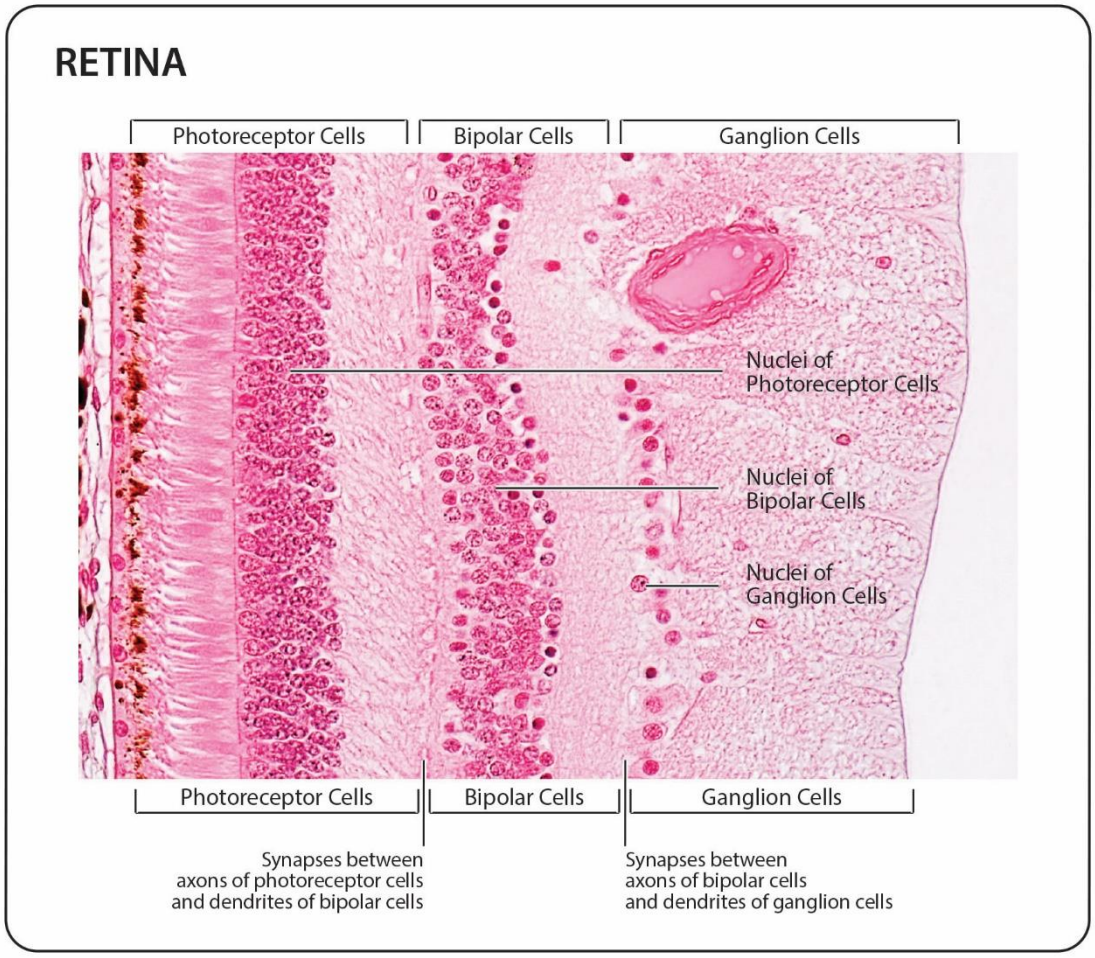

Figure 9.4 © 2018 David G. Ward, Ph.D.

- Imbedded in the pigment layer are the **photoreceptors** which are composed of three major parts.
  - Closest to the pigment layers are the disks which contain light sensitive pigments.
  - In the center of the photoreceptors are the nuclei.
  - Furthest from the pigment layer are the synaptic terminals of the photoreceptors
- Connected to the synaptic terminals of the photoreceptors are the **bipolar cells**.
- Connected to the synaptic terminals of the bipolar cells are the **ganglion cells**.
  - The ganglion cells are the source of the axons in the optic nerve.

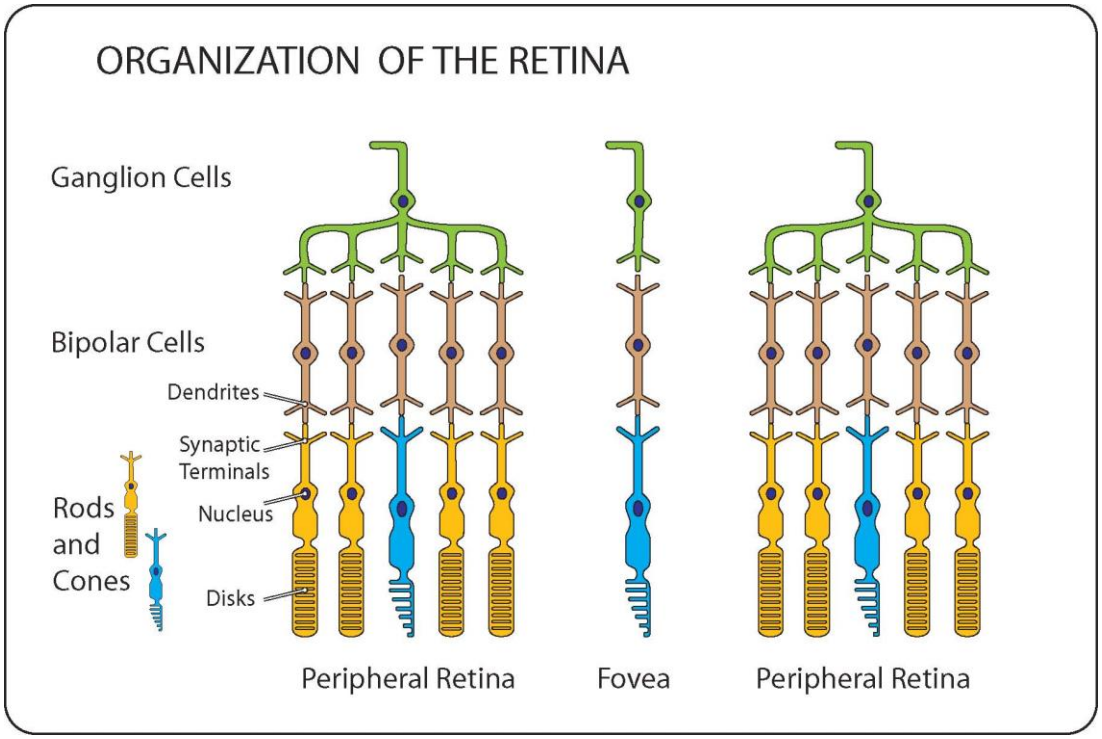

Figure 9.5 © 2007 David G. Ward, Ph.D.

Photoreceptors

The photoreceptors are composed of rods and cones as shown in Figure 9.5.

- Rods contain visual pigments that absorb light in the blue-green range, but do not discriminate colors.

- Cones are found in three varieties that contain visual pigments that absorb different colors of light.

    - Blue cones contain visual pigments with a peak absorption of 430 nm.
    - Green cones contain visual pigments with a peak absorption of 530 nm.
    - Red cones contain visual pigments with a peak absorption of 560 nm.

The visual pigments are opsins (rhodopsin in rods and photopsins in cones) which are a class of G-Protein coupled receptors. The process through which the absorption of light by a photoreceptor affects the release of neurotransmitter from photoreceptors is shown in Figure 9.6.

When a photoreceptor is not absorbing light

- Guanylyl cyclase is continually active and converts GMP to cyclic-GMP (cGMP).
- cGMP opens cGMP gated sodium channels in the disk membrane of the photoreceptors.
- The inflow of sodium ions causes depolarization that opens voltage gated calcium channels which leads to the continual release of glutamate.

  - A photoreceptor not absorbing light secretes more glutamate.

When a photoreceptor is absorbing light

- Retinal changes from cis form to trans form and opsin changes shape leading to activation of the G-protein transducin.
- G-protein alpha is activated (releases GDP and binds to GTP).
- Activated G-protein alpha activates phosphodiesterase.
- Phosphodiesterase breaks down cyclic-GMP.
- Without as much cyclic-GMP the gated sodium channels close.
- Sodium no longer enters the photoreceptor and hyperpolarization occurs.
- In response to decreasing positive charge (+) voltage gated calcium channels close, calcium no longer enters the photoreceptors, and the release of the neurotransmitter glutamate is decreased.

  - A photoreceptor absorbing light secretes less glutamate.

At first, what we have just said sounds counterintuitive, but this is a fundamental way the photoreceptors work. As we will describe later (in "Retinal Processing of Visual Information"), the photoreceptors use glutamate to communicate with bipolar cells.

The bipolar cells and retinal ganglion cells are responsible for additional processing. For example, some bipolar cells are depolarized (stimulated) by glutamate, and other bipolar cells are hyperpolarized (inhibited) by glutamate. You may or may not find it useful to read "Retinal Processing of Visual Information". However, you should read "Central processing of visual signals".

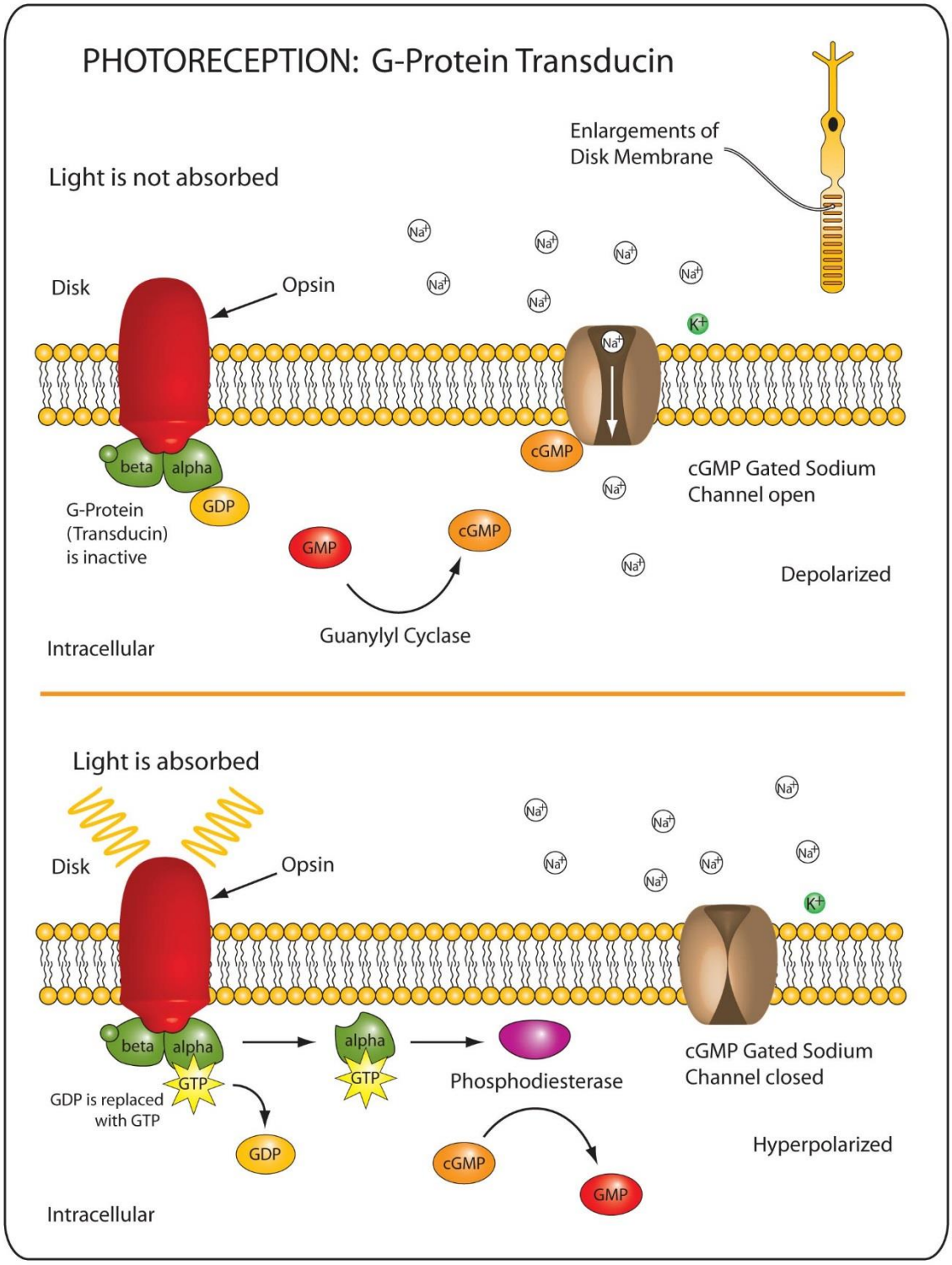

Figure 9.6 © 2014 David G. Ward, Ph.D.

Retinal Processing of Visual Information

As shown in Figure 9.5, rods are more common in peripheral parts of the retina. Cones are more common in central parts of the retina where the fovea contains the highest density of cones.

- In the peripheral parts of the retina, as many as 1000 rods may connect to a single ganglion cell via their bipolar cells.
- In the fovea a single cone may connect via a single bipolar cell to a single ganglion cell.

As a result of this organization, vision in fovea is extremely acute and clear and vision in the periphery is imprecise and blurred.

- Although not illustrated, the retina also contains horizontal cells and amacrine cells.
- Horizontal cells receive signals from photoreceptors and project laterally to inhibit or facilitate bipolar cells.
- Amacrine cells receive signals from bipolar cells and inhibit or facilitate ganglion cells.

Bipolar Cells

Both photoreceptors and bipolar cells generate graded potentials. Some bipolar cells (OFF- bipolar cells) respond to glutamate released from photoreceptors by depolarizing (exhibit EPSPs). Other bipolar cells (ON- bipolar cells) respond to glutamate released from photoreceptors by hyperpolarizing (exhibit IPSPs).

- Members of the first group are called **OFF-Bipolar cells** and use glutamate gated cation channels that open in response to glutamate, and thus respond to more glutamate with more depolarization (larger EPSPs). When photoreceptors absorb less light, they secrete more glutamate and thus cause these off-bipolar cells to depolarize.
- Members of the second group are called **ON-bipolar cells** and use G-protein coupled metabotropic receptors that close cation channels (and open Cl^- channels) in response to glutamate, and thus respond to more glutamate with more hyperpolarization (larger IPSPs). When photoreceptors absorb more light, they secrete less glutamate and thus cause these on-bipolar cells to depolarize.

The receptive field of a bipolar cell consists of two parts: a circular area of retina providing direct photoreceptor input called the receptive field center, and a surrounding area of retina providing input via horizontal cells called the receptive fields surround. The responses of the membrane potential of a bipolar neuron to light absorption in the receptive field center are the opposite of the response to light absorption in the receptive field surround. For example:

- Bipolar cells that exhibit EPSPs in response to glutamate when photoreceptors absorb light in the receptive field center, will exhibit IPSPs when photoreceptors absorb light in the receptive field surround.
- Bipolar cells that exhibit IPSPs in response to glutamate when photoreceptors absorb light in the receptive field center, will exhibit EPSPs when photoreceptors absorb light in the receptive field surround.

Retinal Ganglion Cells

Most retinal ganglion cells have the center-surround receptive field organization described above for bipolar cells. Most ganglion cells are not particularly responsive to changes in illumination that include both the receptive field center and the receptive field surround. In contrast, it appears that the ganglion cells are mostly responsive to differences in illumination that occur within their receptive fields. Furthermore, in contrast to photoreceptors and bipolar cells, ganglion cells generate actions potentials.

- The center-surround organization of the receptive fields leads to a neural response that emphasizes the contrast at light-dark edges.

Some retinal ganglion cells also have a color center-surround receptive field organization. The responses of cells to one wavelength in the receptive field center are cancelled by an opposing wavelength in the receptive field surround. These cells are called color-opponent cells. For example:

- Retinal ganglion cells that depolarize in response to exposure to red light in the receptive field center will hyperpolarize in response to exposure to green light in the receptive field surround.
- Retinal ganglion cells that depolarize in response to exposure to blue light in the receptive field center will hyperpolarize in response to exposure to yellow light in the receptive field surround.

The perception of color appears to be the result of the relative activity of retinal ganglion cells whose receptive field centers receive signals from red, green, and blue cones.

Central processing of visual signals

Ganglion cells are the only cells of the retina that transmit signals by way of action potential. Axons of the retinal ganglion provide the only route through which information leaves the retina.

Thalamus and Primary Visual (Striate) Cortex

The major visual pathways between the retina and the thalamus and between the thalamus and primary visual cortex are shown in Figure 9.7

- Axons from the retinal ganglion cells travel through the optic nerves, optic chiasm, and optic tracts to reach the lateral geniculate nucleus of the thalamus
    - Axons from the retinal ganglion cells of the left half of each retina, travel through the left optic tract to synapse on neurons in the left lateral geniculate nucleus of the thalamus.
    - Axons from the retinal ganglion cells of the right half of each retina, travel through the right optic tract to synapse on neurons in the right lateral geniculate nucleus of the thalamus.

- Axons from the retinal ganglion cells also synapse on neurons in the superior colliculus to coordinate orientation of the eyes, head and neck toward visual stimuli (not shown in Figure 9.7).
- Axons from neurons in the lateral geniculate nucleus of the thalamus travel through the optic radiations to reach the primary visual cortex

    - Axons from the left lateral geniculate nucleus of the thalamus synapse on neurons in the left primary visual cortex.
    - Axons in the right lateral geniculate nucleus of the thalamus synapse on neurons in the right primary visual cortex.

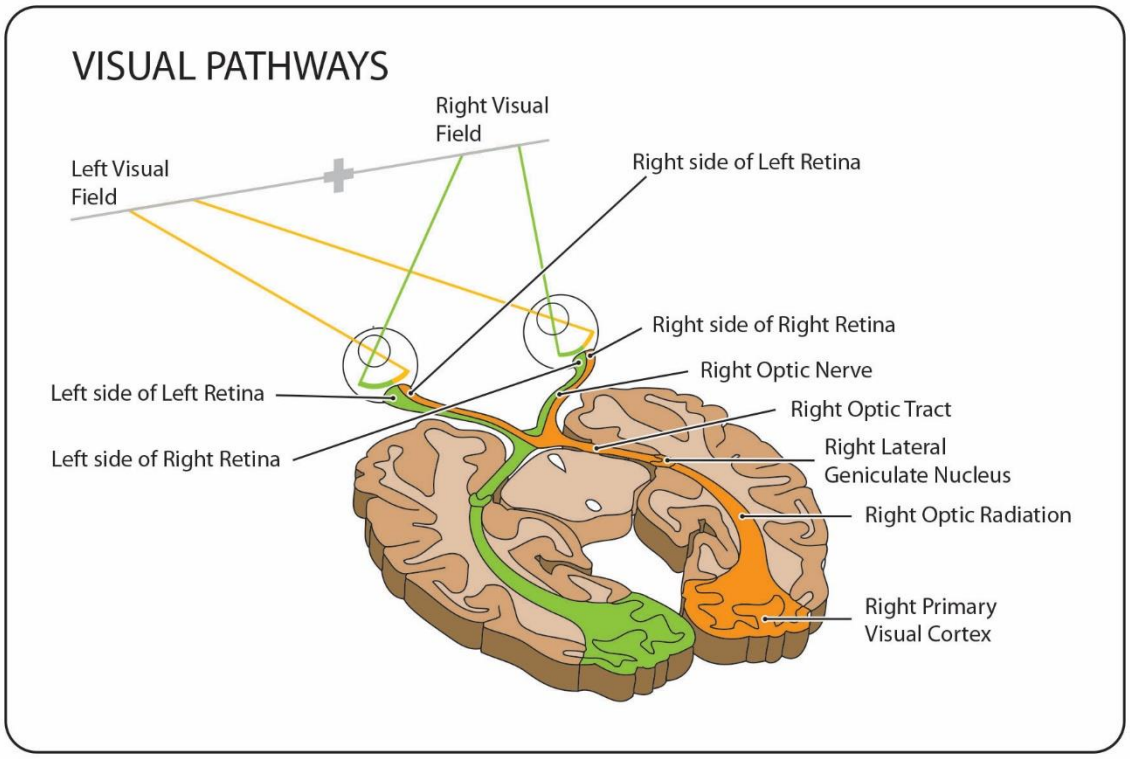

Figure 9.7 © 2016 David G. Ward, Ph.D.

Receptive fields and visual processing in thalamus and cortex

The receptive fields of the neurons of the lateral geniculate nucleus are almost identical to those of the retinal ganglion cells that feed them.

- The retina is not the major source of synaptic input to the lateral geniculate nucleus, rather

    - About 80% of the excitatory synapses within the lateral geniculate nucleus come from the primary visual cortex.

The receptive fields of neurons of the primary visual cortex are similar to many of the neurons of the lateral geniculate nucleus that feed them. There are three distinguishable pathways:

- A "magnocellular" pathway that seems to be involved in the analysis of object motion and guidance of motor actions
- A "parvocellular-interblob" pathway that seems to be involved in analysis of fine object shape
- A "blob" pathway that appears to be involved in analysis of object color.

As we saw for the processing of somatosensory signals, the central nervous system, acting through descending pathways, filters visual sensory information in the thalamus, brainstem, and possibly even in the retina. The thalamus is again seen anatomically and functionally as the "gateway" to the cerebral cortex.

Extrastriate Cortex

Processing of visual information continues far past the primary visual (striate) cortex and continues into parietal and temporal lobes. These areas are often referred to as the dorsal and ventral streams

- The **Dorsal Stream** extends from the primary visual cortex (V1) into the middle temporal lobe (V5) and posterior parietal cortex.
    - Neurons in these areas have properties similar to "magnocellular" neurons of the primary visual cortex.
    - Appear to be involved in the analysis of visual motion and visual control of action.
- The **Ventral Stream** extends from the primary visual cortex (V1) into cortical area V4 and into the inferior temporal lobe.
    - Neurons in these areas have properties similar to "parvocellular-interblob" neurons and "blob" neurons of the primary visual cortex.
    - Appear to be involved in perception of the visual world and recognition of objects and their color.

Ear, Cochlea and Hearing

Organization of the Ear

The ear is composed of three major regions, as shown in Figure 9.8. These regions are commonly called the outer ear, the middle ear, and the inner ear.

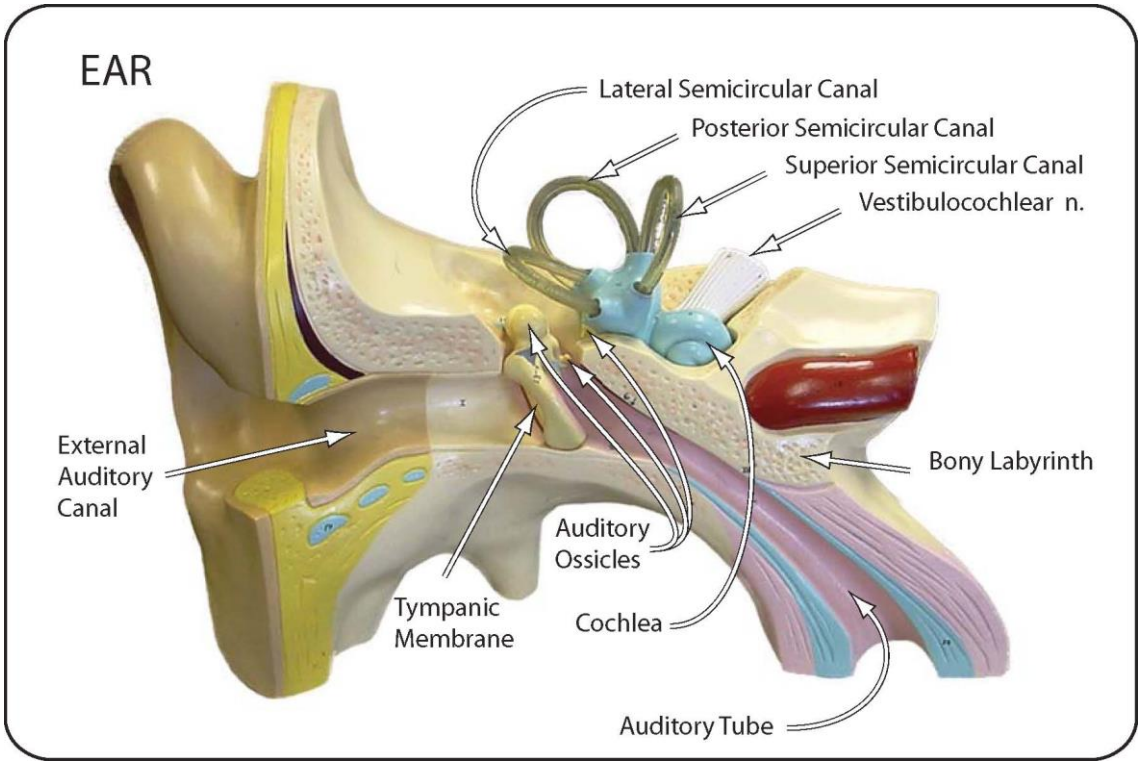

Figure 9.8 © 2007 David G. Ward, Ph.D.

The outer ear includes the **external auditory canal** and the **tympanic membrane**. The middle ear includes the **auditory ossicles** (malleus, incus and stapes) and the **auditory tube** (Eustachian tube). The inner ear includes the **cochlea**, the vestibular apparatus (**semicircular canals**), and the **vestibulocochlear** nerve. The inner ear and portions of the middle and outer ear are surrounded by the **bony labyrinth** of the temporal bone.

- Sound waves enter the external auditory canal where they are funneled to the tympanic membrane.

Auditory Ossicles

- The malleus, incus, and stapes transfer and mechanically amplify movement of tympanic membrane to the oval window of the cochlea.
- The movement is further amplified because the diameter of the tympanic membrane is larger than the diameter of the oval window of the cochlea

Cochlea

As shown in the photomicrograph in Figure 9.9, the cochlea is contained within the bony labyrinth of the temporal bone. Three ducts can be easily seen; the vestibular duct, the tympanic duct, and the cochlear duct.

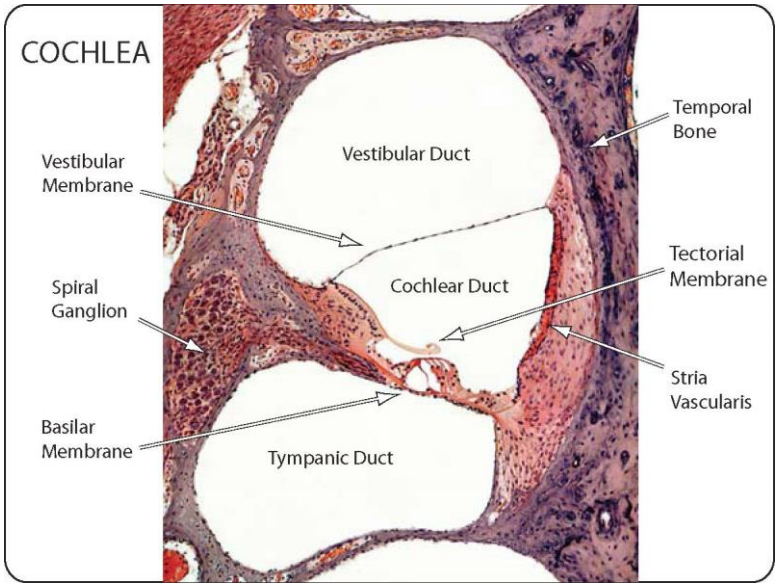

Figure 9.9 © 2007 David G. Ward, Ph.D.

- The vestibular duct contains perilymph and is connected to the oval window.
- The tympanic duct contains perilymph and is connected to the round window.
- The cochlear duct contains endolymph and the organ of Corti.
- The vestibular membrane separates vestibular duct and cochlear duct.
- The **basilar membrane** separates the tympanic duct and cochlear duct.

As shown in the photomicrograph in Figure 9.10, the basilar membrane also supports the organ of Corti.

- The **organ of Corti** is a raised region within the cochlear duct that contains the hair cells.
- There are three **outer hair cells** for every one **inner hair cell**.
- The **tectorial membrane** overlies the organ of Corti and attaches to the stereocilia of the hair cells.

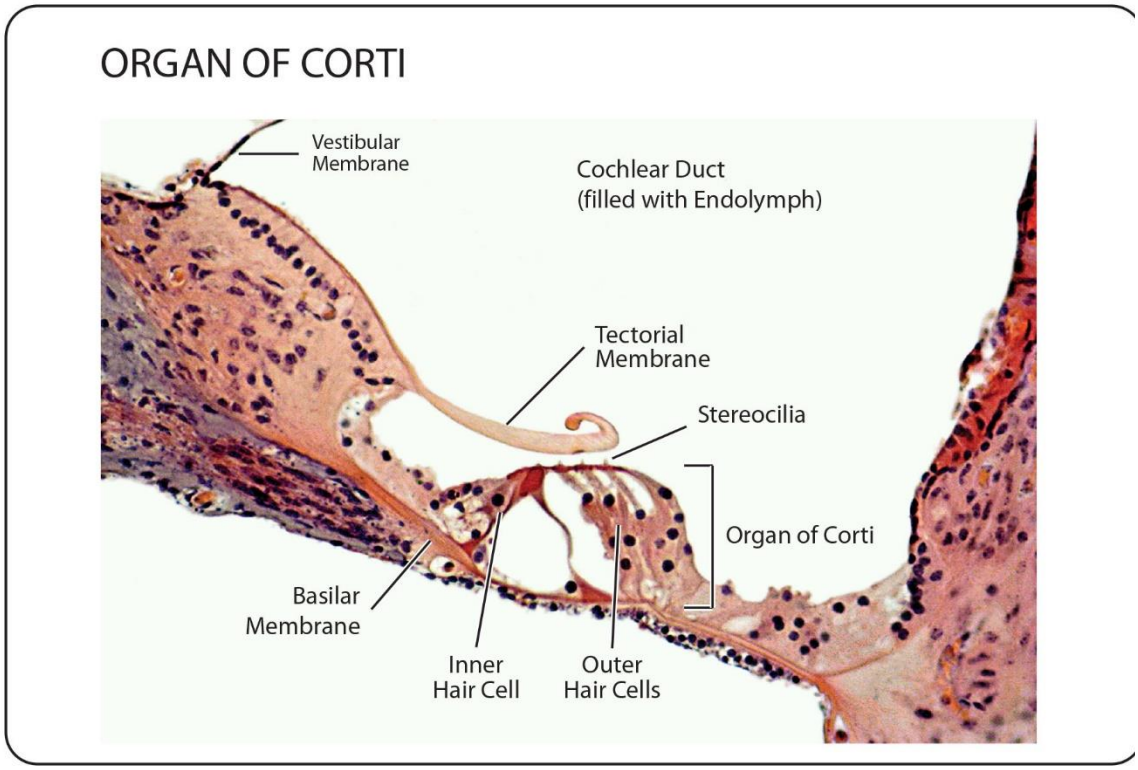

Figure 9.10 © 2014 David G. Ward, Ph.D.

Detection of sound, pitch and amplitude

The cochlea is shown uncoiled in Figure 9.11. Movement of the oval window of the cochlea leads to movement of the perilymph in the vestibular duct and tympanic duct. Movement of the perilymph has two effects. 1) Movement of the perilymph moves the basilar membrane. 2) Movement of the perilymph moves the vestibular membrane which will move the endolymph in the cochlear duct. Movement of the basilar membrane and the endolymph moves the stereocilia of the hair cells. As shown in Figure 9.11, the basilar membrane is stiffest near the oval window (the base) and most flexible far away from the oval window (the apex).

- High frequency pulses vibrate the basilar membrane preferentially near the oval window where the membrane is stiffest.
- Low frequency pulses vibrate the basilar membrane preferentially further from the oval window where the membrane is most flexible.

As a result of this organization, a place code is established where different locations are maximally deformed by different frequencies.

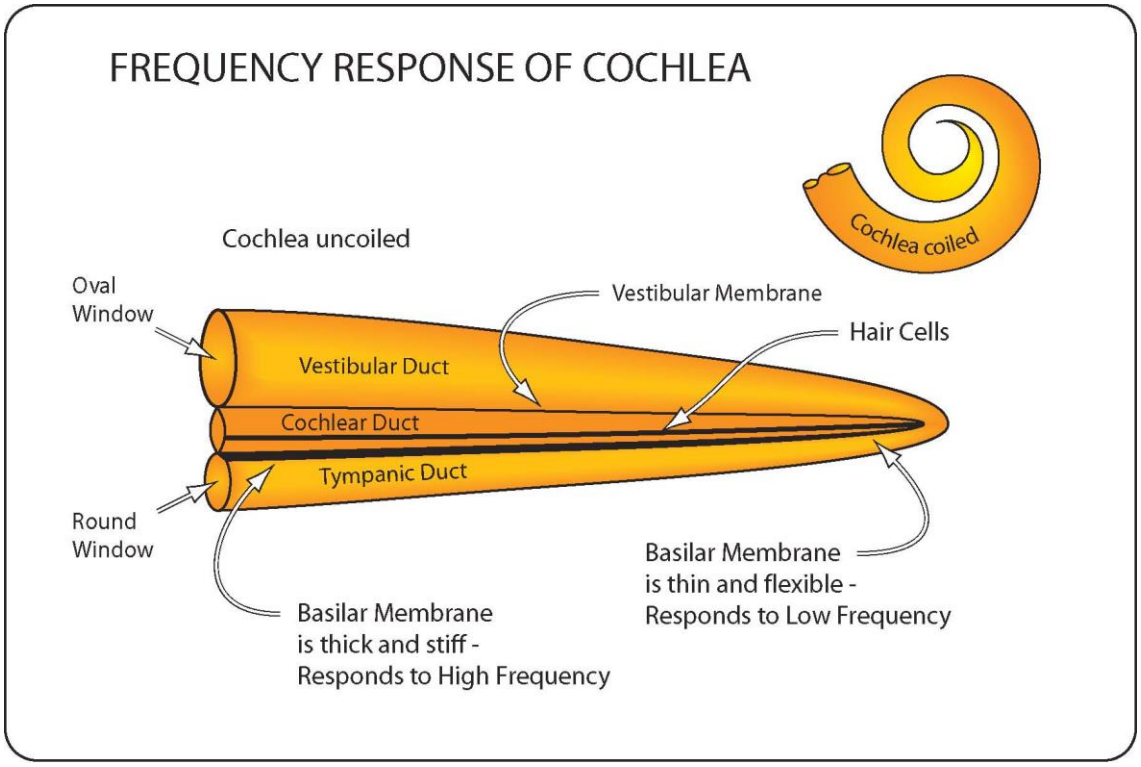

Figure 9.11 © 2007 David G. Ward, Ph.D.

In addition to responding to different frequencies and thus allowing for the neural encoding of pitch, the cochlea can easily distinguish different amplitudes of sound.

- High amplitude (loud) sound causes the most distortion of the stereocilia of the hair cells and the largest receptor potential. In addition, more adjacent hair cells respond.
- Low amplitude (quiet) sound lead to the least distortion of the stereocilia of the hair cells and the smallest receptor potential. In addition, few adjacent hair cells respond.

Detection of movement by the hair cells

Deformation of the basilar membrane leads to movement of the stereocilia of the hair cells, as shown in Figure 9.12. In the absence of distortion, the stereocilia of the hair cells are pulled straight.

- Upward movement of the basilar membrane pushes the stereocilia of the outer hair cells against the tectorial membrane and bends them outward.
- Movement of the endolymph is most likely responsible for pushing the stereocilia of the inner hair cells outward.

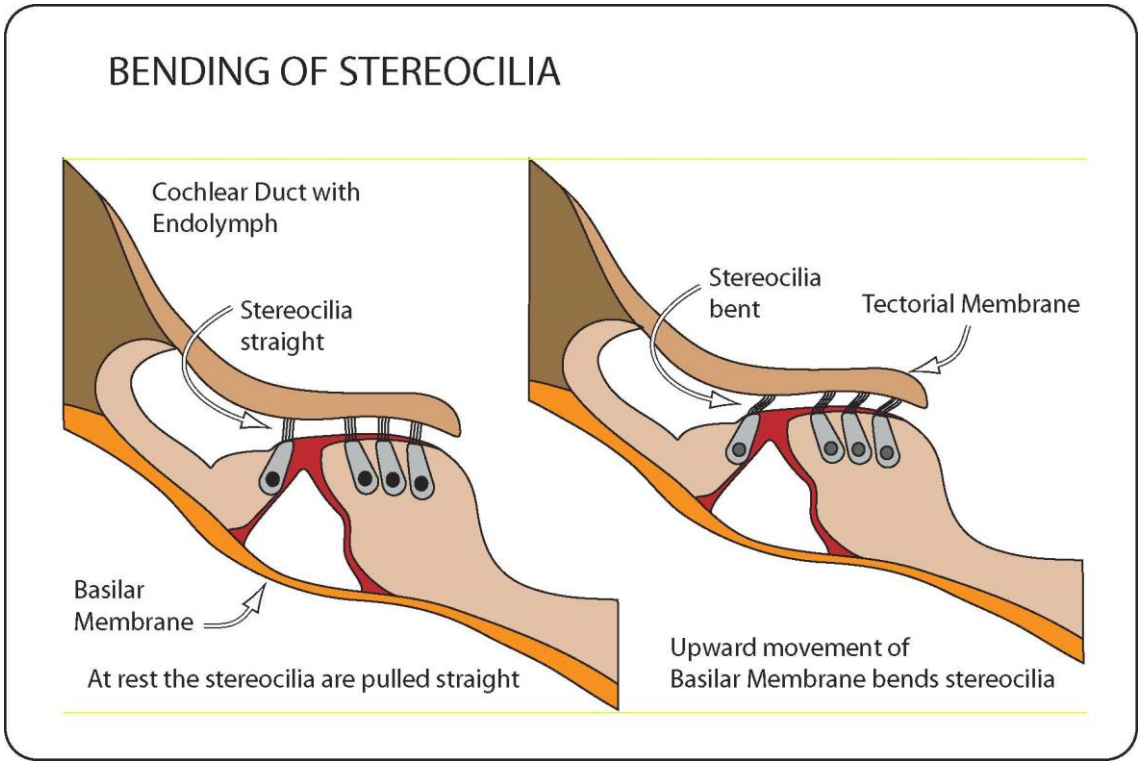

Figure 9.12 © 2007 David G. Ward, Ph.D.

Bending of the stereocilia outward causes depolarization of the hair cells, as shown in Figure 9.13. The endolymph is relatively unique in containing a high concentration of potassium.

- Movement of the stereocilia toward the tallest cilia opens movement gated potassium channels and allows potassium ions to enter the cell causing depolarization.
    - The positive charge from the entry of potassium opens voltage gated calcium channels.
    - Calcium ions trigger the fusion of synaptic vesicles with the presynaptic membrane and the release of an excitatory neurotransmitter, most likely glutamate.

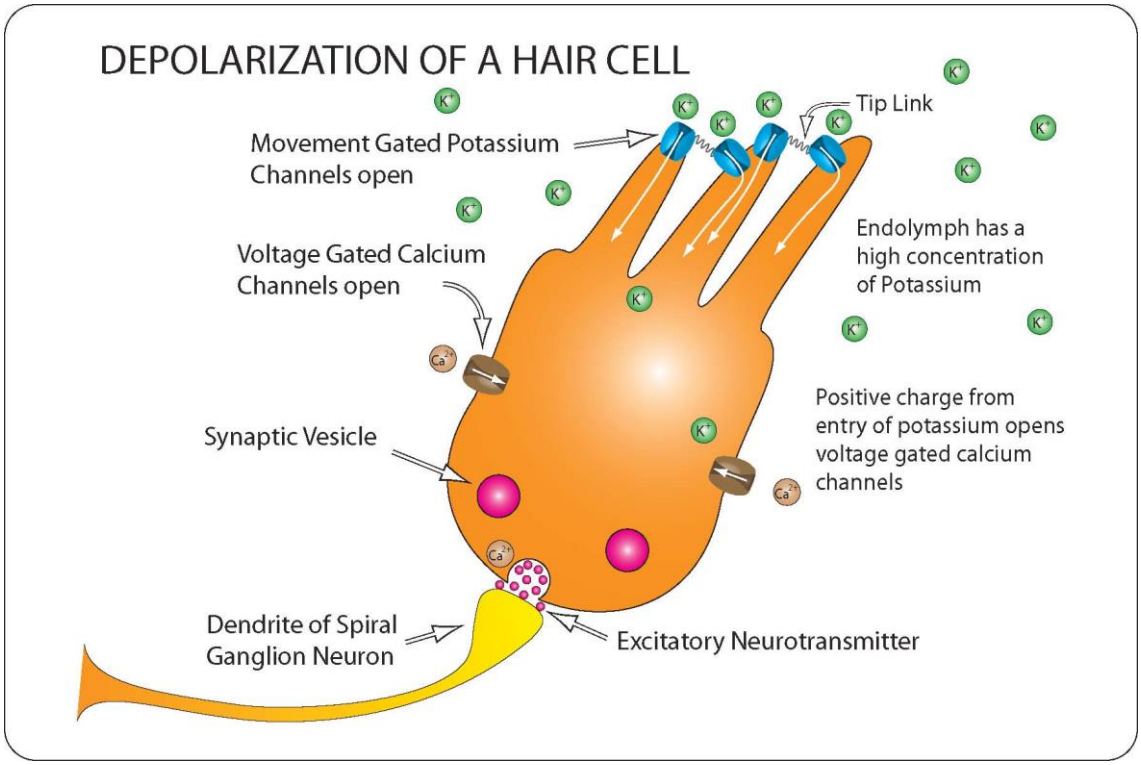

Figure 9.13 © 2007 David G. Ward, Ph.D.

Movement of the stereocilia toward the shortest cilia closes the movement gated potassium channels and leads to hyperpolarization.

The hair cells do not generate action potentials. They release an excitatory neurotransmitter (glutamate) at synaptic connections with the dendrites of spiral ganglion neurons.

- About 95% of the neurons of the cochlear nerve form synaptic connections with the inner hair cells.
- Only about 5% of the neurons of the cochlear nerve form synaptic connections with the outer hair cells, although the outer hair cells outnumber the inner hair cells by a factor of 3:1. The outer hair cells seem to play a critical role in amplifying the movement of the basilar membrane.

Central processing of auditory signals

Spiral ganglion cells transmit signals by way of actions potentials generated in response to glutamate from the hair cells. The major auditory pathways are shown in Figure 9.14.

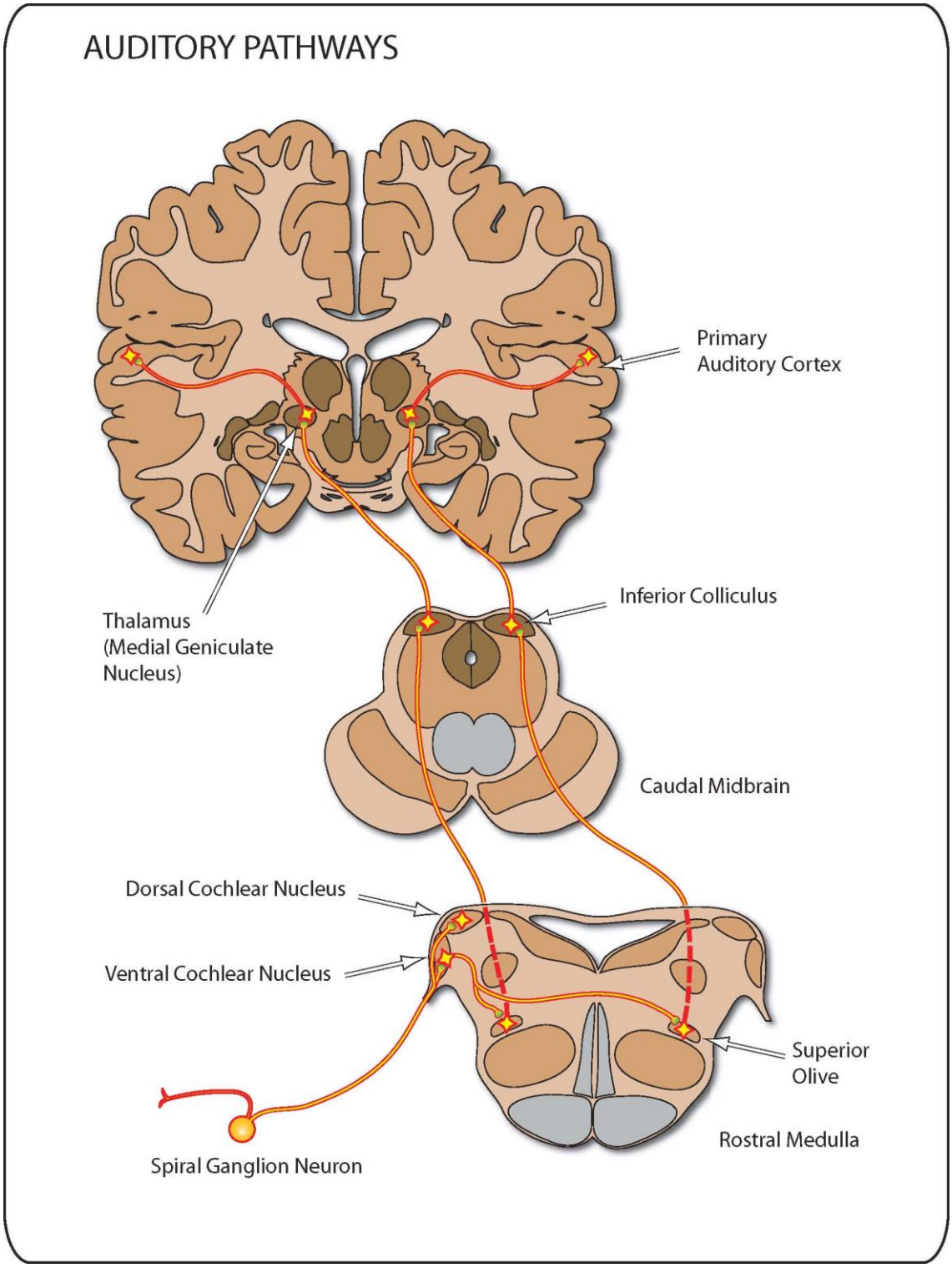

Figure 9.14 © 2007 David G. Ward, Ph.D.

- Axons from spiral ganglion cells (first order neurons) travel through the cochlear nerve into the Pons, ipsilateral.
- Axons from the spiral ganglion cells synapse on second order neurons in the ventral cochlear nucleus and dorsal cochlear nucleus.
- The axons of second order neurons in the ventral cochlear nucleus synapse on neurons in the superior olive, both ipsilateral and contralateral, to calculate the location of sound.
    - The medial superior olive compares the arrival times of sound from the two ears.
    - The lateral superior olive compares the intensity of sound from the two ears,
- Axons of neurons of the superior olive synapse on neurons in the inferior colliculus to coordinate orientation of the head toward sounds.
    - Axons of second order neurons in the dorsal cochlear nuclei synapse on neurons in the inferior colliculus (not shown in Figure 9.14).
- Axons of neurons in the inferior colliculus synapse on neurons in the medial geniculate nucleus of the thalamus to process and filter auditory signals.
- The axons of the "third order" neurons in medial geniculate nucleus of the thalamus synapse on neurons in the auditory cortex (temporal lobe) that lead to conscious awareness of sound.

Quiz Yourself

1-5. Matching

A)	emmetropic eye	eyeball is normal length	1) _____
B)	hyperopic eye	eyeball is longer than normal	2) _____
C)	myopic eye	eyeball is shorter then normal	3) _____
		Eye lens cannot become more convex as needed for near vision	4) _____
		Eye lens cannot become less convex as needed for distance vision	5) _____

6-10. Matching (connects to)

A)	left retina of left eye	left optic tract	6) _____
B)	left retina of right eye	left optic nerve	7) _____
C)	right retina of left eye	left superior colliculus	8) _____
D)	A and B	left primary visual cortex	9) _____
E)	A and C	left lateral geniculate nucleus	10) _____

11-15. Place in order the events following exposure of a photoreceptor to light.

A)	release of glutamate is reduced	11) _____
B)	phosphodiesterase is activated	12) _____
C)	opsin activates G-protein (transducin)	13) _____
D)	Phosphodiesterase breaks down cyclic-GMP	14) _____
E)	voltage gated sodium and calcium channels close	15) _____

16-20. Place in order the events following exposure of the basilar membrane to movement.

A)	movement of the stereocilia toward the tallest cilia opens K^+ channels	16) _____
B)	stereocilia of hair cells bend against tectorial membrane	17) _____
C)	synaptic vesicles fuse with the presynaptic membrane	18) _____
D)	voltage gated calcium channels open	19) _____
E)	glutamate is released	20) _____

Fill in

21. Near sightedness is corrected with _____ lenses.

22. Yellow causes a (n) _____ in glutamate release from blue sensitive photoreceptors.

23. Damage to the left optic nerve would cause blindness in the _____ eye.

24. High frequency sound is detected by portions of the cochlea _____ the oval window.

25. Movement of the head is detected by _____ cells in the semicircular canals.

Study Questions

1. Explain the mechanisms responsible for accommodation of the lens.
2. Describe the organization of the retina and explain the mechanisms responsible for the detection of light by the photoreceptors.
3. Describe the organization of the cochlea and explain the mechanisms responsible for the detection of sound by the hair cells. Include the detection of different frequencies.