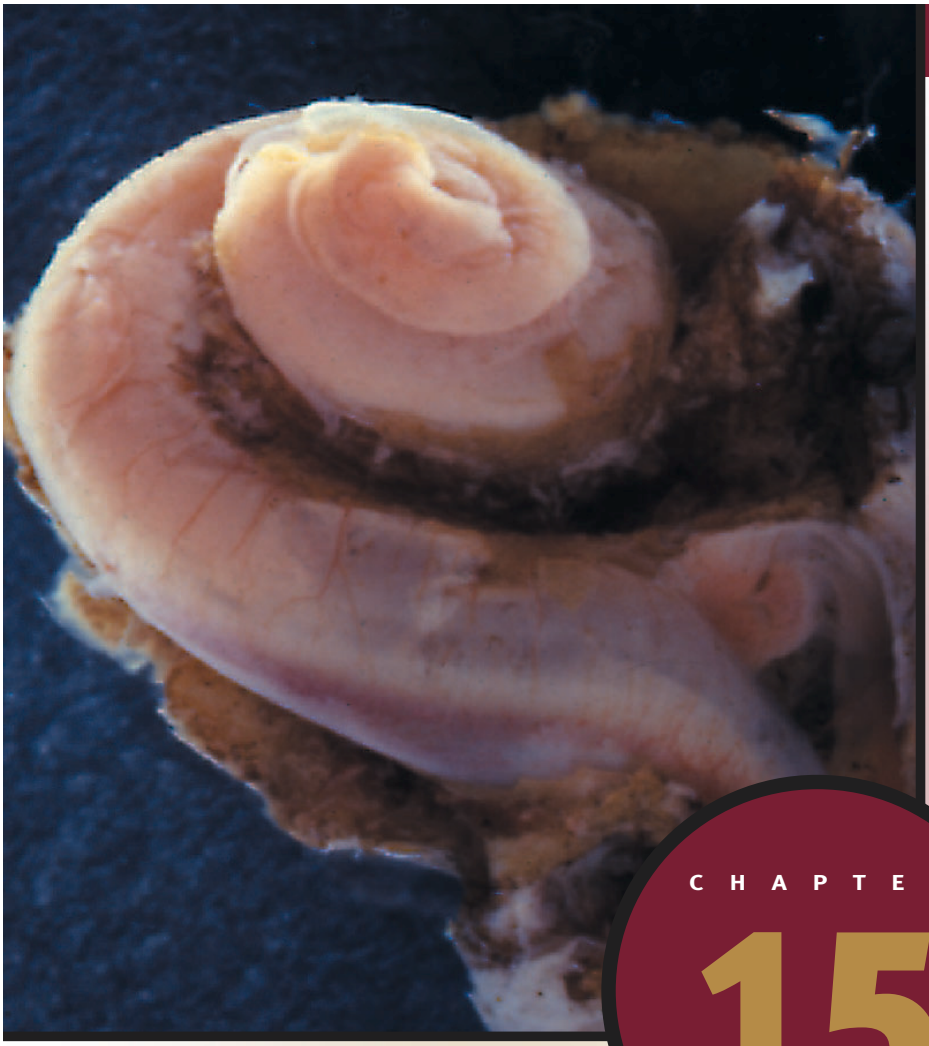


Photograph of an isolated cochlea from the inner ear.

The Special Senses

CHAPTER 15

Historically, it was thought that we had just five senses: smell, taste, sight, hearing, and touch. Today we recognize many more. Some specialists suggest that there are at least 20, or perhaps as many as 40, different senses. Most of these senses are part of what was originally classified as "touch." These "general senses" were discussed in chapter 14. The sense of balance is now recognized as a "special sense," making a total of five special senses: smell, taste, sight, hearing, and balance. **Special senses** are defined as those senses with highly localized receptors that provide specific information about the environment. This chapter describes *olfaction* (502), *taste* (504), the *visual system* (508), and *hearing and balance* (527). We conclude the chapter with a look at the *effects of aging on the special senses* (540).

Olfaction

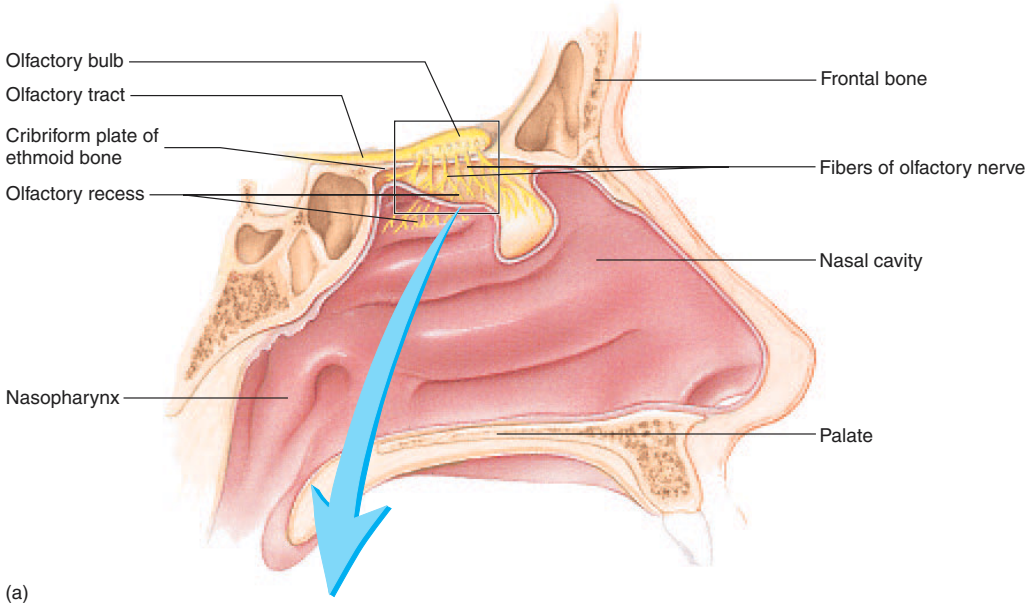
Objectives

- *Describe the histologic structure and function of the olfactory epithelium and the olfactory bulb.*
- *Describe the CNS connections for smell.*

Olfaction (ol-fak′shŭn), the sense of smell, occurs in response to odors that stimulate sensory receptors located in the extreme superior region of the nasal cavity, called the **olfactory recess** (figure 15.1*a*). Most of the nasal cavity is involved in respiration, with only a small superior part devoted to olfaction. During normal respiration, air passes through the nasal cavity without much of it entering the olfactory recess. The major anatomic features of the nasal cavity are described in chapter 23 in relation to respiration. The specialized nasal epithelium of the olfactory recess is called the **olfactory epithelium.**

P R E D I C T 1

Explain why it sometimes helps to inhale slowly and deeply through the nose when trying to identify an odor.



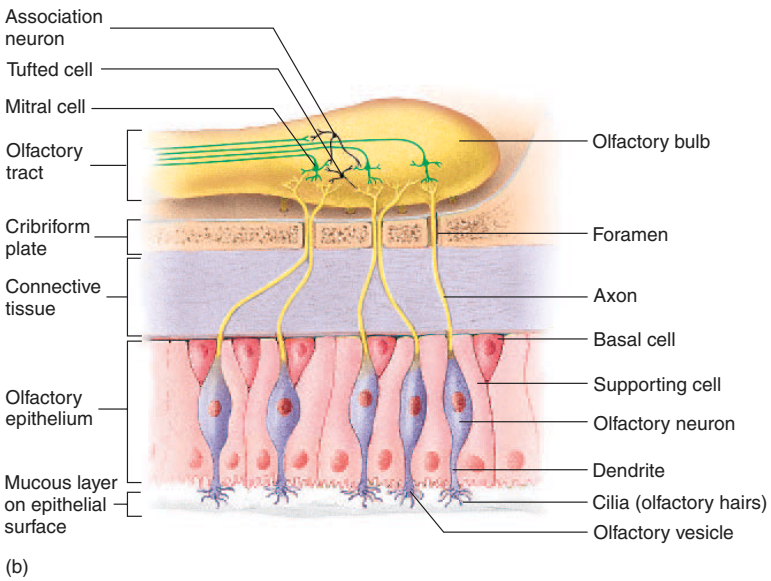


Figure 15.1 Olfactory Recess, Epithelium, and Bulb

(*a*) The lateral wall of the nasal cavity (cut in sagittal section), showing the olfactory recess and olfactory bulb. (*b*) The olfactory cells within the olfactory epithelium are shown. The olfactory nerve processes passing through the cribriform plate and the fine structure of the olfactory bulb are also shown.

Olfactory Epithelium and Bulb

Ten million **olfactory neurons** are present within the olfactory epithelium (figure 15.1*b*). The axons of these bipolar neurons project through numerous small foramina of the bony cribriform plate (see chapter 7) to the **olfactory bulbs. Olfactory tracts** project from the bulbs to the cerebral cortex.

The dendrites of olfactory neurons extend to the epithelial surface of the nasal cavity, and their ends are modified into bulbous enlargements called **olfactory vesicles** (see figure 15.1*b*). These vesicles possess cilia called **olfactory hairs,** which lie in a thin mucous film on the epithelial surface.

Airborne molecules enter the nasal cavity and are dissolved in the fluid covering the olfactory epithelium. Some of these molecules, referred to as **odorants** (ō′dŏr-ants; a molecule with an odor), bind to chemoreceptor molecules of the olfactory hair membranes. Although the exact nature of this interaction is not yet fully understood, it appears that the chemoreceptors are membrane receptor molecules that bind to odorants. Once an odorant has become bound to a receptor, the cilia of the olfactory neurons react by depolarizing and initiating action potentials in the olfactory neurons.

The mechanism of olfactory discrimination is not completely known. Most physiologists believe that the wide variety of detectable smells, which is about 4000 for the average person, are actually combinations of a smaller number of primary odors. Seven primary classes of odors have been proposed: (1) camphoraceous, (2) musky, (3) floral, (4) pepperminty, (5) ethereal, (6) pungent, and (7) putrid. It's very unlikely, however, that this list is an accurate representation of all primary odors, and some studies point to the possibility of as many as 50 primary odors.

The threshold for the detection of odors is very low, so very few odorant molecules are required to trigger the response. Apparently there is rather low specificity in the olfactory epithelium. A given receptor may react to more than one type of odorant.

The "Odor" of Natural Gas

Methylmercaptan, which has a nauseating odor similar to that of rotten cabbage, is added to natural gas at a concentration of about 1 part per million. A person can detect the odor of about 1/25 billionth of a milligram of the substance and therefore is aware of the presence of the more dangerous but odorless natural gas.

Odor Survey Results

The National Geographic Society conducted a smell survey in 1986, which was the largest sampling of its kind ever conducted. One and a half million people participated. Of six odors studied, 98%–99% of those responding could smell isoamyl acetate (banana), eugenol (cloves), mercaptans, and rose; but 29% could not smell galaxolide (musk), and 35% could not smell androstenone (contained in sweat). Of those responding to the survey, 1.2% could not smell at all, a disorder called **anosmia** (an-oz′mē-ă).

The primary olfactory neurons have the most exposed nerve endings of any neurons, and they are constantly being replaced. The entire olfactory epithelium, including the neurosensory cells, is lost about every 2 months as the olfactory epithelium degenerates and is lost from the surface. Lost olfactory cells are replaced by a proliferation of **basal cells** in the olfactory epithelium. This replacement of olfactory neurons is unique among neurons, most of which are permanent cells that have a very limited ability to replicate (see chapter 4).

Neuronal Pathways for Olfaction

Axons from the olfactory neurons (cranial nerve I) enter the olfactory bulb (see figure 15.1*b*), where they synapse with **mitral** (mī′trăl; triangular cells; shaped like a bishop's miter or hat) **cells** or **tufted cells.** The mitral and tufted cells relay olfactory information to the brain through the olfactory tracts and synapse with **association neurons** in the olfactory bulb. Association neurons also receive input from nerve cell processes entering the olfactory bulb from the brain. As a result of input from both mitral cells and the brain, association neurons can modify olfactory information before it leaves the olfactory bulb.

Olfaction is the only major sensation that is relayed directly to the cerebral cortex without first passing through the thalamus. Each olfactory tract terminates in an area of the brain called the **olfactory cortex** (figure 15.2). The olfactory cortex is in the frontal lobe, within the lateral fissure of the cerebrum, and can be divided structurally and functionally into three areas: lateral, intermediate, and medial. The **lateral olfactory area** is involved in the conscious perception of smell. The **medial olfactory area** is responsible for visceral and emotional reactions to odors and has connections to the limbic system, through which it connects to the hypothalamus. Axons extend from the **intermediate olfactory area** along the olfactory tract to the bulb, synapse with the association neurons, and thus constitute a major mechanism by which sensory information is modulated within the olfactory bulb.

1. *Describe the initiation of an action potential in an olfactory neuron. Name all the structures and cells that the action potential would encounter on the way to the olfactory cortex.*
2. *What is a primary odor? Name seven possible examples. How do the primary odors relate to our ability to smell many different odors?*
3. *What type of neurons are olfactory neurons? What is unique about olfactory neurons with respect to replacement?*
4. *How is the sense of smell modified in the olfactory bulb?*
5. *Name the three areas of the olfactory cortex, and give their functions.*
6. *Explain how the CNS connections elicit various visceral and conscious responses to smell.*

P R E D I C T 2

The olfactory system quickly adapts to continued stimulation, and a particular odor becomes unnoticed before very long, even though the odor molecules are still present in the air. Describe as many sites as you can in the olfactory pathways where such adaptation can occur.

1. Axons of the olfactory neurons in the olfactory epithelium project through foramina in the cribriform plate to the olfactory bulb.
2. Axon of neurons in the olfactory bulb project through the olfactory tract to the olfactory cortex.
3. The lateral olfactory area is involved in the conscious perception of smell.
4. The medial olfactory area is involved in the visceral and emotional reaction to odors.
5. The intermediate olfactory area receives input from the medial and lateral olfactory areas.
6. Axons from the intermediate olfactory area project along the olfactory tract to the olfactory bulb. Action potentials carried by those axons modulate the activity of the neurons in the olfactory bulb.

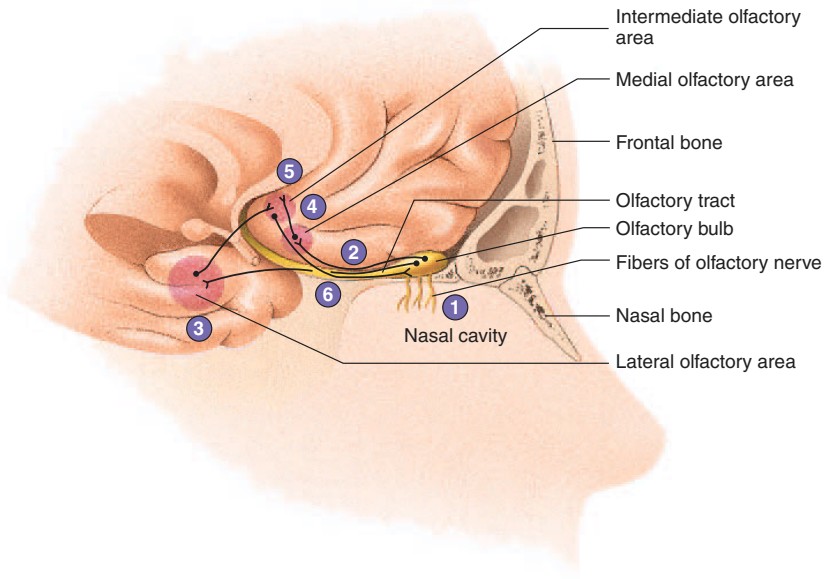


Figure 15.2 Olfactory Neuronal Pathways and Cortex

Taste

Objectives

- *Describe the types and locations of papillae on the tongue, and indicate which types have taste buds associated with them.*
- *Describe the histology and function of a typical taste bud.*
- *List the five primary tastes, and indicate for each taste how depolarization of the taste cell occurs.*
- *Describe the CNS pathways and cortical locations for taste.*

The sensory structures that detect **gustatory,** or **taste,** stimuli are the **taste buds.** Most taste buds are associated with specialized portions of the tongue called **papillae** (pă-pil′ē). Taste buds, however, are also located on other areas of the tongue, the palate, and even the lips and throat, especially in children. The four major types of papillae are named according to their shape (figure 15.3): **vallate** (val′āt; surrounded by a wall), **fungiform** (fŭn′ji-fōrm; mushroom-shaped), **foliate** (fō′lē-āt; leaf-shaped), and **filiform** (fil′i-fōrm; filament-shaped). Taste buds (figure 15.3*c–e*) are associated with vallate, fungiform, and foliate papillae. Filiform papillae are the most numerous papillae on the surface of the tongue but have no taste buds.

Vallate papillae are the largest but least numerous of the papillae. Eight to 12 of these papillae form a V-shaped row along the border between the anterior and posterior parts of the tongue (figure 15.3*a*). Fungiform papillae are scattered irregularly over the entire superior surface of the tongue and appear as small red dots interspersed among the far more numerous filiform papillae. Foliate papillae are distributed in folds on the sides of the tongue and contain the most sensitive of the taste buds. They are most numerous in young children and decrease with age. They are located mostly posteriorly in adults.

Histology of Taste Buds

Taste buds are oval structures embedded in the epithelium of the tongue and mouth (figure 15.3*f*). Each of the 10,000 taste buds on a person's tongue consists of two types of specialized epithelial cells. One type forms the exterior supporting capsule of the taste bud, whereas the interior of each bud consists of about 50 **taste** or **gustatory cells.** Like olfactory cells, cells of the taste buds are replaced continuously, each having a normal life span of about 10 days. Each taste cell has several microvilli, called **gustatory hairs,** extending from its apex into a tiny opening in the epithelium called the **taste** or **gustatory pore.**

Function of Taste

Substances called **tastants** (tās′tants), dissolved in saliva, enter the taste pore and, by various mechanisms, cause the taste cells to depolarize. These cells have no axons and don't generate their own action potentials. Neurotransmitters are released from the taste cells and stimulate action potentials in the axons of sensory neurons associated with them.

The taste of **salt** results when Na^+ diffuse through Na^+ channels (figure 15.4*a*) of the gustatory hairs or other cell surfaces of taste cells, resulting in depolarization of the cells. Hydrogen ions (H^+) of **acids** can cause depolarization of taste cells by one of three mechanisms (figure 15.4*b*): (1) they can enter the cell directly through H^+ channels, (2) they can bind to ligand-gated K^+ channels and block the exit of K^+ from the cell, or (3) they can open ligand-gated channels for other positive ions and allow them to diffuse into the cell. **Sweet** and **bitter** tastants bind to receptors (figure 15.4*c* and *d*) on the gustatory hairs of taste cells and cause depolarization through a G protein mechanism (see chapter 17). A new taste, called **umami** (ū-ma′mē; loosely translated as savory) by the Japanese, results when amino acids, such as glutamate, bind to

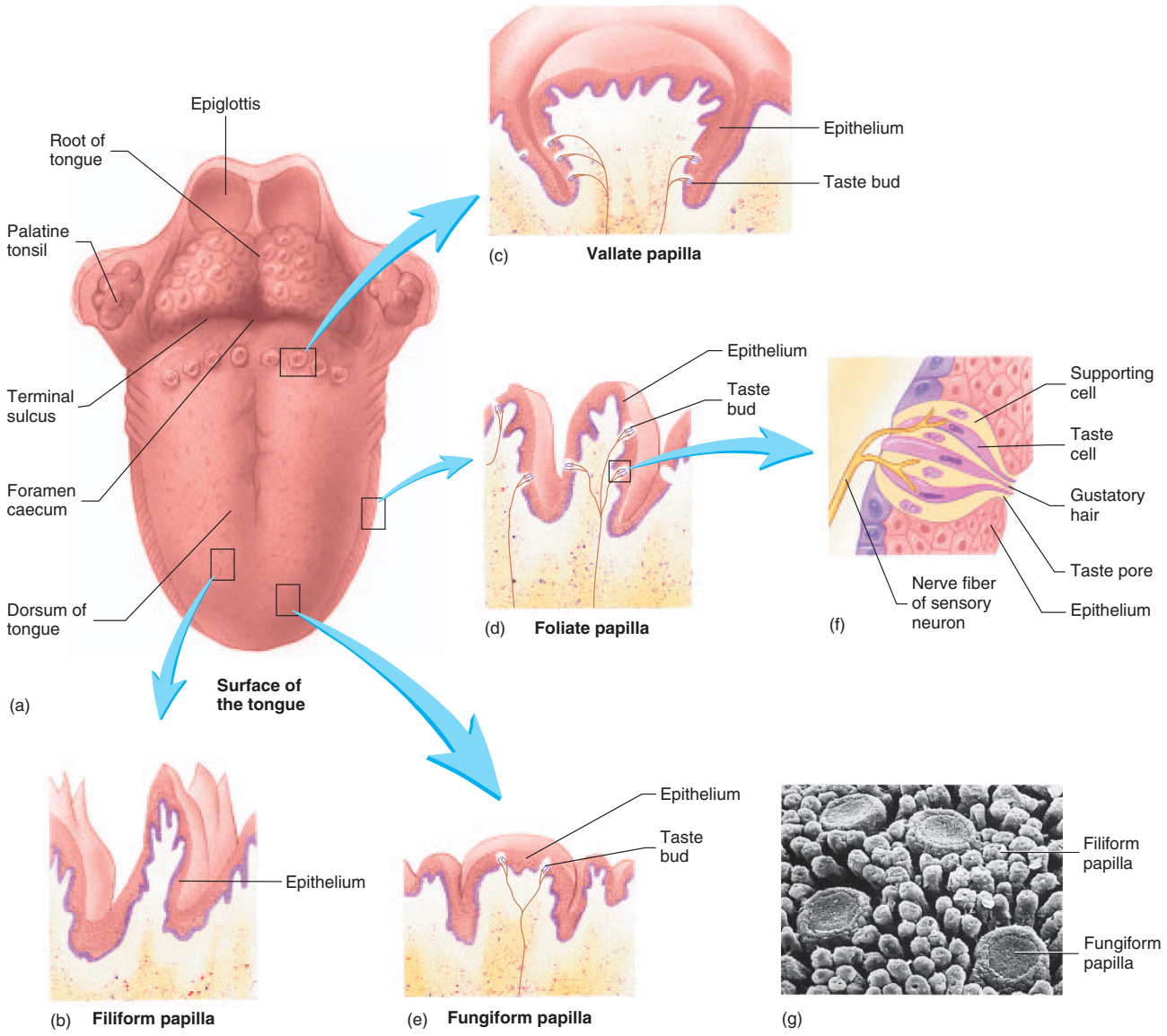


Figure 15.3 Papillae and Taste Buds

(*a*) Surface of the tongue. (*b*) Filiform papillae. (*c*) Vallate papillae. (*d*) Foliate papillae. (*e*) Fungiform papillae. (*f*) A taste bud. (*g*) Scanning electron micrograph of taste buds (fungiform and filiform papillae) on the surface of the tongue.

receptors (figure 15.4*e*) on gustatory hairs of taste cells and cause depolarization through a G protein mechanism.

The texture of food in the oral cavity also affects the perception of taste. Hot or cold food temperatures may interfere with the ability of the taste buds to function in tasting food. If a cold fluid is held in the mouth, the fluid becomes warmed by the body, and the taste becomes enhanced. On the other hand, adaptation is very rapid for taste. This adaptation apparently occurs both at the level of the taste bud and within the CNS. Adaptation may begin within 1 or 2 seconds after a taste sensation is perceived, and complete adaptation may occur within 5 minutes.

Even though only five primary tastes have been identified, humans can perceive a fairly large number of different tastes, presumably by combining the five basic taste sensations. As with olfaction, the specificity of the receptor molecules is not perfect. For example, artificial sweeteners have different chemical structures than the sugars they are designed to replace and are often many times more powerful than natural sugars in stimulating taste sensations.

Many of the sensations thought of as being taste are strongly influenced by olfactory sensations. This phenomenon can be demonstrated by pinching one's nose to close the nasal passages, while trying to taste something. With olfaction blocked, it's difficult to distinguish

(a) **Salt:** Na^+ diffuse through Na^+ channels, resulting in depolarization.

(b) **Acid:** Hydrogen ions (H^+) from acids can cause depolarization by one of three mechanisms: (1) they can enter the cell directly through H^+ channels, (2) they can bind to gated K^+ channels, closing the gate, and preventing K^+ from entering the cell, or (3) they can open ligand-gated channels for other positive ions.

(c) **Sweet:** Sugars, such as glucose, or artificial sweeteners bind to receptors and cause the cell to depolarize by means of a G protein mechanism. (GDP = guanosine diphosphate)

(d) **Bitter:** Bitter tastants, such as quinine, bind to receptors and cause depolarization of the cell through a G protein mechanism.

(e) **Glutamate (umami):** Amino acids, such as glutamate, bind to receptors and cause depolarization through a G protein mechanism.

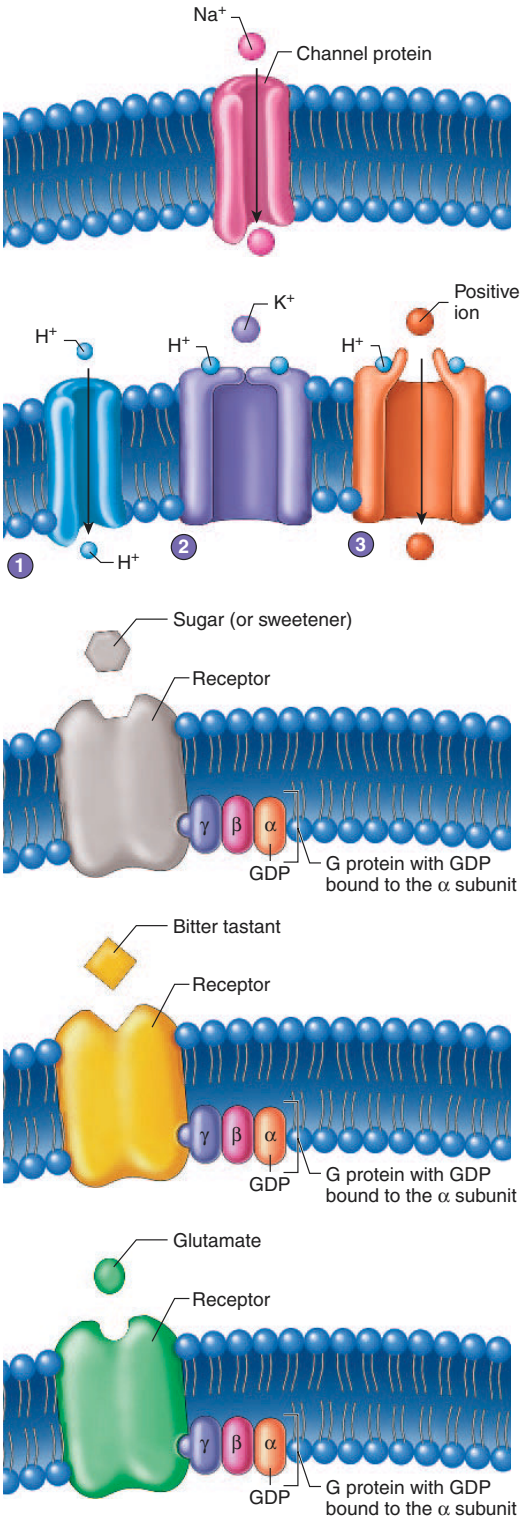


Figure 15.4 Actions of the Major Tastants

between the taste of a piece of apple and a piece of potato. Much of the "taste" is lost by this action. Although all taste buds are able to detect all five of the basic tastes, each taste cell is usually most sensitive to one.

Thresholds vary for the five primary tastes. Sensitivity for bitter substances is the highest; sensitivities for sweet and salty tastes are the lowest. Sugars, some other carbohydrates, and some proteins produce sweet tastes; many proteins and amino acids produce umami tastes; acids produce sour tastes; metal ions tend to produce salty tastes; and alkaloids (bases) produce bitter tastes. Many alkaloids are poisonous; thus the high sensitivity for bitter tastes may be protective. On the other hand, humans tend to crave sweet, salty, and umami tastes, perhaps in response to the body's need for sugars, carbohydrates, proteins, and minerals.

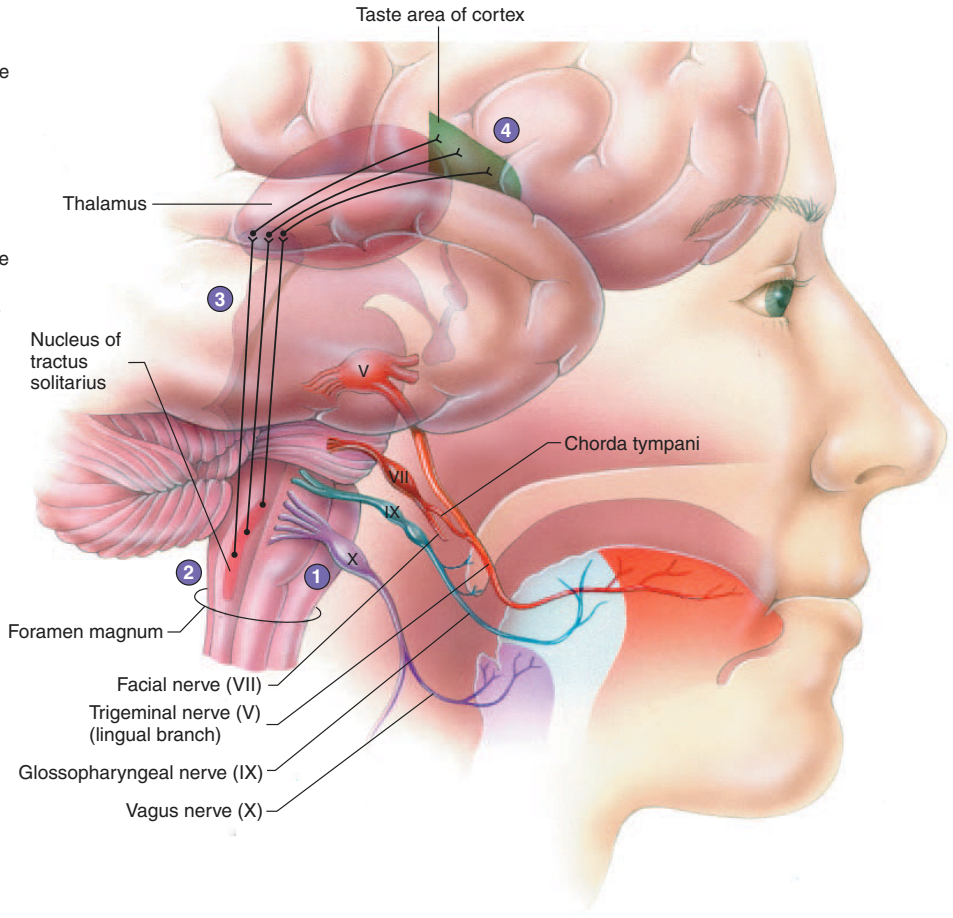
Neuronal Pathways for Taste

Taste from the anterior two-thirds of the tongue, except from the circumvallate papillae, is carried by means of a branch of the facial nerve (VII) called the **chorda tympani** (kōr′dă tim′pă-nē; so named because it crosses over the surface of the tympanic membrane of the middle ear). Taste from the posterior one-third of the tongue, the circumvallate papillae, and the superior pharynx is carried by means of the glossopharyngeal nerve (IX). In addition to these two major nerves, the vagus nerve (X) carries a few fibers for taste sensation from the epiglottis.

These nerves extend from the taste buds to the tractus solitarius of the medulla oblongata (figure 15.5). Fibers from this nucleus decussate and extend to the thalamus. Neurons from the thalamus project to the taste area of the cortex, which is at the extreme inferior end of the postcentral gyrus.

7. *Name and describe the four kinds of papillae found on the tongue. Which ones have taste buds associated with them?*
8. *Starting with the gustatory hair, name the structures and cells that an action potential would encounter on the way to the taste area of the cerebral cortex.*
9. *What is the life span of a normal gustatory cell?*
10. *What are the five primary tastes? Describe how each type of tastant causes depolarization of a taste cell.*
11. *How is the sense of taste related to the sense of smell?*

1. Axons of sensory neurons, which synapse with taste receptors, pass through cranial nerves VII, IX, and X and through the ganglion of each nerve (enlarged portion of each nerve).
2. The axons enter the brainstem and synapse in the nucleus of the tractus solitarius.
3. Axons from the nucleus solitarius synapse in the thalamus.
4. Axons from the thalamus terminate in the taste area of the cortex.



Process Figure 15.5 Pathways for the Sense of Taste

The facial nerve (anterior two-thirds of the tongue), glossopharyngeal nerve (posterior one-third of the tongue), and vagus nerve (root of the tongue) all carry taste sensations. The trigeminal nerve is also shown. It carries tactile sensations from the anterior two-thirds of the tongue. The chorda tympani from the facial nerve (carrying taste input) joins the trigeminal nerve.

Visual System

Objective

- ***List the accessory structures of the eye, and explain their functions.***

The visual system includes the eyes, the accessory structures, and the optic nerves (II), tracts, and pathways. The eyes respond to light and initiate afferent action potentials, which are transmitted from the eyes to the brain by the optic nerves and tracts. The accessory structures, such as eyebrows, eyelids, eyelashes, and tear glands, help protect the eyes from direct sunlight and damaging particles. Much of the information about the world around us is detected by the visual system. Our education is largely based on visual input and depends on our ability to read words and numbers. Visual input includes information about light and dark, color and hue.

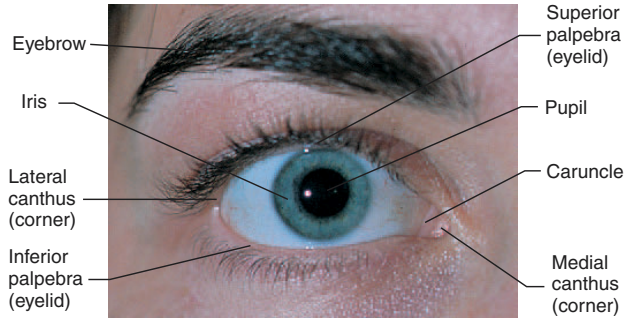


Figure 15.6 The Right Eye and Its Accessory Structures

Accessory Structures

Accessory structures protect, lubricate, move, and in other ways aid in the function of the eye. These structures include the eyebrows, eyelids, conjunctiva, lacrimal apparatus, and extrinsic eye muscles.

Eyebrows

The **eyebrows** (figure 15.6) protect the eyes by preventing perspiration, which can irritate the eyes, from running down the forehead and into them, and they help shade the eyes from direct sunlight.

Eyelids

The **eyelids,** also called **palpebrae** (pal-pē′brē), with their associated lashes, protect the eyes from foreign objects. The space between the two eyelids is called the **palpebral fissure,** and the angles where the eyelids join at the medial and lateral margins of the eye are called **canthi** (kan′thī; corners of the eye) (see figure 15.6). The medial canthus contains a small reddish-pink mound called the **caruncle** (kar′ŭng-kl; a mound of tissue). The caruncle contains some modified sebaceous and sweat glands.

The eyelids consist of five layers of tissue (figure 15.7). From the outer to the inner surface, they are (1) a thin layer of integument on the external surface; (2) a thin layer of areolar connective tissue; (3) a layer of skeletal muscle consisting of the orbicularis oculi and levator palpebrae superioris muscles; (4) a crescent-shaped layer of dense connective tissue called the **tarsal** (tar′săl) **plate,** which helps maintain the shape of the eyelid; and (5) the palpebral conjunctiva (described in the next section), which lines the inner surface of the eyelid and the anterior surface of the eyeball.

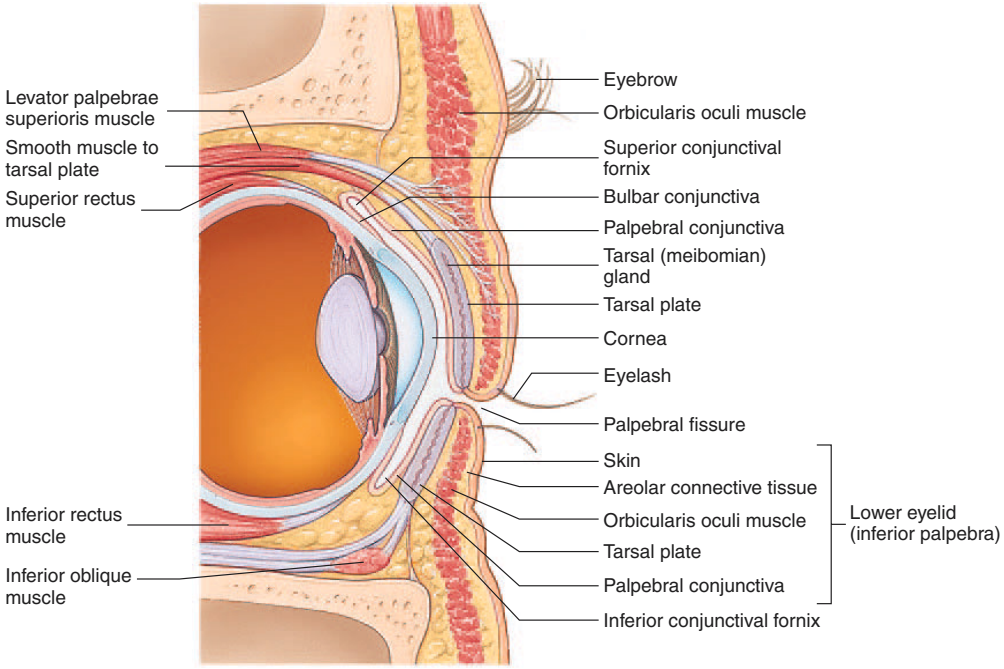


Figure 15.7 Sagittal Section Through the Eye Showing Its Accessory Structures

If an object suddenly approaches the eye, the eyelids protect the eye by rapidly closing and then opening (blink reflex). Blinking, which normally occurs about 25 times per minute, also helps keep the eye lubricated by spreading tears over the surface of the eye. Movements of the eyelids are a function of skeletal muscles. The orbicularis oculi muscle closes the lids, and the levator palpebrae superioris elevates the upper lid (see chapter 10). The eyelids also help regulate the amount of light entering the eye.

Eyelashes (see figures 15.6 and 15.7) are attached as a double or triple row of hairs to the free edges of the eyelids. **Ciliary glands** are modified sweat glands that open into the follicles of the eyelashes to keep them lubricated. When one of these glands becomes inflamed, it's called a **sty. Meibomian** (mī-bō′mē-an; also called tarsal) **glands** are sebaceous glands near the inner margins of the eyelids and produce **sebum** (sē′bŭm; an oily semifluid substance), which lubricates the lids and restrains tears from flowing over the margin of the eyelids. An infection or blockage of a meibomian gland is called a **chalazion** (ka-lā′zē-on), or **meibomian cyst.**

Conjunctiva

The **conjunctiva** (kon-jŭnk-tī′vă) (see figure 15.7) is a thin, transparent mucous membrane. The **palpebral conjunctiva** covers the inner surface of the eyelids, and the **bulbar conjunctiva** covers the anterior surface of the eye. The points at which the palpebral and bulbar conjunctivae meet are the superior and inferior **conjunctival fornices.**

Conjunctivitis

Conjunctivitis is an inflammation of the conjunctiva caused by infection or some other irritation. An example of conjunctivitis caused by a bacterium is **acute contagious conjunctivitis,** also called **pinkeye.**

Lacrimal Apparatus

The **lacrimal** (lak′ri-măl) **apparatus** (figure 15.8) consists of a lacrimal gland situated in the superolateral corner of the orbit and a nasolacrimal duct beginning in the inferomedial corner of the orbit. The **lacrimal gland** is innervated by parasympathetic fibers from the facial nerve (VII). The gland produces tears, which leave the gland through several ducts and pass over the anterior surface of the eyeball. Tears are produced constantly by the gland at the rate of about 1 mL/day to moisten the surface of the eye, lubricate the eyelids, and wash away foreign objects. Tears are mostly water, with some salts, mucus, and lysozyme, an enzyme that kills certain bacteria. Most of the fluid produced by the lacrimal glands evaporates from the surface of the eye, but excess tears are collected in the medial corner of the eye by the **lacrimal canaliculi.** The opening of each lacrimal canaliculus is called a **punctum** (pŭngk′tŭm). The upper and lower eyelids each have a punctum near the medial canthus. Each punctum is located on a small lump called the **lacrimal papilla.** The lacrimal canaliculi open into a **lacrimal sac,** which in turn continues into the **nasolacrimal duct** (see figure 15.8). The nasolacrimal duct opens into the inferior meatus of the nasal cavity beneath the inferior nasal concha (see chapter 23).

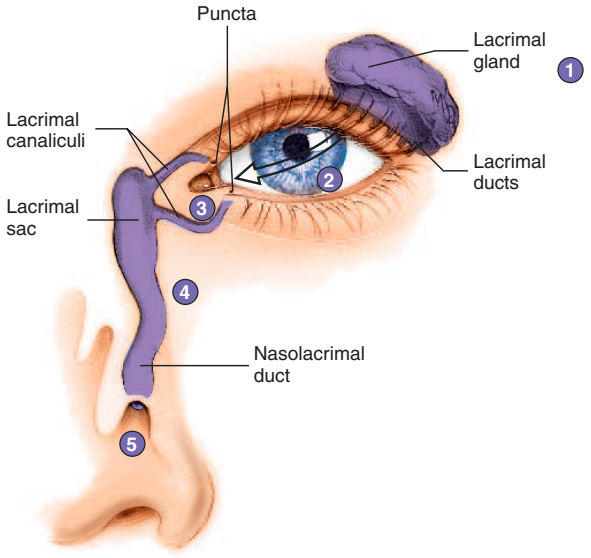
Facial Nerve Damage

Facial nerve damage results in the inability to close the eyelid on the affected side. With the ability to blink being lost, tears cannot be washed across the eye, and the conjunctiva and cornea become dry. A dry cornea may become ulcerated, and, if not treated, eyesight may be lost.

P R E D I C T 3

Explain why it's often possible to "taste" medications, such as eyedrops, that have been placed into the eyes. Why does a person's nose "run" when he or she cries?

1. Tears are produced in the lacrimal gland.
2. The tears pass over the surface of the eye.
3. Tears enter the lacrimal canaliculi.
4. Tears are carried through the nasolacrimal duct.
5. Tears enter the nasal cavity from the nasolacrimal duct.



Process Figure 15.8 The Lacrimal Apparatus

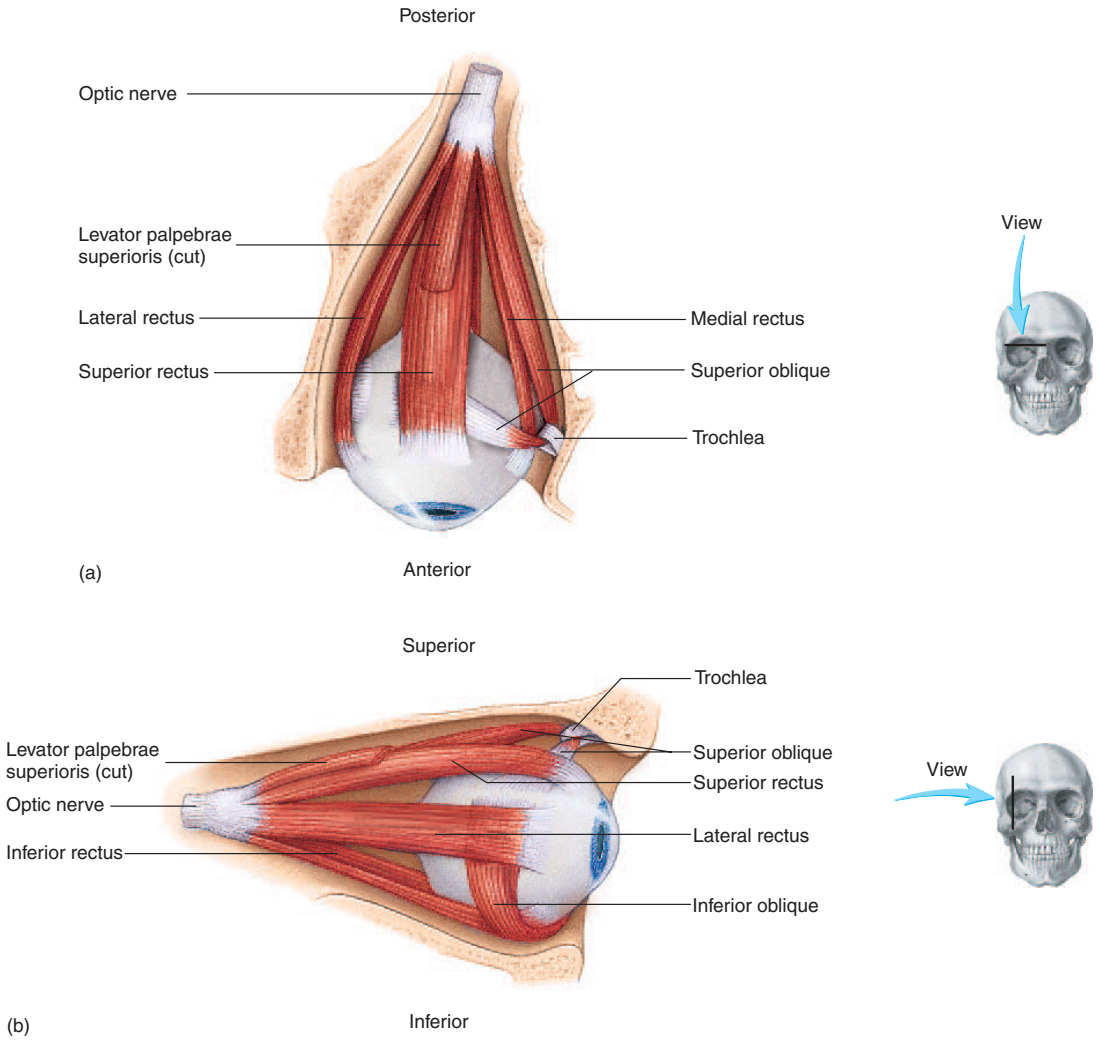


Figure 15.9 Extrinsic Muscles of the Eye

(*a*) Superior view. (*b*) Lateral view.

Extrinsic Eye Muscles

Six **extrinsic muscles** of the eye (figures 15.9 and 15.10; also see chapter 10) cause the eyeball to move. Four of these muscles run more or less straight anteroposteriorly. They are the superior, inferior, medial, and lateral **rectus muscles.** Two muscles, the superior and inferior **oblique muscles,** are placed at an angle to the globe of the eye.

The movements of the eye can be described graphically by a figure resembling the letter *H.* The clinical test for normal eye movement is therefore called the **H test.** A person's inability to move his eye toward one part of the H may indicate dysfunction of an extrinsic eye muscle or the cranial nerve to the muscle (the actions of the eye muscles are listed in table 10.7).

The superior oblique muscle is innervated by the trochlear nerve (IV). The nerve is so named because the superior oblique muscle goes around a little pulley, or trochlea, in the superomedial

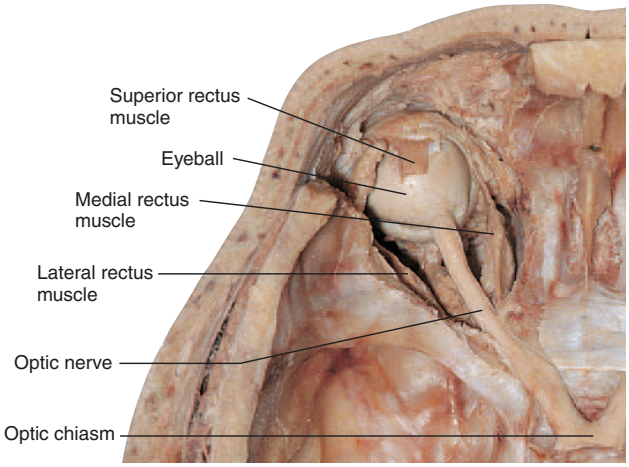


Figure 15.10 Photograph of the Eye and Its Associated Structures from a Superior View

corner of the orbit. The lateral rectus muscle is innervated by the abducens nerve (VI), so named because the lateral rectus muscle abducts the eye. The other four extrinsic eye muscles are innervated by the oculomotor nerve (III).

12. *Describe and state the functions of the eyebrows, eyelids, conjunctiva, lacrimal apparatus, and extrinsic eye muscles.*

Anatomy of the Eye

Objectives

- *Describe the tunics of the eye, and give the function of each of their parts.*
- *What are light refraction and reflection, and how are images focused on the retina?*
- *Describe the structure and function of the cells in the layers of the retina.*

The eye is composed of three coats, or tunics (figure 15.11). The outer, or **fibrous, tunic** consists of the sclera and cornea; the middle, or **vascular, tunic** consists of the choroid, ciliary body, and iris; and the inner, or **nervous, tunic** consists of the retina.

Fibrous Tunic

The **sclera** (sklēr′ă) is the firm, opaque, white outer layer of the posterior five-sixths of the eye. It consists of dense collagenous connective tissue with elastic fibers. The sclera helps maintain the shape of the eye, protects its internal structures, and provides an attachment point for the muscles that move it. Usually, a small portion of the sclera can be seen as the "white of the eye" when the eye and its surrounding structures are intact (see figure 15.6).

The sclera is continuous anteriorly with the cornea. The **cornea** (kōr′nē-ă) is an avascular, transparent structure that permits light to enter the eye and bends, or refracts, that light as part of the focusing system of the eye. The cornea consists of a connective tissue matrix containing collagen, elastic fibers, and proteoglycans, with a layer of stratified squamous epithelium covering the outer surface and a layer of simple squamous epithelium on the inner surface. Large collagen fibers are white, whereas smaller collagen fibers and proteoglycans are transparent. The cornea is transparent, rather than white like the sclera, in part because fewer large collagen fibers and more proteoglycans are present in the cornea than in the sclera. The transparency of the cornea also results from its low water content. In the presence of water, proteoglycans trap water and expand, which scatters light. In the absence of water, the proteoglycans decrease in size and do not interfere with the passage of light through the matrix.

PREDICT 4

Predict the effect of inflammation of the cornea on vision.

The Cornea

The central part of the cornea receives oxygen from the outside air. Soft plastic contact lenses worn for long periods must therefore be permeable to air so that air can reach the cornea.

The most common eye injuries are cuts or tears of the cornea caused by foreign objects like stones or sticks hitting the cornea. Extensive injury to the cornea may cause connective tissue deposition, thereby making the cornea opaque.

The cornea was one of the first organs transplanted. Several characteristics make it relatively easy to transplant: It's easily accessible and relatively easily removed; it's avascular and therefore does not require as extensive circulation as do other tissues; and it's less immunologically active and therefore less likely to be rejected than other tissues.

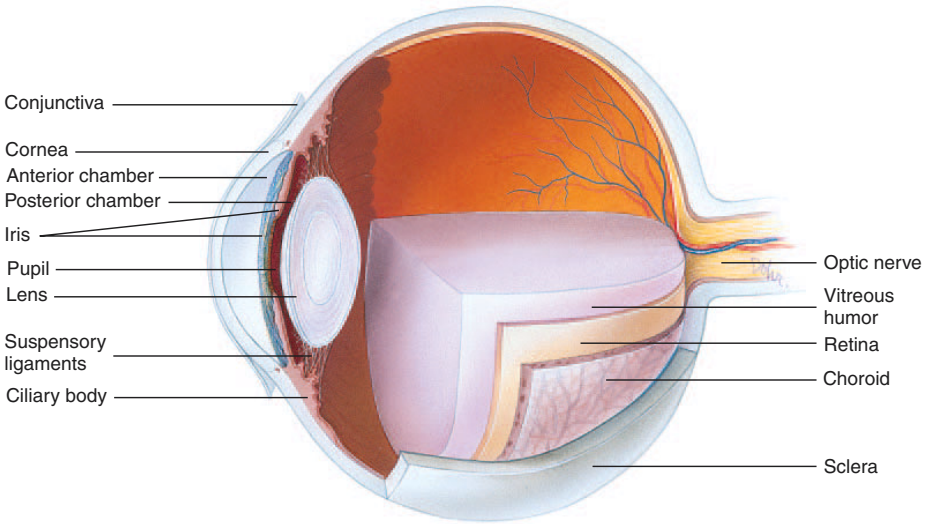


Figure 15.11 Sagittal Section of the Eye Demonstrating Its Layers

Vascular Tunic

The middle tunic of the eyeball is called the vascular tunic because it contains most of the blood vessels of the eyeball (see figure 15.11). The arteries of the vascular tunic are derived from a number of arteries called **short ciliary arteries,** which pierce the sclera in a circle around the optic nerve. These arteries are branches of the **ophthalmic** (of-thal′mik) **artery,** which is a branch of the internal carotid artery. The vascular tunic contains a large number of melanin-containing pigment cells and appears black in color. The portion of the vascular tunic associated with the sclera of the eye is the **choroid** (ko′royd). The term *choroid* means membrane and suggests that this layer is relatively thin (0.1–0.2 mm thick). Anteriorly, the vascular tunic consists of the ciliary body and iris.

The **ciliary** (sil′ē-ar-ē) **body** is continuous with the choroid, and the **iris** is attached at its lateral margins to the ciliary body (figure 15.12*a* and *b*). The ciliary body consists of an outer **ciliary ring** and an inner group of **ciliary processes,** which are attached to the lens by **suspensory ligaments.** The ciliary body contains smooth muscles called the **ciliary muscles,** which are arranged with the outer muscle fibers oriented radially and the central fibers oriented circularly. The ciliary muscles function as a sphincter, and contraction of these muscles can change the shape of the lens. (This

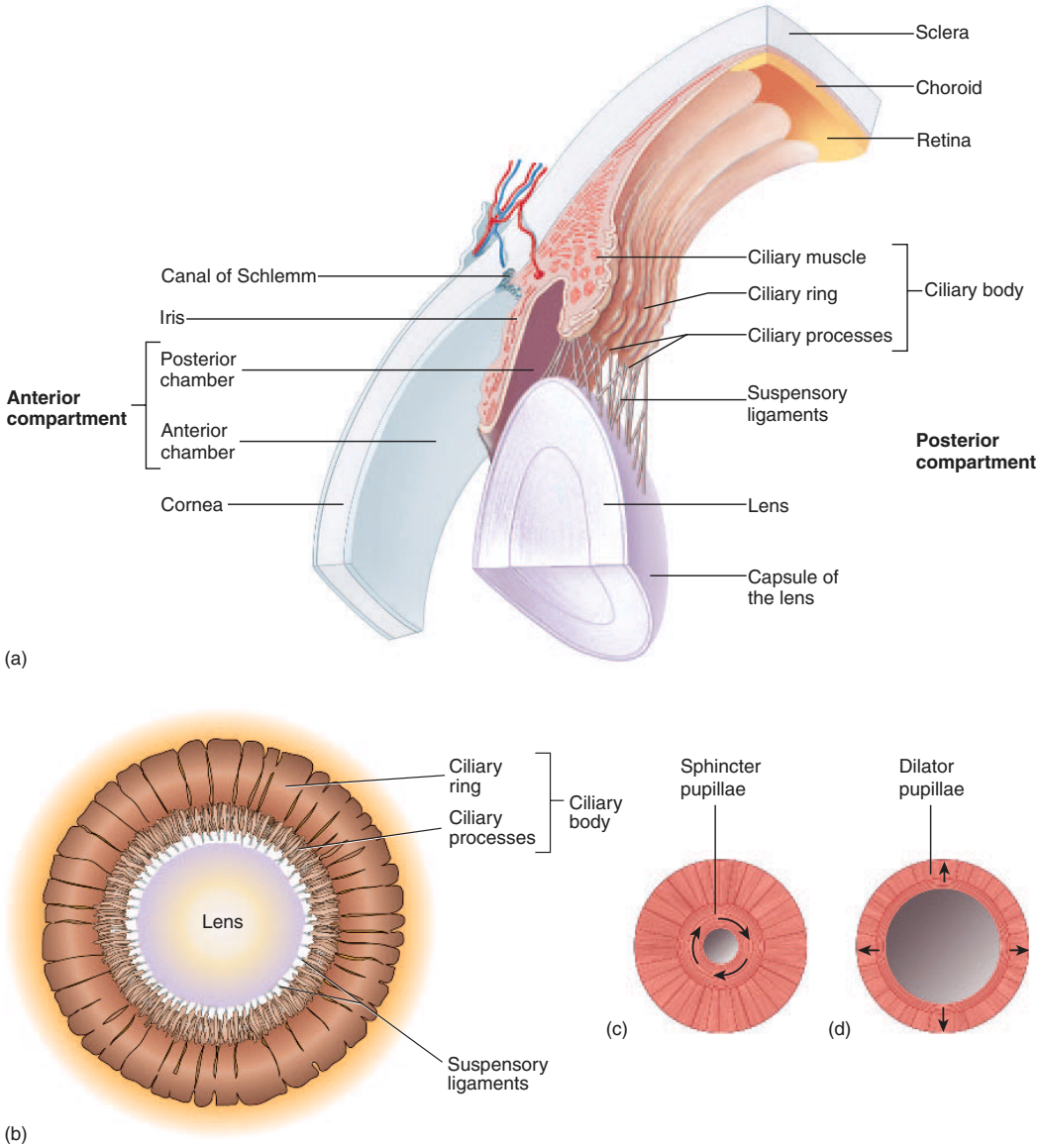


Figure 15.12 Lens, Cornea, Iris, and Ciliary Body

(*a*) The orientation is the same as in figure 15.11. (*b*) The lens and ciliary body. (*c*) The sphincter pupillae muscles of the iris constrict the pupil. (*d*) The dilator pupillae muscles of the iris dilate the pupil.

function is described in more detail on p. 515.) The ciliary processes are a complex of capillaries and cuboidal epithelium that produces aqueous humor.

The **iris** is the "colored part" of the eye, and its color differs from person to person. Brown eyes have brown melanin pigment in the iris. Blue eyes are not caused by a blue pigment but result from the scattering of light by the tissue of the iris, overlying a deeper layer of black pigment. The blue color is produced in a fashion similar to the scattering of light as it passes through the atmosphere to form the blue skies from the black background of space.

The iris is a contractile structure, consisting mainly of smooth muscle, surrounding an opening called the **pupil.** Light enters the eye through the pupil, and the iris regulates the amount of light by controlling the size of the pupil. The iris contains two groups of smooth muscles: a circular group called the **sphincter pupillae** (pū-pil′ē), and a radial group called the **dilator pupillae** (figure 15.12*c* and *d*). The sphincter pupillae are innervated by parasympathetic fibers from the oculomotor nerve (III). When they contract, the iris decreases or constricts the size of the pupil. The dilator pupillae are innervated by sympathetic fibers. When they contract, the pupil is dilated. The ciliary muscles, sphincter pupillae, and dilator pupillae are sometimes referred to as the intrinsic eye muscles.

Retina

The **retina** is the innermost, nervous tunic of the eye (see figure 15.11). It consists of the outer **pigmented retina,** which is pigmented simple cuboidal epithelium, and the inner **sensory retina,** which responds to light. The sensory retina contains 120 million photoreceptor cells called **rods** and another 6 or 7 million **cones,** as well as numerous relay neurons. The retina covers the inner surface of the eye posterior to the ciliary body. A more detailed description of the histology and function of the retina is presented on page 516 and following.

Eye Pigment

The pupil appears black when you look into a person's eye because of the pigment in the choroid and the pigmented portion of the retina. The eye is a closed chamber, which allows light to enter only through the pupil. Light is absorbed by the pigmented inner lining of the eye; thus looking into it is like looking into a dark room. If a bright light is directed into the pupil, however, the reflected light is red because of the blood vessels on the surface of the retina. This is why the pupils of a person looking directly at a flash camera often appear red in a photograph. People with albinism lack the pigment melanin, and the pupil always appears red because no melanin is present to absorb light and prevent it from being reflected from the back of the eye. The diffusely lighted blood vessels in the interior of the eye contribute to the red color of the pupil.

When the posterior region of the retina is examined with an **ophthalmoscope** (of-thal′mō-skōp) (figure 15.13), several important features can be observed. Near the center of the posterior retina is a small yellow spot approximately 4 mm in diameter, the **macula lutea** (mak′ū-lă lū′tē-ă). In the center of the macula lutea is a small pit, the **fovea** (fō′vē-ă) **centralis.** The fovea and macula make up the region of the retina where light is focused. The fovea is the portion of the retina with the greatest visual acuity, the ability to see fine images, because the photoreceptor cells are more tightly packed in that portion of the retina than anywhere else. Just medial to the macula lutea is a white spot, the **optic disc,** through which blood vessels enter the eye and spread over the surface of the retina. This is also the spot where nerve processes from the sensory retina meet, pass through the outer two tunics, and exit the eye as the optic nerve. The optic disc contains no photoreceptor cells and does not respond to light; therefore it's called the **blind spot** of the eye.

Ophthalmoscopic Examination of the Retina

Ophthalmoscopic examination of the posterior retina can reveal some general disorders of the body. **Hypertension,** or high blood pressure, results in "nicking" (compression) of the retinal veins where the abnormally pressurized arteries cross them. **Increased cerebrospinal fluid (CSF) pressure** associated with hydrocephalus may cause swelling of the optic disc. This swelling is referred to as **papilledema** (pă-pil-e-dē′mă).

Compartments of the Eye

Two major compartments exist within the eye, a larger compartment posterior to the lens and a much smaller compartment anterior to the lens (see figure 15.11). The **anterior compartment** is divided into two chambers: the **anterior chamber** lies between the cornea and iris, and a smaller **posterior chamber** lies between the iris and lens (see figure 15.12). These two chambers are filled with **aqueous humor,** which helps maintain intraocular pressure. The

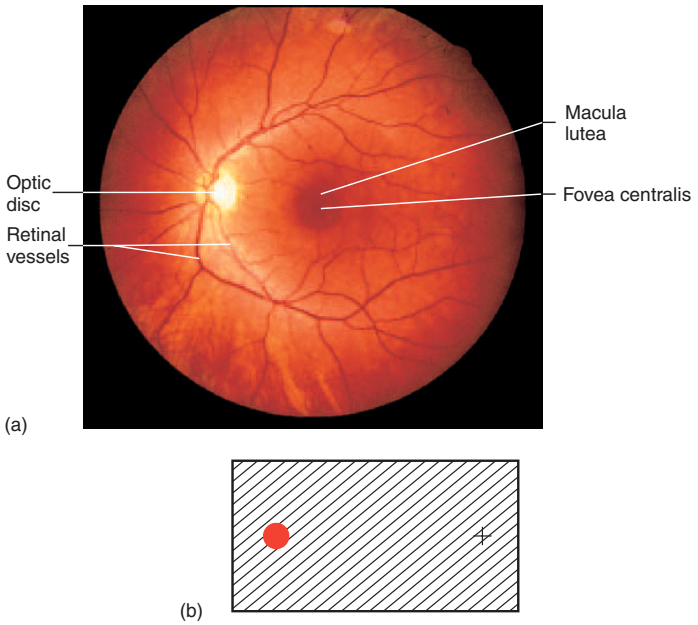


Figure 15.13 Ophthalmoscopic View of the Left Retina

(*a*) The posterior wall of the retina as seen when looking through the pupil. Notice the vessels entering the eye through the optic disc (the optic nerve) and the macula lutea with the fovea (the part of the retina with the greatest visual acuity). (*b*) Demonstration of the blind spot. Close your right eye. Hold the figure in front of your left eye and stare at the +. Move the figure toward your eye. At a certain point, when the image of the spot is over the optic disc, the red spot seems to disappear.

pressure within the eye keeps the eye inflated and is largely responsible for maintaining the shape of the eye. The aqueous humor also refracts light and provides nutrition for the structures of the anterior chamber, such as the cornea, which has no blood vessels. Aqueous humor is produced by the ciliary processes as a blood filtrate and is returned to the circulation through a venous ring at the base of the cornea called the **canal of Schlemm** (shlem), or the **scleral venous sinus** (see figure 15.12). The production and removal of aqueous humor results in "circulation" of aqueous humor and maintenance of a constant intraocular pressure. If circulation of the aqueous humor is inhibited, a defect called **glaucoma** (glaw-kō′mă), which is an abnormal increase in intraocular pressure, can result (see the Clinical Focus on "Eye Disorders").

The posterior compartment of the eye is much larger than the anterior compartment. It's surrounded almost completely by the retina and is filled with a transparent jellylike substance, the **vitreous** (vit′rē-ŭs) **humor.** The vitreous humor is not produced as rapidly as is the aqueous humor, and its turnover is extremely slow. The vitreous humor helps maintain intraocular pressure and therefore the shape of the eyeball, and it holds the lens and the retina in place. It also functions in the refraction of light in the eye.

Lens

The **lens** is an unusual biologic structure. Transparent and biconvex, with the greatest convexity on its posterior side, the lens consists of a layer of cuboidal epithelial cells on its anterior surface and a posterior region of very long columnar epithelial cells called **lens fibers.** Cells from the anterior epithelium proliferate and give rise to the lens fibers at the equator of the lens. The lens fibers lose their nuclei and other cellular organelles and accumulate a special set of proteins called **crystallines.** This crystalline lens is covered by a highly elastic transparent **capsule.**

The lens is suspended between the two eye compartments by the suspensory ligaments of the lens, which are connected from the ciliary body to the lens capsule.

13. *Name the three layers (tunics) of the eye, describe the parts or structures each forms, and explain their functions.*
14. *How does the pupil constrict? How does it dilate? What is the blind spot?*
15. *Name the two compartments of the eye and the substances that fill each compartment.*
16. *What is the function of the canal of Schlemm and the ciliary processes?*
17. *Describe the lens of the eye, and explain how the lens is held in place.*

Functions of the Complete Eye

The eye functions much like a camera. The iris allows light into the eye, and the lens, cornea, and humors focus the light onto the retina. The light striking the retina is converted into action potentials that are relayed to the brain.

Light

The electromagnetic spectrum is the entire range of wavelengths or frequencies of electromagnetic radiation from very short gamma waves at one end of the spectrum to the longest radio waves at the other end (figure 15.14). **Visible light** is the portion of the electromagnetic spectrum that can be detected by the human eye. Light has characteristics of both particles (photons) and

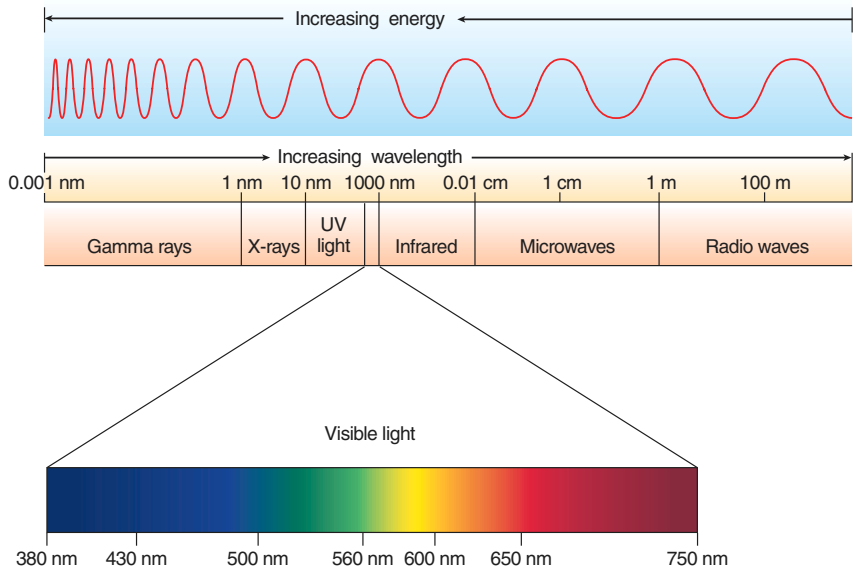


Figure 15.14 The Electromagnetic Spectrum

The spectrum of visible light is pulled out and expanded. The wavelengths of the various colors are also depicted.

waves, with a wavelength between 400 and 700 nm. This range sometimes is called the range of visible light or, more correctly, the **visible spectrum.** Within the visible spectrum, each color has a different wavelength.

Light Refraction and Reflection

An important characteristic of light is that it can be refracted (bent). As light passes from air to a denser substance like glass or water, its speed is reduced. If the surface of that substance is at an angle other than 90 degrees to the direction the light rays are traveling, the rays are bent as a result of variation in the speed of light as it encounters the new medium. This bending of light is called **refraction.**

If the surface of a lens is concave, with the lens thinnest in the center, the light rays diverge as a result of refraction. If the surface is convex, with the lens thickest in the center, the light rays tend to converge. As light rays converge, they finally reach a point at which they cross. This point is called the **focal point,** and causing light to converge is called **focusing.** No image is formed exactly at the focal point, but an inverted, focused image can form on a surface located some distance past the focal point. How far past the focal point the focused image forms depends on a number of factors. A biconvex lens causes light to focus closer to the lens than does a lens with a single convex surface. Furthermore, the more nearly spherical the lens, the closer to the lens the light is focused; the more flattened the biconcave lens, the more distant is the point where the light is focused.

If light rays strike an object that is not transparent, they bounce off the surface. This phenomenon is called **reflection.** If the surface is very smooth, such as the surface of a mirror, the light rays bounce off in a specific direction. If the surface is rough, the light rays are reflected in several directions and produce a more diffuse reflection. We can see most solid objects because of the light reflected from their surfaces.

Focusing of Images on the Retina

The focusing system of the eye projects a clear image on the retina. Light rays converge as they pass from the air through the convex cornea. Additional convergence occurs as light encounters the aqueous humor, lens, and vitreous humor. The greatest contrast in media density is between the air and the cornea; therefore, the greatest amount of convergence occurs at that point. The shape of the cornea and its distance from the retina are fixed, however, so that no adjustment in the location of the focal point can be made by the cornea. Fine adjustment in focal point location is accomplished by changing the shape of the lens. In general, focusing can be accomplished in two ways. One is to keep the shape of the lens constant and move it nearer or farther from the point at which the image will be focused, such as occurs in a camera, microscope, or telescope. The second way is to keep the distance constant and to change the shape of the lens, which is the technique used in the eye.

As light rays enter the eye and are focused, the image formed just past the focal point is inverted (figure 15.15). Action potentials that represent the inverted image are passed to the visual cortex of the cerebrum, where they are interpreted by the brain as being right side up.

Visual Image Inversion

Because the visual image is inverted when it reaches the retina, the image of the world focused on the retina is upside down. The brain processes information from the retina so that the world is perceived the way "it really is." If, as an experiment, a person wears glasses that invert the image entering the eye, he or she will see the world upside down for a few days, after which time the brain adjusts to the new input to set the world right side up again. If the glasses are then removed, another adjustment period is required before the world is made right by the brain.

When the ciliary muscles are relaxed, the suspensory ligaments of the ciliary body maintain elastic pressure on the lens, thereby keeping it relatively flat and allowing for distant vision (figure 15.15*a*). The condition in which the lens is flattened so that nearly parallel rays from a distant object are focused on the retina

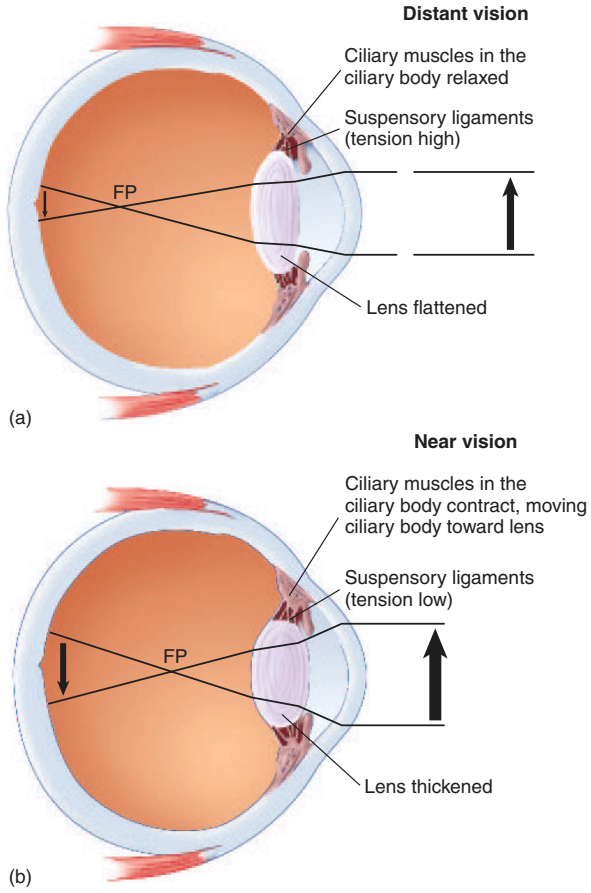


Figure 15.15 Focus and Accommodation by the Eye

The focal point (FP) is where light rays cross. (*a*) Distant image. The lens is flattened, and the image is focused on the retina. (*b*) Accommodation for near vision. The lens is more rounded, and the image is focused on the retina.

is referred to as **emmetropia** (em-ĕ-trō′pē-ă; measure) and is the normal resting condition of the lens. The point at which the lens does not have to thicken for focusing to occur is called the **far point of vision** and normally is 20 feet or more from the eye.

When an object is brought closer than 20 feet to the eye, three events occur to bring the image into focus on the retina: accommodation by the lens, constriction of the pupil, and convergence of the eyes.

1. *Accommodation.* When focusing on a nearby object, the ciliary muscles contract as a result of parasympathetic stimulation from the oculomotor nerve (III). This sphincterlike contraction pulls the choroid toward the lens to reduce the tension on the suspensory ligaments. This allows the lens to assume a more spherical form because of its own elastic nature (figure 15.15*b*). The more spherical lens then has a more convex surface, causing greater refraction of light. This process is called accommodation.

   As light strikes a solid object, the rays are reflected in every direction from the surface of the object. Only a small portion of the light rays reflected from a solid object, however, pass through the pupil and enter the eye of any given person. An object far away from the eye appears small compared to a nearby object because only nearly parallel light rays enter the eye from a distant object (see figure 15.15*a*). Converging rays leaving an object closer to the eye can also enter the eye (see figure 15.15*b*), and the object appears larger.

   When rays from a distant object reach the lens, they don't have to be refracted to any great extent to be focused on the retina, and the lens can remain fairly flat. When an object is closer to the eye, the more obliquely directed rays must be refracted to a greater extent to be focused on the retina.

   As an object is brought closer and closer to the eye, accommodation becomes more and more difficult because the lens cannot become any more convex. At some point, the eye no longer can focus the object, and it's seen as a blur. The point at which this blurring occurs is called the **near point of vision,** which is usually about 2–3 inches from the eye for children, 4–6 inches for a young adult, 20 inches for a 45-year-old adult, and 60 inches for an 80-year-old adult. This increase in the near point of vision, called **presbyopia,** occurs because the lens becomes more rigid with increasing age, which is primarily why some older people say they could read with no problem if they only had longer arms.

Vision Charts

When a person's vision is tested, a chart is placed 20 feet from the eye, and the person is asked to read a line of letters that is standardized for normal vision. If the person can read the line, the vision is considered to be 20/20, which means that the person can see at 20 feet what people with normal vision can see at 20 feet. If, on the other hand, the person can see words only at 20 feet that people with normal vision can see at 40 feet, the vision is considered 20/40.

2. *Pupil constriction.* Another factor involved in focusing is the **depth of focus,** which is the greatest distance through which an object can be moved and still remain in focus on the retina. The main factor affecting the depth of focus is the size of the pupil. If the pupillary diameter is small, the depth of focus is greater than if the pupillary diameter is large. With a smaller pupillary opening, an object may therefore be moved slightly nearer or farther from the eye without disturbing its focus. This is particularly important when viewing an object at close range because the interest in detail is much greater, and therefore the acceptable margin for error is smaller. When the pupil is constricted, the light entering the eye tends to pass more nearly through the center of the lens and is more accurately focused than light passing through the edges of the lens. Pupillary diameter also regulates the amount of light entering the eye. The dimmer the light, the greater the pupil diameter must be. As the pupil constricts during close vision, therefore, more light is required on the object being observed.
3. *Convergence.* Because the light rays entering the eyes from a distant object are nearly parallel, both pupils can pick up the light rays when the eyes are directed more or less straight ahead. As an object moves closer, however, the eyes must be rotated medially so that the object is kept focused on corresponding areas of each retina. Otherwise the object appears blurry. This medial rotation of the eyes is accomplished by a reflex which stimulates the medial rectus muscle of each eye. This movement of the eyes is called convergence. Convergence can easily be observed. Have someone stand facing you. Have the person reach out one hand and extend an index finger as far in front of his face as possible. While the person keeps his gaze fixed on the finger, have him slowly bring the finger in toward his nose until he finally touches it. Notice the movement of his pupils during this movement. What happens?

PREDICT 5

Explain how several hours of reading can cause eyestrain, or eye fatigue. Describe what structures are involved.

18. What causes light to refract? What is a focal point? What is emmetropia?

19. Describe the changes that occur in the lens, pupil, and extrinsic eye muscles as an object moves from 25 feet away to 6 inches away. What is meant by the terms near point and far point of vision?

Structure and Function of the Retina

Leonardo da Vinci, in speaking of the eye, said, "Who would believe that so small a space could contain the images of all the universe?" The retina of each eye, which gives us the potential to see the whole world, is about the size and thickness of a postage stamp.

The retina consists of a pigmented retina and a sensory retina. The **sensory retina** contains three layers of neurons: photoreceptor, bipolar, and ganglionic. The cell bodies of these neurons form nuclear layers separated by plexiform layers, where the neurons of adjacent layers synapse with each other (figure 15.16). The outer plexiform (plexuslike) layer is between the photoreceptor and bipolar cell layers. The inner plexiform layer is between the bipolar and ganglionic cell layers.

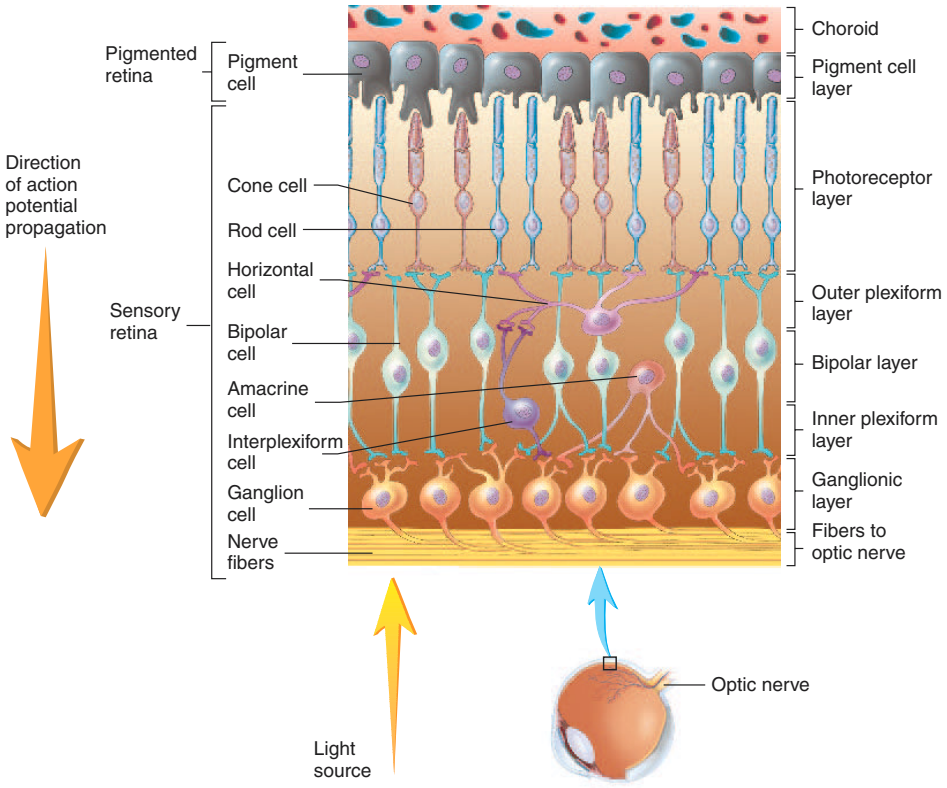


Figure 15.16 Retina

Section through the retina with its major layers labeled.

The **pigmented retina,** or pigmented epithelium, consists of a single layer of cells. This layer of cells is filled with melanin pigment and, together with the pigment in the choroid, provides a black matrix, which enhances visual acuity by isolating individual photoreceptors and reducing light scattering. Pigmentation is not strictly necessary for vision, however. People with albinism (lack of pigment) can see, although their visual acuity is reduced because of some light scattering.

The layer of the sensory retina nearest the pigmented retina is the layer of rods and cones. The rods and cones are photoreceptor cells, which are sensitive to stimulation from "visible" light. The light-sensitive portion of each photoreceptor cell is adjacent to the pigmented layer.

Rods

Rods are bipolar photoreceptor cells involved in noncolor vision and are responsible for vision under conditions of reduced light (table 15.1). The modified, dendritic, light-sensitive part of rod cells is cylindrical, with no taper from base to apex (figure 15.17*a*). This rod-shaped photoreceptive part of the rod cell contains about 700 double-layered membranous discs. The discs contain **rhodopsin** (rō-dop′sin), which consists of the protein **opsin** covalently bound to a pigment called **retinal** (derived from vitamin A).

Function of Rhodopsin

Figure 15.18 depicts the changes that rhodopsin undergoes in response to light. In the resting (dark) state, the shape of opsin keeps 11-*cis*-retinal tightly bound to the internal surface of opsin. As light is absorbed by rod cells, opsin changes shape from 11-*cis*-retinal to all-*trans*-retinal. These changes activate the attached G protein, called **transducin** (trans-doo′sin), which closes Na^+ channels, resulting in hyperpolarization of the cell (figure 15.19).

Opsin Mutants

Opsin is a protein composed of 338 amino acids. Mutation at amino acid 23 or 28, in the extracellular plug covering the external opening of the molecule, which keeps retinal associated with opsin, causes **retinitis pigmentosa.** This is a genetic disorder consisting of progressive retinal degeneration. During this degeneration, pigment infiltrates the sensory retina, decreasing its function and constricting the visual fields. **Night blindness,** or nyctalopia, (the decreased ability to see in reduced light) may also occur in retinitis pigmentosa. Night blindness also may occur as a result of vitamin A deficiency or as the result of another mutation at amino acid 90 of the opsin molecule. This mutation occurs in the second of the seven helical regions of the protein opsin and may affect the attachment of retinal to opsin.

Table 15.1 Rods and Cones

Photoreceptive End	Photoreceptive Molecule	Function	Location
Rod			
Cylindrical	Rhodospin	Noncolor vision; vision under conditions of low light	Over most of retina; none in fovea
Cone			
Conical	Iodopsin	Color vision; visual acuity	Numerous in fovea and macula lutea; sparse over rest of retina

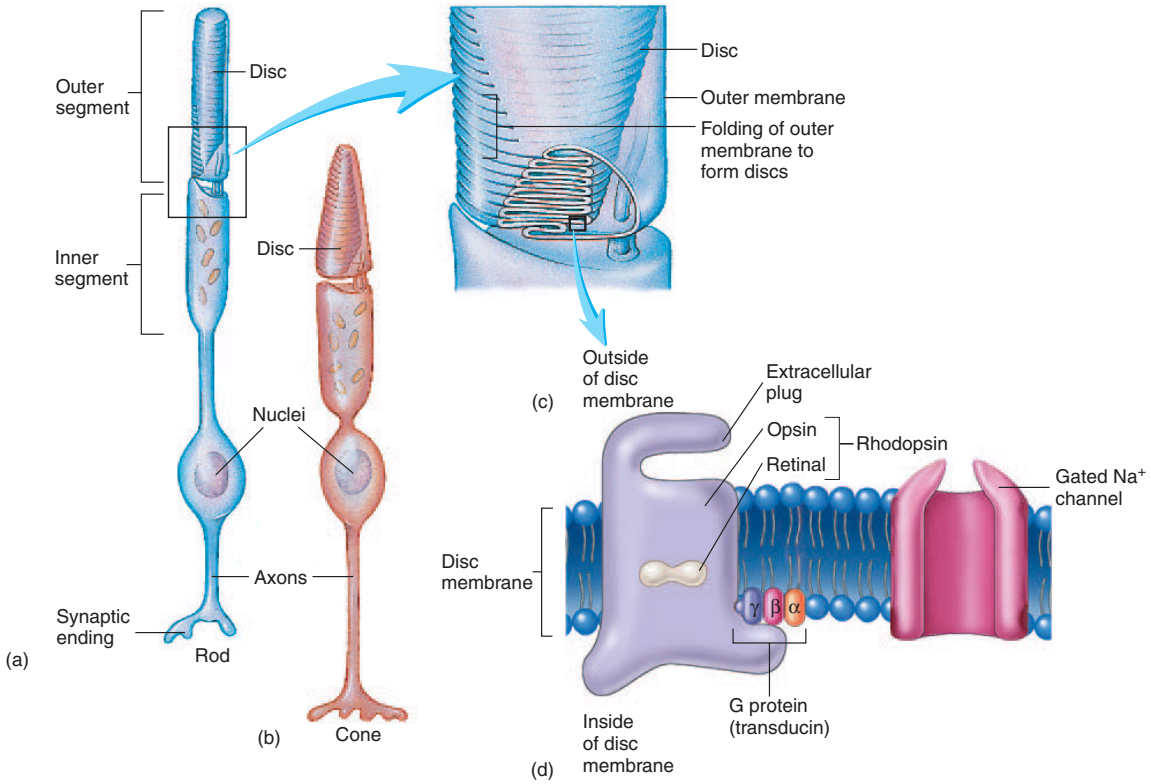


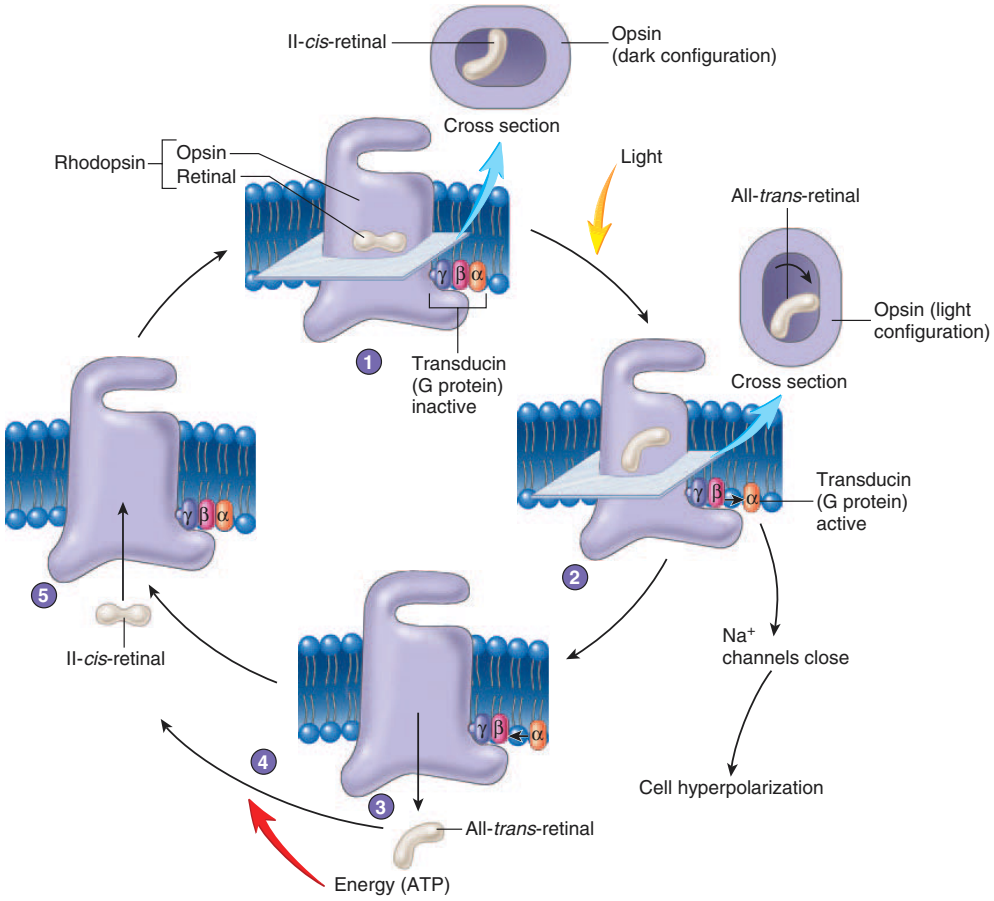
Figure 15.17 Sensory Receptor Cells of the Retina

(*a*) Rod cell. (*b*) Cone cell. (*c*) An enlargement of the discs in the outer segment. (*d*) An enlargement of one of the discs, showing the relation of rhodopsin and a gated Na^+ channel to the membrane.

This hyperpolarization in the photoreceptor cells is somewhat remarkable, because most neurons respond to stimuli by depolarizing. When photoreceptor cells are not exposed to light and are in a resting, nonactivated state, some of the Na^+ channels in their membranes are open, and Na^+ flow into the cell. This influx of Na^+ causes the photoreceptor cells to release the neurotransmitter glutamate from their presynaptic terminals (see figure 15.19). Glutamate binds to receptors on the postsynaptic membranes of the bipolar cells of the retina, causing them to hyperpolarize. Thus, glutamate causes an inhibitory postsynaptic potential (IPSP) in the bipolar cells.

When photoreceptor cells are exposed to light, the Na^+ channels close, fewer Na^+ enter the cell, and the amount of glutamate released from the presynaptic terminals decreases. As a result, the hyperpolarization in the bipolar cells decreases, and the cells depolarize sufficiently to release neurotransmitters, which

1. Retinal (in an inactive configuration called II-*cis*-) is attached inside opsin to make rhodopsin.
2. Light causes opsin to change shape, and retinal changes shape from II-*cis*-retinal to all-*trans*-retinal. This activated rhodopsin also activates the attached G protein (called transducin), which closes Na^+ channels, resulting in hyperpolarization of the cell.
3. All-*trans*-retinal detaches from opsin.
4. All-*trans*-retinal is converted to II-*cis*-retinal, a process that requires energy.
5. II-*cis*-retinal attaches to opsin, which returns to its original (dark) configuration



Process Figure 15.18 Rhodopsin Cycle

stimulate ganglionic cells to generate action potentials. The number of Na^+ channels that close and the degree to which they close is proportional to the amount of light exposure.

At the final stage of this light-initiated reaction, retinal is completely released from the opsin. This free retinal may then be converted back to vitamin A, from which it was originally derived. The total vitamin A/retinal pool is in equilibrium so that under normal conditions the amount of free retinal is relatively constant. To create more rhodopsin, the altered retinal must be converted back to its original shape, a reaction that requires energy. Once the retinal resumes its original shape, its recombination with opsin is spontaneous, and the newly formed rhodopsin can again respond to light.

Light and **dark adaptation** is the adjustment of the eyes to changes in light. Adaptation to light or dark conditions, which occurs when a person comes out of a darkened building into the sunlight or vice versa, is accomplished by changes in the amount of available rhodopsin. In bright light excess rhodopsin is broken down so that not as much is available to initiate action potentials, and the eyes become "adapted" to bright light. Conversely, in a dark room more rhodopsin is produced, making the retina more light-sensitive.

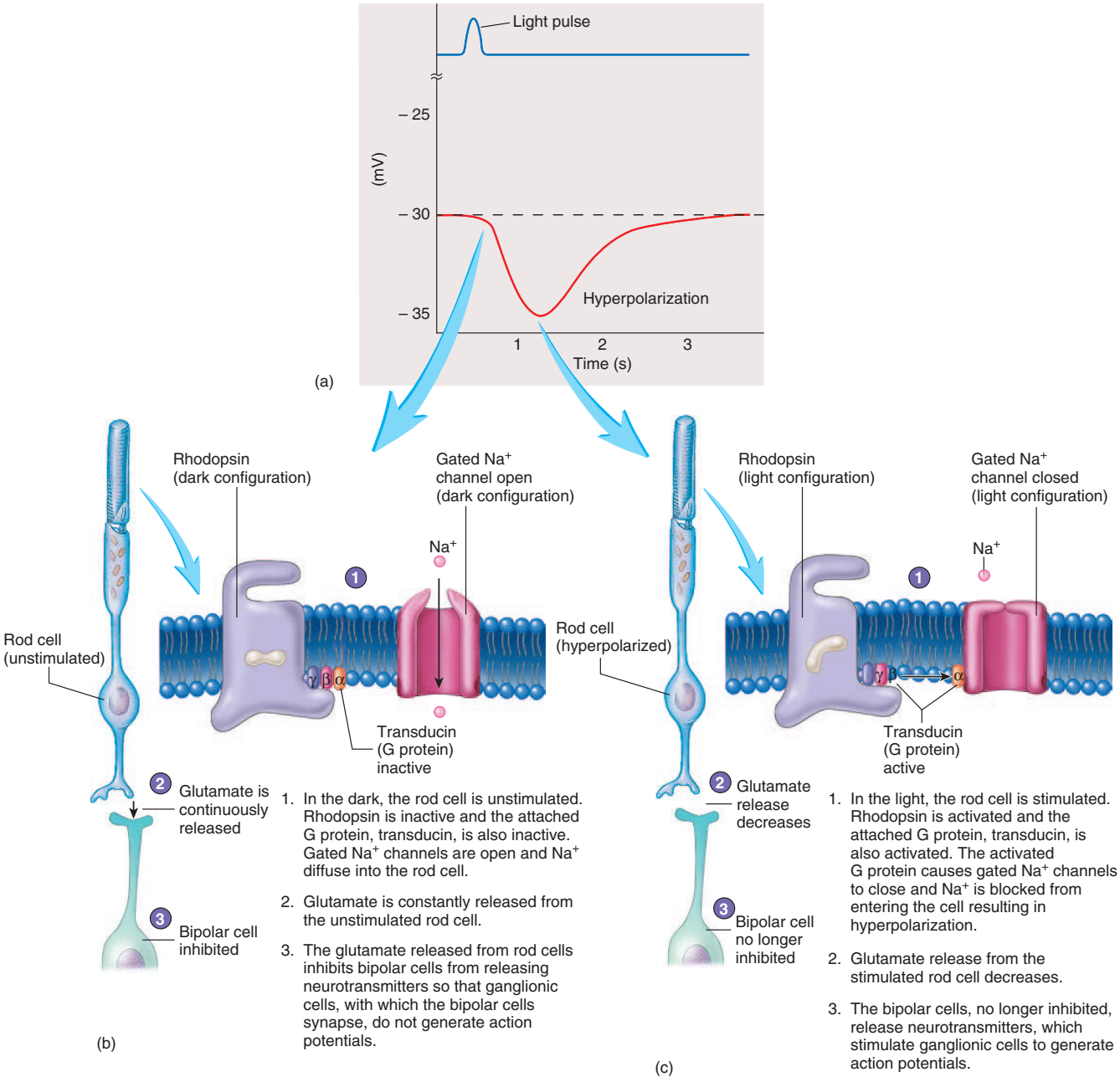
P R E D I C T 6

If breakdown of rhodopsin occurs rapidly and production is slow, do eyes adapt more rapidly to light or dark conditions?

Light and dark adaptation also involves pupil reflexes. The pupil enlarges in dim light to allow more light into the eye and contracts in bright light to allow less light into the eye. In addition, rod function decreases and cone function increases in light conditions, and vice versa during dark conditions. This occurs because rod cells are more sensitive to light than cone cells and because rhodopsin is depleted more rapidly in rods than in cones.

Cones

Color vision and visual acuity are functions of cone cells. Color is a function of the wavelength of light, and each color results from a certain wavelength within the visible spectrum. Even though rods are very sensitive to light, they cannot detect color, and sensory input that ultimately reaches the brain from these cells is interpreted by the brain as shades of gray. Cones require relatively bright light to function. As a result, as the light decreases, so does the color of objects that can be seen until, under conditions of very low



Process Figure 15.19 Rod Cell Hyperpolarization

(*a*) Changes in the rod cell membrane potential following the opsin and retinal cell shape changes is a hyperpolarization. (*b*) Unstimulated rod cell (dark). (*c*) Stimulated rod cell (light).

illumination, the objects appear gray. This occurs because as the light decreases, fewer cone cells respond to the dim light.

Cones are bipolar photoreceptor cells with a conical light-sensitive part that tapers slightly from base to apex (see figure 15.17*b*). The outer segments of the cone cells, like those of the rods, consist of double-layered discs. The discs are slightly more numerous and more closely stacked in the cones than in the rods. Cone cells contain a visual pigment, **iodopsin** (ī-ō-dop′sin), which consists of retinal combined with a photopigment opsin protein. Three major types of color-sensitive opsin exist: blue, red, and green; each closely resembles the opsin proteins of rod cells but with somewhat different amino acid sequences. These color photopigments

function in much the same manner as rhodopsin, but whereas rhodopsin responds to the entire spectrum of visible light, each iodopsin is sensitive to a much narrower spectrum.

Most people have one red pigment gene and one or more green pigment genes located in a tandem array on each X chromosome. An enhancer gene on the X chromosome apparently determines that only one color opsin gene is expressed in each cone cell. Only the first or second gene in the tandem array is expressed in each cone cell, so that some cone cells express only the red pigment gene and others express only one of the green pigment genes.

As can be seen in figure 15.20, although considerable overlap occurs in the wavelength of light to which these pigments are sensitive, each pigment absorbs light of a certain range of wavelengths. As light of a given wavelength, representing a certain color, strikes the retina, all cone cells containing photopigments capable of responding to that wavelength generate action potentials. Because of the overlap among the three types of cones, especially between the green and red pigments, different proportions of cone cells respond to each wavelength, thus allowing color perception over a wide range. Color is interpreted in the visual cortex as combinations of sensory input originating from cone cells. For example, when orange light strikes the retina, 99% of the red-sensitive cones respond, 42% of the green-sensitive cones respond, and no blue cones respond. When yellow light strikes the retina, the response is shifted so that a greater number of green-sensitive cones respond. The variety of combinations created allows humans to distinguish several million gradations of light and shades of color.

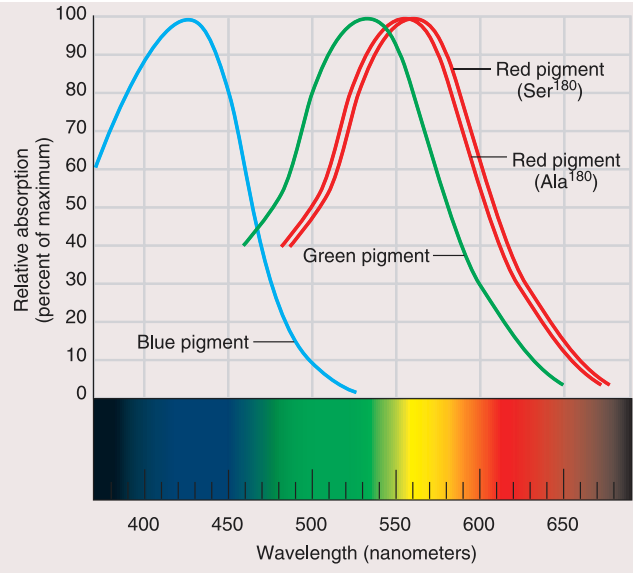


Figure 15.20 **Wavelengths to Which Each of the Three Visual Pigments are Sensitive: Blue, Green, Red**

There are actually two forms of the red pigment. One, found in 60% of the population, has a serine at position 180; and the other, found in 40% of the population, has an alanine at position 180. Each red pigment has a slightly different wavelength sensitivity.

Seeing Red

Not everyone sees the same red. Two forms of the red photopigment are common in humans. Approximately 60% of people have the amino acid serine in position 180 of the red opsin protein, whereas 40% have alanine in that position. That subtle difference in the protein results in slightly different absorption characteristics (see figure 15.20). Even though we were each taught to recognize red when we see a certain color, we apparently don't see that color in quite the same way. This difference may contribute to people having different favorite colors.

Distribution of Rods and Cones in the Retina

Cones are involved in visual acuity, in addition to their role in color vision. The fovea centralis is used when visual acuity is required, such as for focusing on the words of this page. The fovea centralis has about 35,000 cones and no rods. The 120 million rods are 20 times more plentiful than cones over most of the remaining retina, however. They are more highly concentrated away from the fovea and are more important in low-light conditions.

P R E D I C T 7

Explain why at night a person may notice a movement "out of the corner of her eye," but, when she tries to focus on the area where she noticed the movement, it appears as though nothing is there.

Inner Layers of the Retina

The middle and inner nuclear layers of the retina consist of two major types of neurons: bipolar and ganglion cells. The rod and cone photoreceptor cells synapse with **bipolar cells,** which in turn synapse with **ganglion cells.** Axons from the ganglion cells pass over the inner surface of the retina (see figure 15.16), except in the area of the fovea centralis, converge at the **optic disc,** and exit the eye as the **optic nerve** (II). The fovea centralis is devoid of ganglion cell processes, resulting in a small depression in this area; thus the name *fovea,* meaning small pit. As a result of the absence of ganglion cell processes in addition to the concentration of cone cells mentioned previously, visual acuity is further enhanced in the fovea centralis because light rays don't have to pass through as many tissue layers before reaching the photoreceptor cells.

Rod and cone cells differ in the way they interact with bipolar and ganglion cells. One bipolar cell receives input from numerous rods, and one ganglion cell receives input from several bipolar cells so that spatial summation of the signal occurs and the signal is enhanced, thereby allowing awareness of stimulus from very dim light sources but decreasing visual acuity in these cells. Cones, on the other hand, exhibit little or no convergence on bipolar cells so that one cone cell may synapse with only one bipolar cell. This system reduces light sensitivity but enhances visual acuity.

Within the inner layers of the retina, **association neurons** are present also, which modify the signals from the photoreceptor cells before the signal ever leaves the retina (see figure 15.16). **Horizontal cells** form the outer plexiform layer and synapse with photoreceptor cells and bipolar cells. **Amacrine** (am′ă-krin) **cells** form the inner plexiform layer and synapse with bipolar and ganglion cells. **Interplexiform cells** form the bipolar layer and synapse with amacrine, bipolar, and horizontal cells

to form a feedback loop. Association neurons are either excitatory or inhibitory on the cells with which they synapse. These association cells enhance borders and contours, thereby increasing the intensity at boundaries, such as the edge of a dark object against a light background.

20. *What is the function of the pigmented retina and of the choroid?*
21. *Describe the changes that occur in a rod cell after light strikes rhodopsin. How does rhodopsin re-form? Why is the response of a rod cell to a stimulus unusual?*
22. *How do dark and light adaptation occur?*
23. *What are the three types of cone cells? How do they function to produce the colors we see?*
24. *Describe the arrangement of rods and cones in the fovea, the macula lutea, and the periphery of the eye.*
25. *Starting with a rod or cone cell, name the cells or structures that an action potential encounters while traveling to the visual cortex.*

Motion Pictures

Action potentials pass from the retina through the optic nerve at the rate of 20–25/s. We "see" a given image for a fraction of a second longer than it actually appears. Motion pictures take advantage of these two facts. When still photographs are flashed on a screen at the rate of 24 frames per second, they appear to flow into each other, and a motion picture results.

Neuronal Pathways for Vision

Objective

- *Outline the CNS pathway for visual input, and describe what happens to images from each half of the visual fields.*

The optic nerve (II) (figure 15.21) leaves the eye and exits the orbit through the optic foramen to enter the cranial cavity. Just inside the vault and just anterior to the pituitary, the optic nerves are connected to each other at the **optic chiasm** (kī′azm). Ganglion cell axons from the nasal retina (the medial portion of the retina) cross through the optic chiasm and project to the opposite side of the brain. Ganglion cell axons from the temporal retina (the lateral portion of the retina) pass through the optic nerves and project to the brain on the same side of the body without crossing.

Beyond the optic chiasm, the route of the ganglionic axons is called the **optic tract** (see figure 15.21). Most of the optic tract axons terminate in the **lateral geniculate nucleus** of the thalamus. Some axons do not terminate in the thalamus but separate from the optic tract to terminate in the **superior colliculi,** the center for visual reflexes (see chapter 13). Neurons of the lateral geniculate ganglion form the fibers of the **optic radiations,** which project to the **visual cortex** in the **occipital lobe.** Neurons of the visual cortex integrate the messages coming from the retina into a single message, translate that message into a mental image, and then transfer the image to other parts of the brain, where it is evaluated and either ignored or acted on.

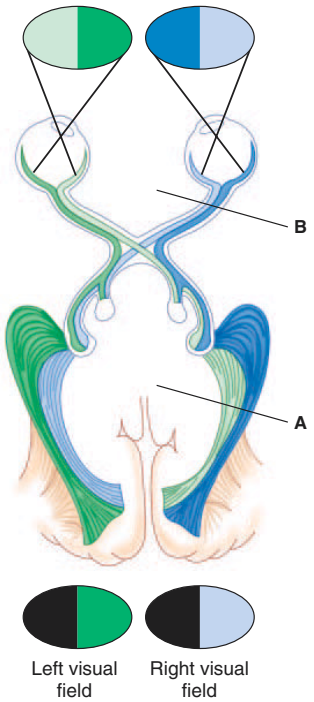
The projections of ganglion cells from the retina can be related to the **visual fields** (see figure 15.21). The visual field of one eye can be evaluated by closing the other eye. Everything that can be seen with the one open eye is the visual field of that eye. The visual field of each eye can be divided into a temporal part (lateral) and a nasal part (medial). In each eye, the temporal part of the visual field projects onto the nasal retina, whereas the nasal part of the visual field projects to the temporal retina. The projections and nerve pathways are arranged in such a way that images entering the eye from the right part of each visual field project to the left side of the brain. Conversely, the left part of each visual field projects to the right side of the brain.

Tunnel Vision

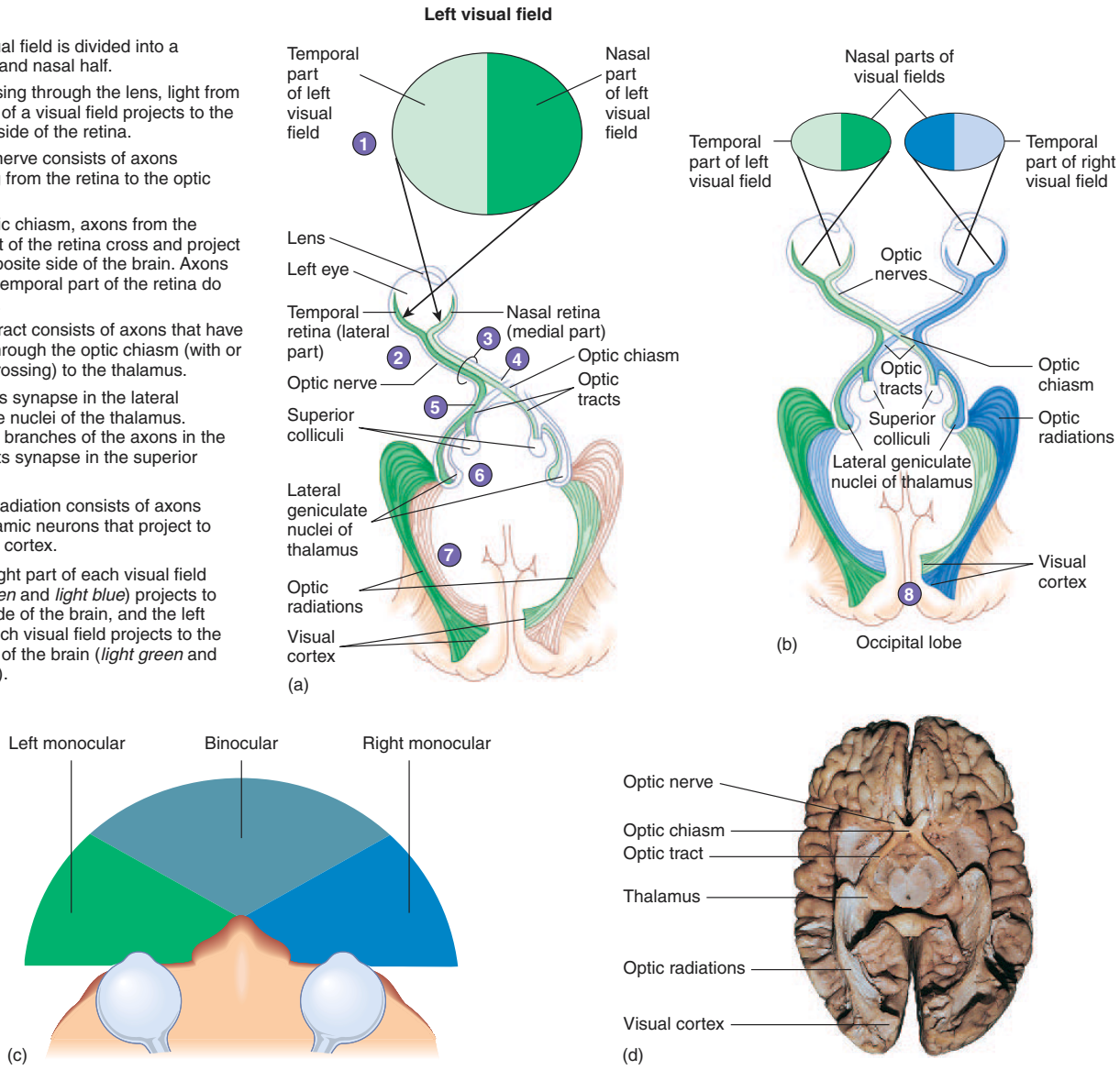
Because the optic chiasm lies just anterior to the pituitary, a pituitary tumor can put pressure on the optic chiasm and may result in visual defects. Because the nerve fibers crossing in the optic chiasm are carrying information from the temporal halves of the visual fields, a person with optic chiasm damage cannot see objects in the temporal halves of the visual fields, a condition called **tunnel vision.** Tunnel vision is often an early sign of a pituitary tumor.

P R E D I C T 8

The lines at *A* and *B* in the figure depict two lesions in the visual pathways. The effect of a lesion at *A* in the optic radiations on the visual fields is depicted (with the right and left fields separated) in the ovals. The black areas indicate what parts of the visual fields are defective. Describe the effect that the lesion at *B* has on the visual fields (see figure 15.21 for help).



1. Each visual field is divided into a temporal and nasal half.
2. After passing through the lens, light from each half of a visual field projects to the opposite side of the retina.
3. An optic nerve consists of axons extending from the retina to the optic chiasm.
4. In the optic chiasm, axons from the nasal part of the retina cross and project to the opposite side of the brain. Axons from the temporal part of the retina do not cross.
5. An optic tract consists of axons that have passed through the optic chiasm (with or without crossing) to the thalamus.
6. The axons synapse in the lateral geniculate nuclei of the thalamus. Collateral branches of the axons in the optic tracts synapse in the superior colliculi.
7. An optic radiation consists of axons from thalamic neurons that project to the visual cortex.
8. (*b*) The right part of each visual field (*dark green* and *light blue*) projects to the left side of the brain, and the left part of each visual field projects to the right side of the brain (*light green* and *dark blue*).



Process Figure 15.21 Visual Pathways

(*a*) Pathways for the left eye (superior view). (*b*) Pathways for both eyes (superior view). (*c*) Overlap of the fields of vision (superior view). (*d*) Photograph of the visual nerves, tracts, and pathways (inferior view).

The visual fields of the eyes partially overlap (see figure 15.21). The region of overlap is the area of **binocular vision,** seen with two eyes at the same time, and it is responsible for **depth perception,** the ability to distinguish between near and far objects and to judge their distance. Because humans see the same object with both eyes, the image of the object reaches the retina of one eye at a slightly different angle from that of the other. With experience, the brain can interpret these differences in angle so that distance can be judged quite accurately.

- ***26. What is a visual field? How do the visual fields project to the brain?***
- ***27. Explain how binocular vision allows for depth perception.***

Clinical Focus Eye Disorders

Myopia

Myopia (mī-ō′pē-ă), or nearsightedness, is the ability to see close objects clearly, but distant objects appear blurry. Myopia is a defect of the eye in which the focusing system, the cornea and lens, is optically too powerful, or the eyeball is too long (axial myopia). As a result, the focal point is too near the lens, and the image is focused in front of the retina (figure A*a*).

Myopia is corrected by a concave lens that counters the refractive power of the eye. Concave lenses cause the light rays coming to the eye to diverge and are therefore called "minus" lenses (figure A*b*).

Another technique for correcting myopia is **radial keratotomy** (ker′ă-tot′ō-mē), which consists of making a series of four to eight radiating cuts in the cornea. The cuts are intended to slightly weaken the dome of the cornea so that it becomes more flattened and eliminates the myopia. One problem with the technique is that it is difficult to predict exactly how much flattening will occur. In one study of 400 patients 5 years after the surgery, 55% had normal vision, 28% were still somewhat myopic, and 17% had become hyperopic. Another problem is that some patients are bothered by glare following radial keratotomy because the slits apparently don't heal evenly.

An alternative procedure being investigated is **laser corneal sculpturing,** in which a thin portion of the cornea is etched away to make the cornea less convex. The advantage of this procedure is that the results can be more accurately predicted than those from radial keratotomy.

Hyperopia

Hyperopia (hī-per-ō′pē-ă), or farsightedness, is the ability to see distant objects clearly, but close objects appear blurry. Hyperopia is a disorder in which the cornea and lens system is optically too weak or the eyeball is too short. The image is focused behind the retina (figure A*c*).

Hyperopia can be corrected by convex lenses that cause light rays to converge as they approach the eye (figure A*d*). Such lenses are called "plus" lenses.

Presbyopia

Presbyopia (prez-bē-ō′pē-ă) is the normal, presently unavoidable, degeneration of the accommodation power of the eye that occurs as a consequence of aging. It occurs because the lens becomes sclerotic and less flexible. The eye is presbyopic when the near point of vision has increased beyond 9 inches. The average age for onset of presbyopia is the midforties. Avid readers or people engaged in fine, close work may develop the symptoms earlier.

Presbyopia can be corrected by the use of "reading glasses" that are worn only for close work and are removed when the person wants to see at a distance. It's sometimes annoying to keep removing and replacing glasses because reading glasses hamper vision of only a few feet away. This

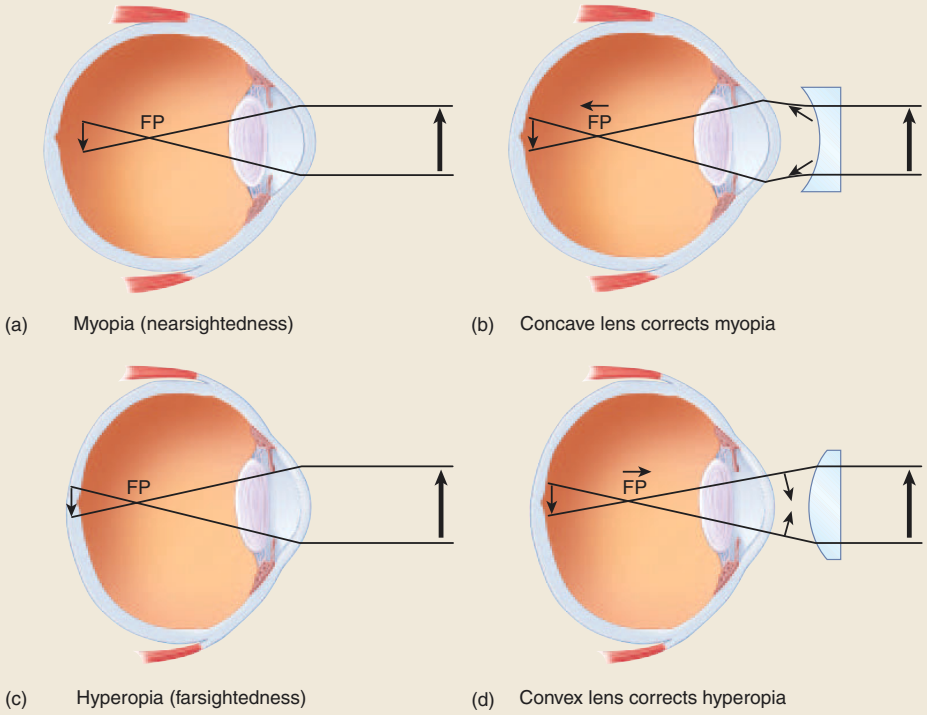


Figure A Visual Disorders and Their Correction by Various Lenses

FP is the focal point. (*a*) Myopia (nearsightedness). (*b*) Correction of myopia with a concave lens. (*c*) Hyperopia (farsightedness). (*d*) Correction of hyperopia with a convex lens.

problem may be corrected by the use of half glasses, or by **bifocals,** which have a different lens in the top and the bottom.

Astigmatism

Astigmatism (ă-stig′mă-tizm) is a type of refractive error in which the quality of focus is affected. If the cornea or lens is not uniformly curved, the light rays don't focus at a single point but fall as a blurred circle. Regular astigmatism can be corrected by glasses that are formed with the opposite curvature gradation. Irregular astigmatism is a situation in which the abnormal form of the cornea fits no specific pattern and is very difficult to correct with glasses.

Strabismus

Strabismus (stra-biz′mŭs) is a lack of parallelism of light paths through the eyes. Strabismus can involve only one eye or both eyes, and the eyes may turn in (convergent) or out (divergent). In **concomitant strabismus,** the most common congenital type, the angle between visual axes remains constant, regardless of the direction of the gaze. In **noncomitant strabismus,** the angle varies, depending on the direction of the gaze, and deviates as the gaze changes.

In some cases, the image that appears on the retina of one eye may be considerably different from that appearing on the other eye. This problem is called **diplopia** (di-plō′pē-ă, -double vision) and is often the result of weak or abnormal eye muscles.

Retinal Detachment

Retinal detachment is a relatively common problem that can result in complete blindness. The integrity of the retina depends on the vitreous humor, which keeps the retina pushed against the other tunics of the eye. If a hole or tear occurs in the retina, fluid may accumulate between the sensory and pigmented retina, thereby separating them. This separation, or detachment, may continue until the sensory retina has become totally detached from the pigmented retina and folded into a funnel-like form around the optic nerve. When the sensory retina becomes separated from its nutrient supply in the choroid, it degenerates, and blindness follows. Causes of retinal detachment include a severe blow to the eye or head; a shrinking of the vitreous humor, which may occur with aging; or diabetes. The space between the sensory and pigmented retina, called the subretinal space, is also important in keeping the retina from detaching, as well as in maintaining the health of the retina. The space contains a gummy substance that glues the sensory retina to the pigmented retina.

Color Blindness

Color blindness results from the dysfunction of one or more of the three photopigments involved in color vision. If one pigment is dysfunctional and the other two are functional, the condition is called **dichromatism.** An example of dichromatism is red-green color blindness (figure B).

The genes for the red and green photopigments are arranged in tandem on the X chromosome, which explains why color blindness is over eight times more common in males than in females (see chapter 29).

Six exons exist for each gene. The red and green genes are 96%–98% identical and, as a result, the exons may be shuffled to form hybrid genes in some people. Some of the hybrid genes produce proteins with nearly normal function, but others do not. Exon 5 is the most critical for determining normal red-green function. If the fifth exon from a green gene replaces a red pigment gene that has the fifth exon, the protein made from the gene responds to wavelengths more toward the green pigment range. The person has a red perception deficiency and is not able to distinguish between red and green. If the fifth exon from a red gene replaces a green pigment gene that has the fifth exon, the protein made from the gene responds to wavelengths more toward the red pigment range. The person has a green perception deficiency and is also not able to distinguish between red and green.

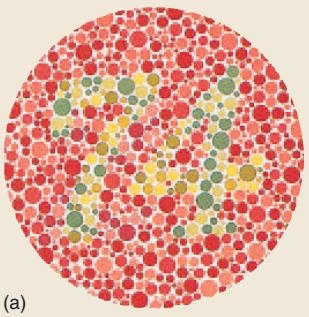
Apparently only about 3 of the over 360 amino acids in the color opsin proteins (those at positions 180 in exon 3 and those at 277 and 285 in exon 5) are key to determining their wavelength absorption characteristics. If those amino acids are altered by hydroxylation, the absorption shifts toward the red end of the spectrum. If they are not hydroxylated, the absorption shifts toward the green end.

Night Blindness

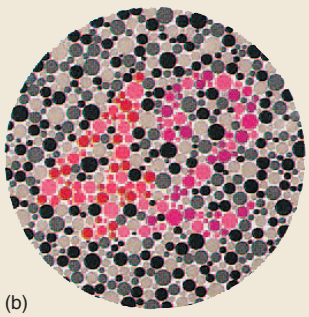
Everyone sees less clearly in the dark than in the light. A person with **night blindness,** however, may not see well enough in a dimly lit environment to function adequately. **Progressive night blindness** results from general retinal degeneration. **Stationary night blindness** results from nonprogressive abnormal rod function. Temporary night blindness can result from a vitamin A deficiency.

Patients with night blindness can now be helped with special electronic optical devices. These include monocular pocket scopes and binocular goggles that electronically amplify light.

Continued



(a)



(b)

Figure B Color Blindness Charts

(*a*) A person with normal color vision can see the number 74, whereas a person with red-green color blindness sees the number 21. (*b*) A person with normal color vision can see the number 42. A person with red color blindness sees the number 2, and a person with green color blindness sees the number 4.

Continued

Glaucoma

Glaucoma (figure C*a*) is a disease of the eye involving increased intraocular pressure caused by a buildup of aqueous humor. It usually results from blockage of the aqueous veins or the canal of Schlemm, restricting drainage of the aqueous humor, or from overproduction of aqueous humor. If untreated, glaucoma can lead to retinal, optic disc, and optic nerve damage. The damage results from the increased intraocular pressure, which is sufficient to close off the blood vessels, causing starvation and death of the retinal cells.

Glaucoma is one of the leading causes of blindness in the United States, affecting 2% of people over age 35, and accounting for 15% of all blindness. Fifty thousand people in the United States are blind as the result of glaucoma, and it occurs three times more often in black people than in white people. The symptoms include a slow closing in of the field of vision. No pain or redness occurs, nor do light flashes occur.

Glaucoma has a strong hereditary tendency but may develop after surgery or with the use of certain eyedrops containing cortisone. Everyone older than 40 should be checked every 2–3 years for glaucoma; those older than 40 who have relatives with glaucoma should have an annual checkup. During a checkup, the field of vision and the optic nerve are examined. Ocular pressures can also be measured. Glaucoma is usually treated with eyedrops, which do not cure the problem but keep it from advancing. In some cases, laser or conventional surgery may be used.

Cataract

Cataract (figure C*b*) is a clouding of the lens resulting from a buildup of proteins. The lens relies on the aqueous humor for its nutrition. Any loss of this nutrient source leads to degeneration of the lens and, ultimately, opacity of the lens (i.e., a cataract). A cataract may occur with advancing age, infection, or trauma.

A certain amount of lens clouding occurs in 65% of patients older than 50 and 95% of patients older than 65. The decision of whether to remove the cataract depends on the extent to which light passage is blocked. Over 400,000 cataracts are removed in the United States each year. Surgery to remove a cataract is actually the removal of the lens. The posterior portion of the lens capsule is left intact. Although the cornea can still accomplish light convergence, with the lens gone, the rays cannot be focused as well, and an artificial lens must be supplied to help accomplish focusing. In most cases, an artificial lens is implanted into the remaining portion of the lens capsule at the time that the natural lens is removed. The implanted lens helps to restore normal vision, but glasses may be required for near vision.

Macular Degeneration

Macular degeneration (figure C*c*) is very common in older people. It does not cause total blindness but results in the loss of acute vision. This degeneration has a variety of causes, including hereditary disorders, infections, trauma, tumor, or most often, poorly understood degeneration associated with aging. Because no satisfactory medical treatment has been developed, optical aids, such as magnifying glasses, are used to improve visual function.

Diabetes

Loss of visual function is one of the most common consequences of diabetes because a major complication of the disease is dysfunction of the peripheral circulation. Defective circulation to the eye may result in retinal degeneration or detachment. Diabetic retinal degeneration (figure C*d*) is one of the leading causes of blindness in the United States.

Infections

Trachoma (tr ă-k ō′m ă) is the leading cause of blindness worldwide. It is caused by an intracellular microbial infection *(Chlamydia trachomatis)* of the corneal epithelial cells, resulting in scar tissue formation in the cornea. The bacteria are spread from one eye to another eye by towels, fingers, and other objects. Five hundred million cases of trachoma exist in the world, and 7 million people are blind or visually impaired as a result of it.

Neonatal gonorrheal ophthalmia (ofthal′-mē-ă) is a bacterial infection *(Neisseria gonorrhoeae)* of the eye that causes blindness. If the mother has gonorrhea, which is a sexually transmitted disease of the reproductive tract, the bacteria can infect the newborn during delivery. The disease can be prevented by treating the infant's eyes with silver nitrate, tetracycline, or erythromycin drops.

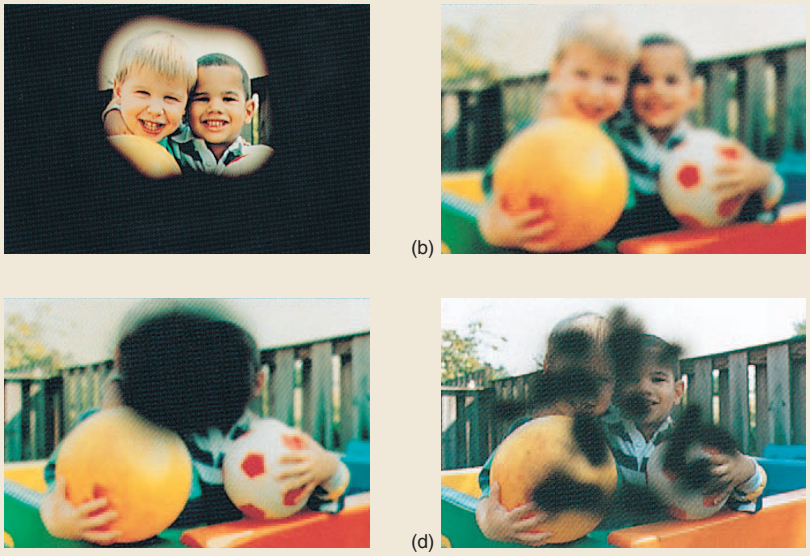


Figure C Defects in Vision

Visual images as seen with various defects in vision. (*a*) Glaucoma. (*b*) Cataract. (*c*) Macular degeneration. (*d*) Diabetic retinopathy.

Hearing and Balance

Objectives

- *Describe the structures that are part of the external, middle, and inner ears.*
- *Explain how the parts of the ear are able to convert sound waves into action potentials.*
- *Describe the auditory pathways in the CNS.*
- *Describe the static and kinetic labyrinths, and explain how they function in balance.*
- *Outline the CNS pathways for balance.*

The organs of hearing and balance are divided into three parts: external, middle, and inner ears (figure 15.22). The external and middle ears are involved in hearing only, whereas the inner ear functions in both hearing and balance.

The **external ear** includes the **auricle** (aw′ri-kl; ear) and the **external auditory meatus** (mē-ā′tŭs; the passageway from the outside to the eardrum). The external ear terminates medially at the **eardrum,** or **tympanic** (tim-pan′ik) **membrane.** The **middle ear** is an air-filled space within the petrous portion of the temporal bone, which contains the **auditory ossicles.** The **inner ear** contains the sensory organs for hearing and balance. It consists of interconnecting fluid-filled tunnels and chambers within the petrous portion of the temporal bone.

Auditory Structures and Their Functions

External Ear

The auricle, or **pinna** (pin′ă), is the fleshy part of the external ear on the outside of the head and consists primarily of elastic cartilage covered with skin (figure 15.23). Its shape helps to collect sound waves and direct them toward the external auditory meatus. The external auditory meatus is lined with **hairs** and **ceruminous** (sĕ-roo′mi-nŭs) **glands,** which produce **cerumen,** a modified sebum commonly called earwax. The hairs and cerumen help prevent foreign objects from reaching the delicate eardrum. Overproduction of cerumen, however, may block the meatus.

The tympanic membrane, or eardrum, is a thin, semitransparent, nearly oval, three-layered membrane that separates the external ear from the middle ear. It consists of a low, simple cuboidal epithelium on the inner surface and a thin stratified squamous epithelium on the outer surface, with a layer of connective tissue between. Sound waves reaching the tympanic membrane through the external auditory meatus cause it to vibrate.

Tympanic Membrane Rupture

Rupture of the tympanic membrane results in deafness. Foreign objects thrust into the ear, pressure, or infections of the middle ear can rupture the tympanic membrane. Sufficient differential pressure between the middle ear and the outside air can also cause rupture of the tympanic membrane. This can occur in flyers, divers, or individuals who are hit on the side of the head by an open hand.

Middle Ear

Medial to the tympanic membrane is the air-filled cavity of the middle ear (see figure 15.22). Two covered openings, the round and oval windows, on the medial side of the middle ear separate it from the inner ear. Two openings provide air passages from the middle ear. One passage opens into the **mastoid air cells** in the mastoid process of the temporal bone. The other passageway, the **auditory,** or **eustachian** (ū-stā′shŭn) **tube,** opens into the pharynx and equalizes air pressure between the outside air and the middle ear cavity. Unequal pressure between the middle ear and the outside environment can distort the eardrum, dampen its vibrations, and make hearing difficult. Distortion of the eardrum, which occurs under these conditions, also stimulates pain fibers associated with it. Because of this distortion, when a person changes altitude, sounds seem muffled, and the eardrum may become painful. These symptoms can be relieved by opening the auditory tube to allow air to pass through the auditory tube to equalize air pressure. Swallowing, yawning, chewing, and holding the nose and mouth shut while gently trying to force air out of the lungs are methods used to open the auditory tube.

The middle ear contains three auditory ossicles: the **malleus** (mal′ē-ŭs; hammer), **incus** (ing′kŭs; anvil), and **stapes** (stā′pēz; stirrup), which transmit vibrations from the tympanic membrane to the **oval window.** The handle of the malleus is attached to the inner surface of the tympanic membrane, and vibration of the membrane causes the malleus to vibrate as well. The head of the malleus is attached by a very small synovial joint to the incus, which in turn is attached by a small synovial joint to the stapes. The foot plate of the stapes fits into the oval window and is held in place by a flexible **annular ligament.**

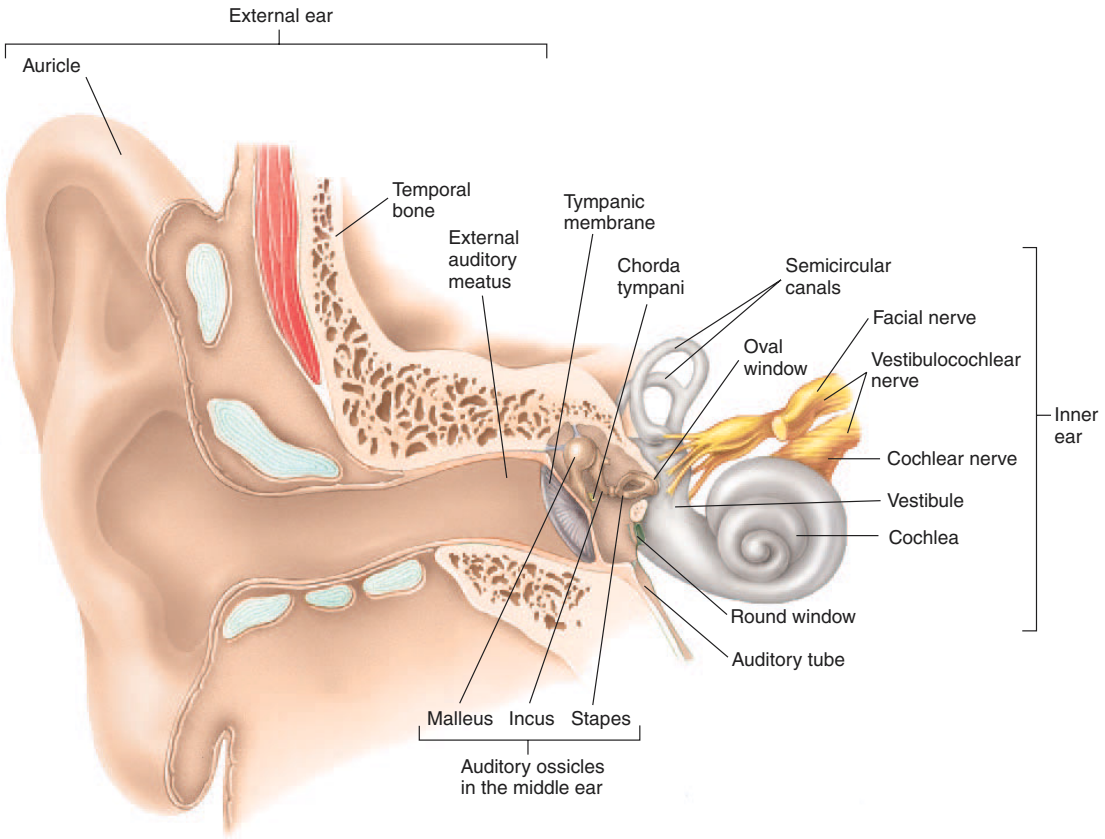


Figure 15.22 External, Middle, and Inner Ear

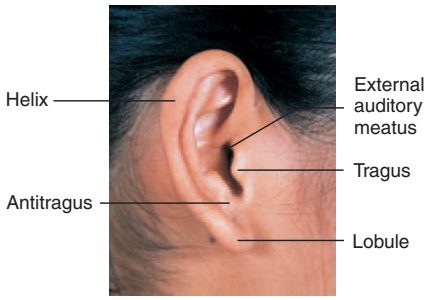


Figure 15.23 Structures of the Auricle (the Right Ear)

Chorda Tympani

A structure that students might be somewhat surprised to find in the middle ear is the **chorda tympani.** It's a branch of the facial nerve carrying taste impulses from the anterior two-thirds of the tongue. It crosses over the inner surface of the tympanic membrane (see figures 15.22 and 15.29). The chorda tympani has nothing to do with hearing but is just passing through. This nerve can be damaged, however, during ear surgery or by a middle ear infection, resulting in loss of taste sensation from the anterior two-thirds of the tongue on the side innervated by that nerve.

Inner Ear

The tunnels and chambers inside the temporal bone are called the **bony labyrinth** (lab′i-rinth; a maze; figure 15.24). Because the bony labyrinth consists of tunnels within the bone, it cannot easily be removed and examined separately. The bony labyrinth is lined with periosteum, and when the inner ear is shown separately (figure 15.25*a*), the periosteum is what is depicted. Inside the bony labyrinth is a similarly shaped but smaller set of membranous tunnels and chambers called the **membranous labyrinth.** The membranous labyrinth is filled with a clear fluid called **endolymph,** and the space between the membranous and bony labyrinth is filled with a fluid called **perilymph.** Perilymph is very similar to cerebrospinal fluid, but endolymph has a high concentration of potassium and a low concentration of sodium, which is opposite from perilymph and cerebrospinal fluid.

The bony labyrinth is divided into three regions: cochlea, vestibule, and semicircular canals. The **vestibule** (ves′ti-bool) and **semicircular canals** are involved primarily in balance, and the **cochlea** (kok′lē-ă) is involved in hearing. The membranous labyrinth of the cochlea is divided into three parts: the scala vestibuli, the scala tympani, and the cochlear duct.

The oval window communicates with the vestibule of the inner ear, which in turn communicates with a cochlear chamber, the **scala vestibuli** (skā′lă ves-tib′ū-lē; see figure 15.25*a*). The scala

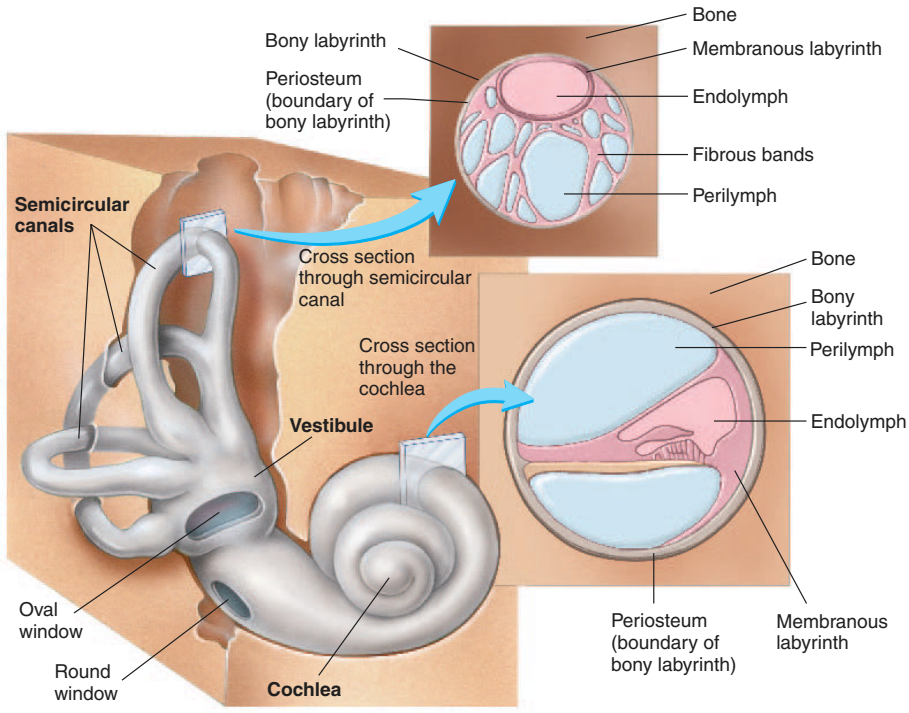


Figure 15.24 The Inner Ear: Bony and Membranous Labyrinths

The cross sections are taken through a semicircular canal and the cochlea to show the relationship between the bony and membranous labyrinths.

vestibuli extends from the oval window to the **helicotrema** (hel′i-kō-trē′mă; a hole at the end of a helix or spiral) at the apex of the cochlea; a second cochlear chamber, the **scala tympani** (tim′pă-nē), extends from the helicotrema, back from the apex, parallel to the scala vestibuli, to the membrane of the **round window.**

The scala vestibuli and the scala tympani are the perilymph-filled spaces between the walls of the bony and membranous labyrinths. A layer of simple squamous epithelium is attached to the periosteum of the bone surrounding each of these chambers. The wall of the membranous labyrinth that bounds the scala vestibuli is called the **vestibular membrane** (Reissner's membrane); the wall of the membranous labyrinth bordering the scala tympani is the **basilar membrane** (figure 15.25*b* and *c*). The space between the vestibular membrane and the basilar membrane is the interior of the membranous labyrinth and is called the **cochlear duct** or **scala media,** which is filled with endolymph.

The vestibular membrane consists of a double layer of squamous epithelium and is the simplest region of the membranous labyrinth. The vestibular membrane is so thin that it has little or no mechanical effect on the transmission of sound waves through the inner ear; therefore, the perilymph and endolymph on the two sides of the vestibular membrane can be thought of mechanically as one fluid. The role of the vestibular membrane is to separate the two chemically different fluids. The basilar membrane is somewhat more complex and is of much greater physiologic interest in relation to the mechanics of hearing. It consists of an acellular portion with collagen fibers, ground substance, and sparsely dispersed elastic fibers and a cellular part with a thin layer of vascular connective tissue that is overlaid with simple squamous epithelium.

The basilar membrane is attached at one side to the bony **spiral lamina,** which projects from the sides of the **modiolus** (mō′dī′ō-lus), the bony core of the cochlea, like the threads of a screw, and at the other side to the lateral wall of the bony labyrinth by the **spiral ligament,** a local thickening of the periosteum. The distance between the spiral lamina and the spiral ligament (i.e., the width of the basilar membrane) increases from 0.04 mm near the oval window to 0.5 mm near the helicotrema. The collagen fibers of the basilar membrane are oriented across the membrane between the spiral lamina and the spiral ligament, somewhat like the strings of a piano. The collagen fibers near the oval window are both shorter and thicker than those near the helicotrema. The diameter of the collagen fibers in the membrane decreases as the basilar membrane widens. As a result, the basilar membrane near the oval window is short and stiff, and responds to high-frequency vibrations, whereas that part near the helicotrema is wide and limber and responds to low-frequency vibrations.

The cells inside the cochlear duct are highly modified to form a structure called the **spiral organ,** or the **organ of Corti** (figure 15.25*b* and *c*). The spiral organ contains supporting epithelial cells and specialized sensory cells called **hair cells,** which have hairlike projections at their apical ends. In children, these projections consist of one cilium (kinocilium) and about 80 very long microvilli, often referred to as **stereocilia;** but in adults the cilium is absent from most hair cells (figures 15.25*d* and 15.26). The hair

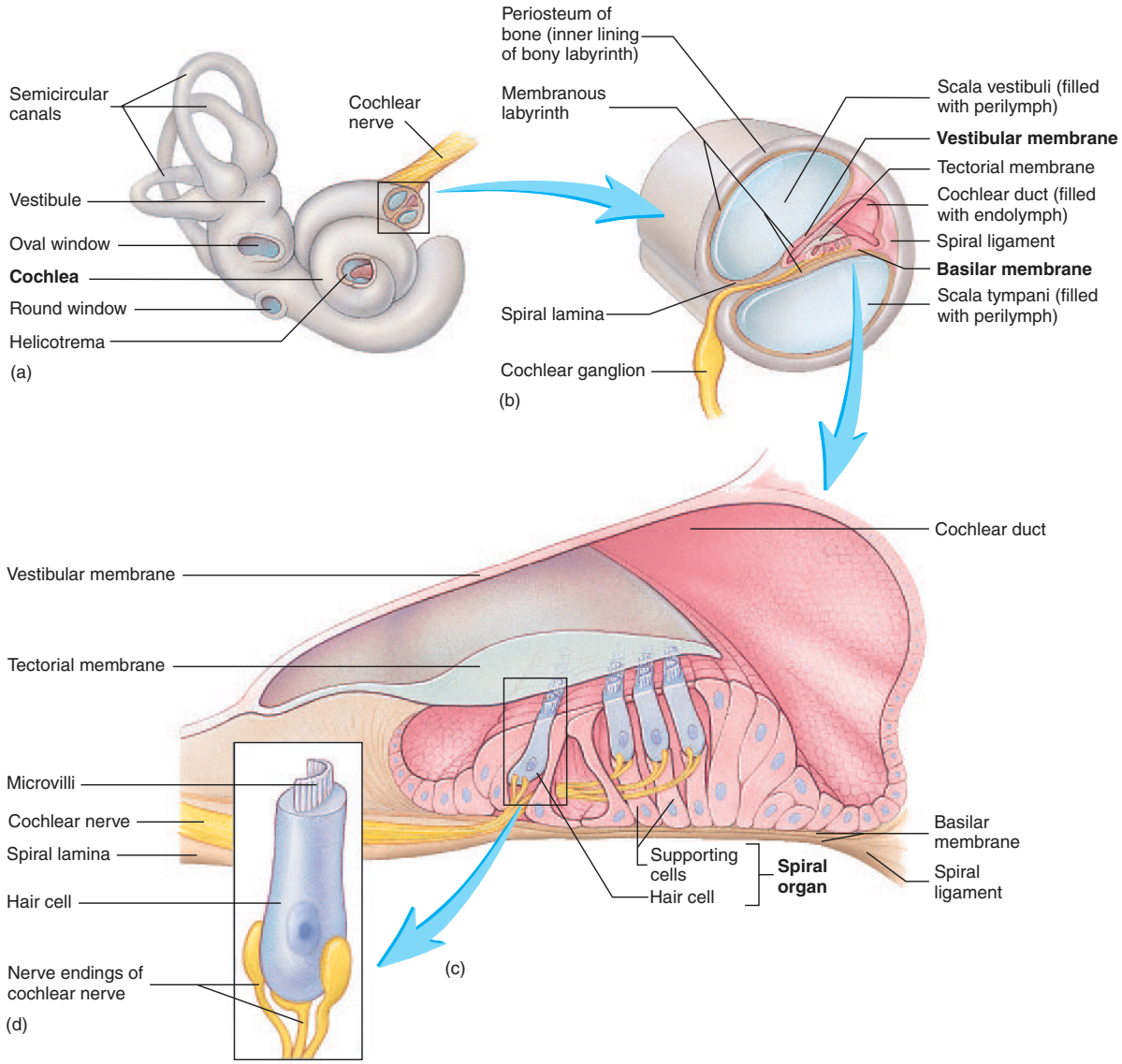


Figure 15.25 Structure of the Cochlea

(*a*) **The inner ear.** The outer surface (*gray*) is the periosteum lining the inner surface of the bony labyrinth. (*b*) **A cross section of the cochlea.** The outer layer is the periosteum lining the inner surface of the bony labyrinth. The membranous labyrinth is very small in the cochlea and consists of the vestibular and basilar membranes. The space between the membranous and bony labyrinth consists of two parallel tunnels: the scala vestibuli and scala tympani. (*c*) An enlarged section of the cochlear duct (membranous labyrinth). (*d*) A greatly enlarged individual sensory hair cell.

cells are arranged in four long rows extending the length of the cochlear duct. The tips of the hairs are embedded within an acellular gelatinous shelf called the **tectorial** (tek-tōr′ē-ăl) **membrane,** which is attached to the spiral lamina.

Hair cells have no axons, but the basilar regions of each hair cell are covered by synaptic terminals of sensory neurons, the cell bodies of which are located within the cochlear modiolus and are grouped into a **cochlear,** or **spiral ganglion** (see figures 15.25*b* and 15.31). Afferent fibers of these neurons join to form the **cochlear nerve.** This nerve then joins the vestibular nerve to become the **vestibulocochlear nerve** (VIII), which traverses the internal auditory meatus and enters the cranial vault.

28. *Name the three regions of the ear, and list each region's parts.*
29. *Describe the relationship between the tympanic membrane, the ear ossicles, and the oval window of the ear.*
30. *What is the function of the external auditory meatus and of the auditory tube?*
31. *Explain how the cochlear duct is divided into three compartments. What is found in each compartment?*

Figure 15.26 Scanning Electron Micrograph of Cochlear Hair Cell Microvilli

Auditory Function

Vibration of matter such as air, water, or a solid material creates sound. No sound occurs in a vacuum. When a person speaks, the vocal cords vibrate, causing the air passing out of the lungs to vibrate. The vibrations consist of bands of compressed air followed by bands of less compressed air (figure 15.27*a*). These vibrations are propagated through the air as sound waves, somewhat like ripples are propagated over the surface of water. **Volume,** or loudness, is a function of wave amplitude, or height, measured in decibels (figure 15.27*b*). The greater the amplitude, the louder is the sound. **Pitch** is a function of the wave frequency (i.e., the number of waves or cycles per second) measured in hertz (Hz) (figure 15.27*c*). The higher the frequency, the higher the pitch. The normal range of human hearing is 20–20,000 Hz and 0 or more decibels (db). Sounds louder than 125 db are painful to the ear.

Human Speech and Hearing Impairment

The range of normal human speech is 250–8000 Hz. This is the range that is tested for the possibility of hearing impairment because it's the most important for communication.

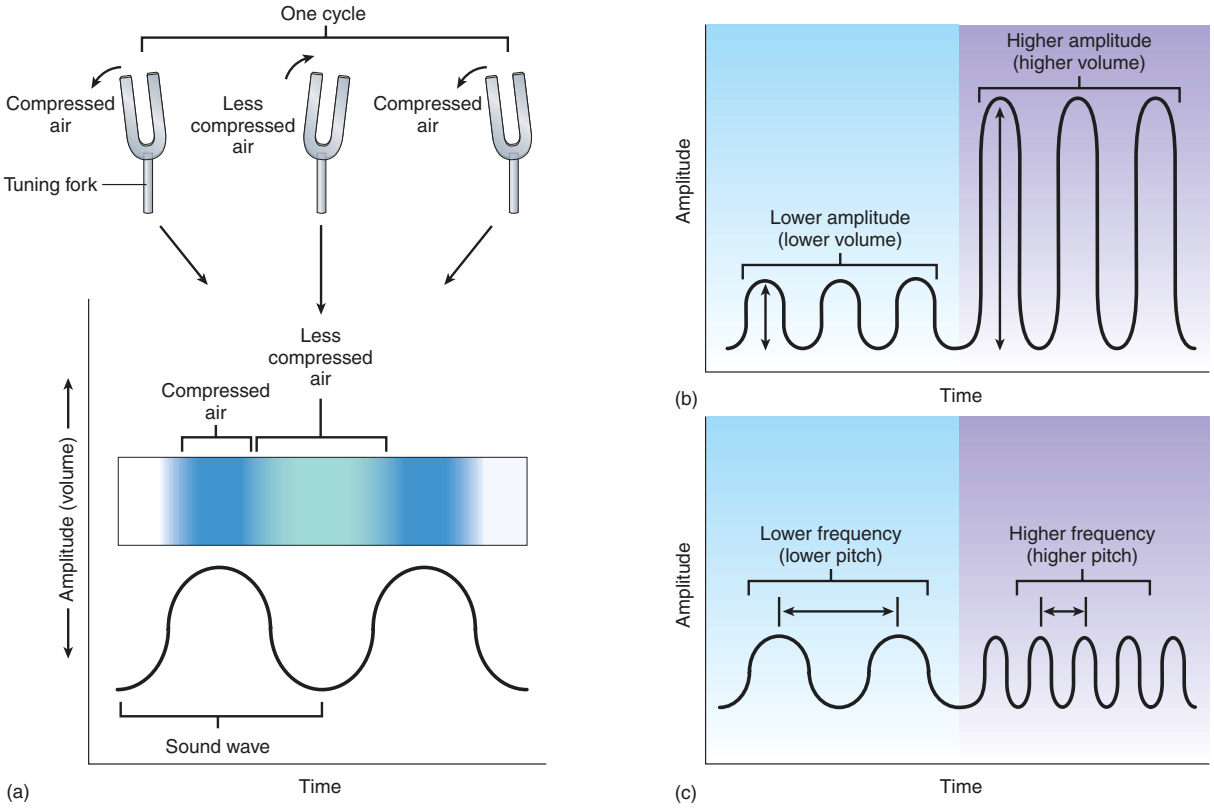


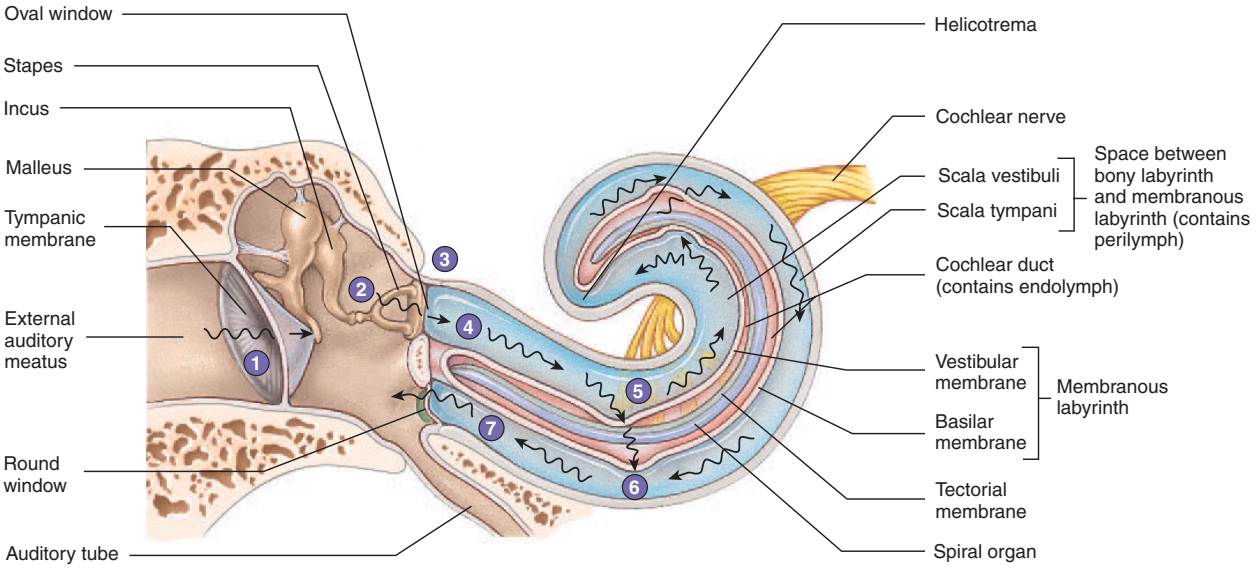
Figure 15.27 Sound Waves

(*a*) Each sound wave consists of a region of compressed air between two regions of less compressed air (*blue bars*). The sigmoid waves correspond to the regions of more compressed air (peaks) and less compressed air (troughs). The *green shadowed area* represents the width of one cycle (distance between peaks). When something like a tuning fork or vocal cords vibrate, the movements of the object alternate between compressing the air and decompressing the air, or making the air less compressed, thus producing sound. (*b*) Depicts low- and high-volume sound waves. Compare the relative lengths of the *arrows* indicating the wave height (amplitude). (*c*) Depicts lower and higher pitch sound. Compare the relative number of peaks (frequency) within a given time interval (*between arrows*).

Timbre (tam′br, tim′br) is the resonance quality or overtones of a sound. A smooth sigmoid curve is the image of a "pure" sound wave, but such a wave almost never exists in nature. The sounds made by musical instruments or the human voice are not smooth sigmoid curves but rather are rough, jagged curves formed by numerous, superimposed curves of various amplitudes and frequencies. The roughness of the curve accounts for the timbre. Timbre allows one to distinguish between, for example, an oboe and a French horn playing a note at the same pitch and volume. The steps involved in hearing are listed in table 15.2 and are illustrated in figure 15.28.

Table 15.2 Steps Involved in Hearing

1. The auricle collects sound waves that are then conducted through the external auditory meatus to the tympanic membrane, causing it to vibrate.
2. The vibrating tympanic membrane causes the malleus, incus, and stapes to vibrate.
3. Vibration of the stapes produces vibration in the perilymph of the scala vestibuli.
4. The vibration of the perilymph produces simultaneous vibration of the vestibular membrane and the endolymph in the cochlear duct.
5. Vibration of the endolymph causes the basilar membrane to vibrate.
6. As the basilar membrane vibrates, the hair cells attached to the membrane move relative to the tectorial membrane, which remains stationary.
7. The hair cell microvilli, embedded in the tectorial membrane, become bent.
8. Bending of the microvilli causes depolarization of the hair cells.
9. The hair cells induce action potentials in the cochlear neurons.
10. The action potentials generated in the cochlear neurons are conducted to the CNS.
11. The action potentials are translated in the cerebral cortex and are perceived as sound.



1. Sound waves strike the tympanic membrane and cause it to vibrate.

2. Vibration of the tympanic membrane causes the three bones of the middle ear to vibrate.

3. The foot plate of the stapes vibrates in the oval window.

4. Vibration of the foot plate causes the perilymph in the scala vestibuli to vibrate.

5. Vibration of the perilymph causes displacement of the basilar membrane. Short waves (high pitch) cause displacement of the basilar membrane near the oval window, and longer waves (low pitch) cause displacement of the basilar membrane some distance from the oval window. Movement of the basilar membrane is detected in the hair cells of the spiral organ, which are attached to the basilar membrane.

6. Vibrations of the perilymph in the scala vestibuli and of the endolymph in the cochlear duct are transferred to the perilymph of the scala tympani.

7. Vibrations in the perilymph of the scala tympani are transferred to the round window, where they are dampened.

Process Figure 15.28 Effect of Sound Waves on Cochlear Structures

External Ear

The auricle collects sound waves that are then conducted through the external auditory meatus toward the tympanic membrane. Sound waves travel relatively slowly in air, 332 m/s, and a significant time interval may elapse between the time a sound wave reaches one ear and the time that it reaches the other. The brain can interpret this interval to determine the direction from which a sound is coming.

Middle Ear

Sound waves strike the tympanic membrane and cause it to vibrate. This vibration causes vibration of the three ossicles of the middle ear, and by this mechanical linkage vibration is transferred to the oval window. More force is required to cause vibration in a liquid like the perilymph of the inner ear than is required in air; thus, the vibrations reaching the perilymph must be amplified as they cross the middle ear. The footplate of the stapes and its annular ligament, which occupy the oval window, are much smaller than the tympanic membrane. Because of this size difference, the mechanical force of vibration is amplified about 20-fold as it passes from the tympanic membrane, through the ossicles, and to the oval window.

Two small skeletal muscles are attached to the ear ossicles and reflexively dampen excessively loud sounds (figure 15.29). This **sound attenuation reflex** protects the delicate ear structures from damage by loud noises. The **tensor tympani** (ten′sōr tim′pănē) muscle is attached to the malleus and is innervated by the trigeminal nerve (V). The **stapedius** (stā-pē′dē-ŭs) muscle is attached to the stapes and is supplied by the facial nerve (VII). The sound attenuation reflex responds most effectively to low-frequency sounds and can reduce by a factor of 100 the energy reaching the oval window. The reflex is too slow to prevent damage from a sudden noise, such as a gunshot, and it cannot function effectively for longer than about 10 minutes, in response to prolonged noise.

P R E D I C T 9

What effect does facial nerve damage have on hearing?

Inner Ear

As the stapes vibrates, it produces waves in the perilymph of the scala vestibuli (see figure 15.28). Vibrations of the perilymph are transmitted through the thin vestibular membrane and cause simultaneous vibrations of the endolymph. The mechanical effect is as though the perilymph and endolymph were a single fluid. Vibration of the endolymph causes distortion of the basilar membrane. Waves in the perilymph of the scala vestibuli are transmitted also through the helicotrema and into the scala tympani. Because the helicotrema is very small, however, this transmitted vibration is probably of little consequence. Distortions of the basilar membrane, together with weaker waves coming through the helicotrema, cause waves in the scala tympani perilymph and ultimately result in vibration of the membrane of the round window. Vibration of the round window membrane is important to hearing because it acts as a mechanical release for waves from within the cochlea. If this window were solid, it would reflect the waves, which would interfere with and dampen later waves. The round window also allows relief of pressure in the perilymph because fluid is not compressible, thereby preventing compression damage to the spiral organ.

The distortion of the basilar membrane is most important to hearing. As this membrane distorts, the hair cells resting on the basilar membrane move relative to the tectorial membrane, which remains stationary. The hair cell microvilli, which are embedded in the tectorial membrane, become bent, causing depolarization of the hair cells. The hair cells then induce action potentials in the cochlear neurons that synapse on the hair cells, apparently by direct electrical excitation through electrical synapses rather than by neurotransmitters.

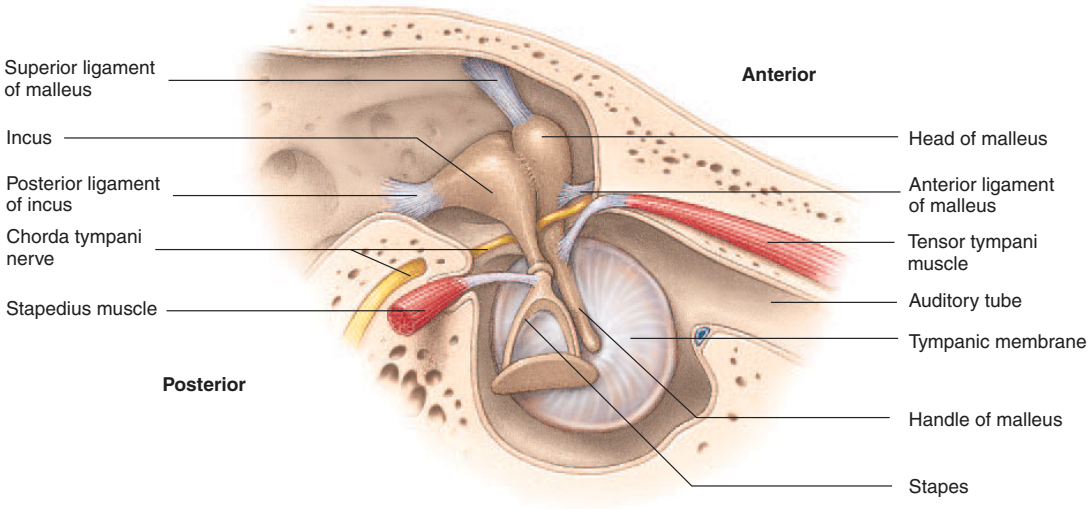


Figure 15.29 Muscles of the Middle Ear

Medial view of the middle ear (as though viewed from the inner ear), showing the three ear ossicles with their ligaments and the two muscles of the middle ear: the tensor tympani and the stapedius.

The hairs of the hair cells are bathed in endolymph. Because of the difference in the potassium and sodium ion concentrations between the perilymph and endolymph, an approximately 80 mV potential exists across the vestibular membrane between the two fluids. This is called the **endocochlear potential.** Because the hair cell hairs are surrounded by endolymph, the hairs have a greater electric potential than if they were surrounded by perilymph. It's believed that this potential difference makes the hair cells much more sensitive to slight movement than they would be if surrounded by perilymph.

The part of the basilar membrane that distorts as a result of endolymph vibration depends on the pitch of the sound that created the vibration and, as a result, on the vibration frequency within the endolymph. The width of the basilar membrane and the length and diameter of the collagen fibers stretching across the membrane at each level along the cochlear duct determine the location of the optimum amount of basilar membrane vibration produced by a given pitch (figure 15.30). Higher-pitched tones cause optimal vibration near the base, and lower-pitched tones cause optimal vibration near the apex of the basilar membrane. As the basilar membrane vibrates, hair cells along a large part of the basilar membrane are stimulated. In areas of minimum vibration, the amount of stimulation may not reach threshold. In other areas, a low frequency of afferent action potentials may be transmitted, whereas in the optimally vibrating regions of the basilar membrane, a high frequency of action potentials is initiated.

Loud Noises and Hearing Loss

Prolonged or frequent exposure to excessively loud noises can cause degeneration of the spiral organ at the base of the cochlea, resulting in high-frequency deafness. The actual amount of damage can vary greatly from person to person. High-frequency loss can cause a person to miss hearing consonants in a noisy setting. Loud music, amplified to 120 db, can impair hearing. The defects may not be detectable on routine diagnosis, but they include decreased sensitivity to sound in specific narrow frequency ranges and a decreased ability to discriminate between two pitches. Loud music, however, is not as harmful as is the sound of a nearby gunshot, which is a sudden sound occurring at 140 db. The sound is too sudden for the attenuation reflex to protect the inner ear structures, and the intensity is great enough to cause auditory damage. In fact, gunshot noise is the most common recreational cause of serious hearing loss.

Afferent action potentials conducted by cochlear nerve fibers from all along the spiral organ terminate in the **superior olivary nucleus** in the medulla oblongata (figure 15.31; see chapter 13). These action potentials are compared to one another, and the strongest action potential, corresponding to the area of maximum basilar membrane vibration, is taken as standard. Efferent action potentials then are sent from the superior olivary nucleus back to the spiral organ to all regions where the maximum vibration did not occur. These action potentials inhibit the hair cells from initiating additional action potentials in the sensory neurons. Thus, only action potentials from regions of maximum vibration are received by the cortex, where they become consciously perceived.

By this process, tones are localized along the cochlea. As a result of this localization, neurons along a given portion of the cochlea send action potentials only to the cerebral cortex in response to specific pitches. Action potentials near the base of the basilar membrane stimulate neurons in a certain part of the auditory cortex, which interpret the stimulus as a high-pitched sound, whereas action potentials from the apex stimulate a different part of the cortex, which interprets the stimulus as a low-pitched sound.

P R E D I C T 10

Suggest some possible sites and mechanisms to explain why certain people have "perfect pitch" and other people are "tone deaf."

Sound volume, or loudness, is a function of sound wave amplitude. As high-amplitude sound waves reach the ear, the perilymph, endolymph, and basilar membrane vibrate more intensely, and the hair cells are stimulated more intensely. As a result of the increased stimulation, more hair cells send action potentials at a higher frequency to the cerebral cortex, where this information is perceived as a greater sound volume.

32. Starting with the auricle, trace a sound wave into the inner ear to the point at which action potentials are generated in the cochlear nerve.

P R E D I C T 11

Explain why it's much easier to perceive subtle musical tones when music is played somewhat softly as opposed to very loudly.

Neuronal Pathways for Hearing

The special senses of hearing and balance are both transmitted by the vestibulocochlear (VIII) nerve. The term *vestibular* refers to the vestibule of the inner ear, which is involved in balance. The term *cochlear* refers to the cochlea and is that portion of the inner ear

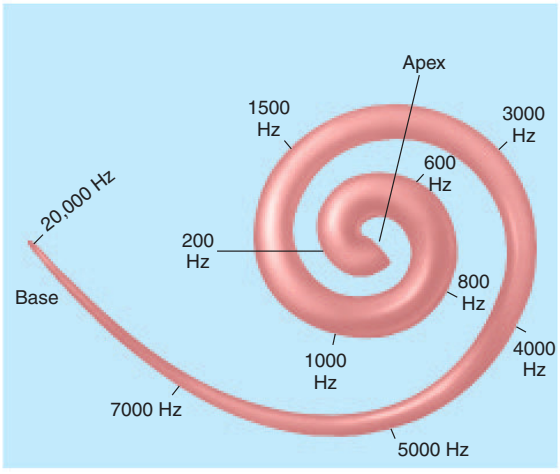
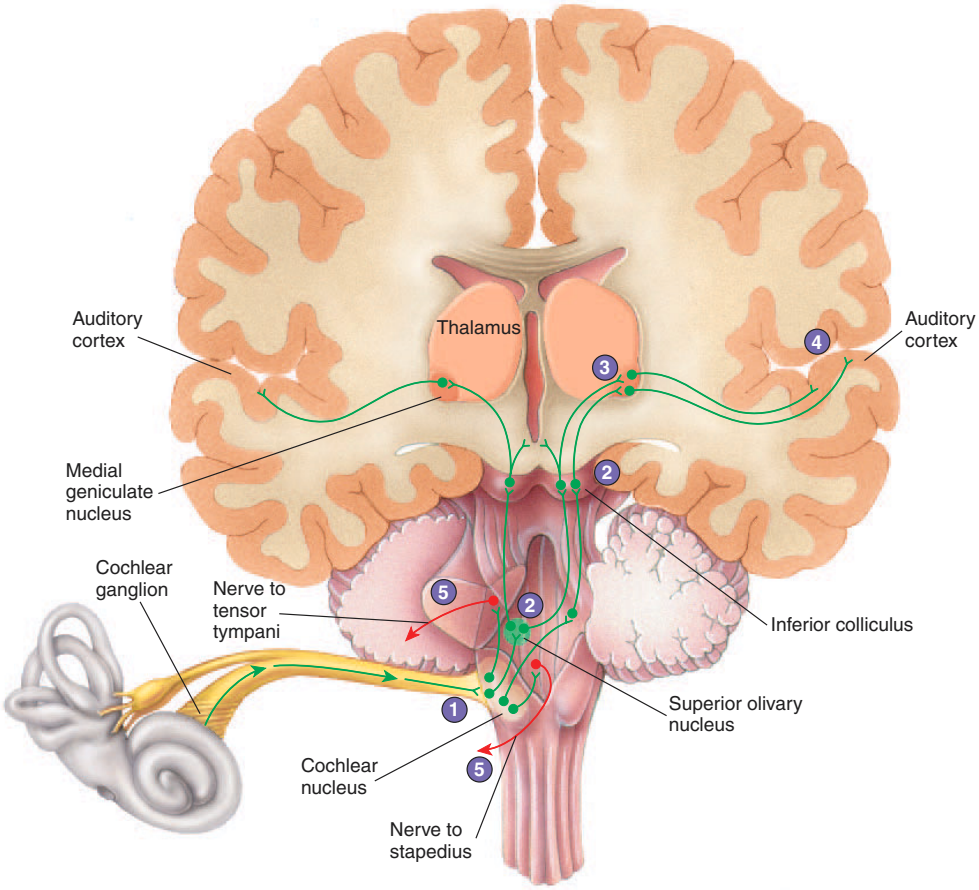


Figure 15.30 Effect of Sound Waves on Points Along the Basilar Membrane

Points of maximum vibration along the basilar membrane resulting from stimulation by sounds of various frequencies (in hertz).

1. Sensory axons from the cochlear ganglion terminate in the cochlear nucleus in the brainstem.
2. Axons from the neurons in the cochlear nucleus project to the superior olivary nucleus or to the inferior colliculus.
3. Axons from the inferior colliculus project to the medial geniculate nucleus of the thalamus.
4. Thalamic neurons project to the auditory cortex.
5. Neurons in the superior olivary nucleus send axons to the inferior colliculus, back to the inner ear, or to motor nuclei in the brainstem that send efferent fibers to the middle ear muscles.



Process Figure 15.31 Central Nervous System Pathways for Hearing

involved in hearing. The vestibulocochlear nerve functions as two separate nerves carrying information from two separate but closely related structures.

The auditory pathways within the CNS are very complex, with both crossed and uncrossed tracts (see figure 15.31). Unilateral CNS damage therefore usually has little effect on hearing. The neurons from the cochlear ganglion synapse with CNS neurons in the dorsal or ventral **cochlear nucleus** in the superior medulla near the inferior cerebellar peduncle. These neurons in turn either synapse in or pass through the superior olivary nucleus. Neurons terminating in this nucleus may synapse with efferent neurons returning to the cochlea to modulate pitch perception. Nerve fibers from the superior olivary nucleus also project to the trigeminal (V) nucleus, which controls the tensor tympani, and the facial (VII) nucleus, which controls the stapedius muscle. This reflex pathway dampens loud sounds by initiating contractions of these muscles. This is the sound attenuation reflex described previously. Neurons synapsing in the superior olivary nucleus may also join other ascending neurons to the cerebral cortex.

Ascending neurons from the superior olivary nucleus travel in the **lateral lemniscus.** All ascending fibers synapse in the **inferior colliculi,** and neurons from there project to the **medial geniculate nucleus** of the **thalamus,** where they synapse with neurons that project to the cortex. These neurons terminate in the **auditory cortex** in the dorsal portion of the temporal lobe within the lateral fissure and, to a lesser extent, on the superolateral surface of the temporal lobe (see chapter 13). Neurons from the inferior colliculus also project to the **superior colliculus,** where reflexes that turn the head and eyes in response to loud sounds are initiated.

33. Describe the neuronal pathways for hearing from the cochlear nerve to the cerebral cortex.

Balance

The organs of balance are divided structurally and functionally into two parts. The first, the **static labyrinth,** consists of the **utricle** (oo′tri-kl) and **saccule** (sak′ūl) of the vestibule and is primarily involved in evaluating the position of the head relative to gravity, although the system also responds to linear acceleration or

Clinical Focus Deafness and Functional Replacement of the Ear

Deafness can have many causes. In general, two categories of deafness exist: conduction and sensorineural (or nerve) deafness. **Conduction deafness** involves a mechanical deficiency in transmission of sound waves from the external ear to the spiral organ and may often be corrected surgically. Hearing aids help people with such hearing deficiencies by boosting the sound volume reaching the ear. **Sensorineural deafness** involves the spiral organ or nerve pathways and is more difficult to correct.

Research is currently being conducted on ways to replace the hearing pathways with electric circuits. One approach involves the direct stimulation of nerves by electric impulses. There has been considerable success in the area of cochlear nerve stimulation. Certain types of sensorineural deafness in which the hair cells of the spiral organ are impaired can now be partially corrected. Prostheses are available that consist of a microphone for picking up the initial sound waves, a microelectronic processor for converting the sound into electric signals, a transmission system for relaying the signals to the inner ear, and a long, slender electrode that is threaded into the cochlea. This electrode delivers electric signals directly to the endings of the cochlear nerve (figure D). High-frequency sounds are picked up by the microphone and transmitted through specific circuits to terminate near the oval window, whereas low-frequency sounds are transmitted farther up the cochlea to cochlear nerve endings near the helicotrema.

Research is currently underway to develop implants directly into the cochlear nucleus of the brainstem for patients with vestibulocochlear nerve damage. These implants have electrodes of various lengths to stimulate parts of the cochlear nucleus, at various depths from the surface, which respond to sounds of different frequencies.

1. A receiver, transmitter, and antenna are implanted under the skin near the auricle.
2. A small lead from the transmitter is fed through the external auditory meatus, tympanic membrane, and middle ear into the cochlea.
3. In the cochlea, the cochlear nerve can be directly stimulated by electric impulses from the receiver.

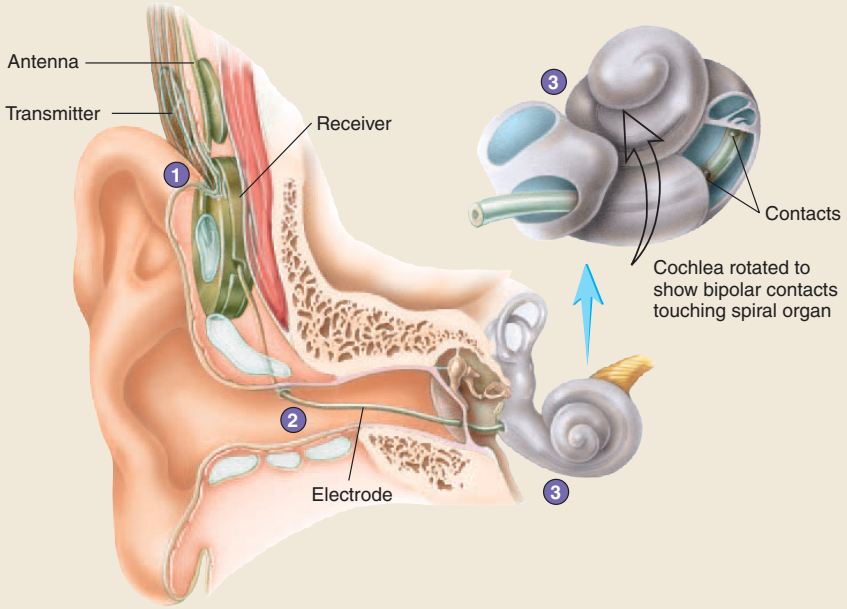


Figure D Cochlear Implant

deceleration, such as when a person is in a car that is increasing or decreasing speed. The second, the **kinetic labyrinth,** is associated with the semicircular canals and is involved in evaluating movements of the head.

Most of the utricular and saccular walls consist of simple cuboidal epithelium. The utricle and saccule, however, each contain a specialized patch of epithelium about 2–3 mm in diameter called the **macula** (mak′ū-lă; figure 15.32*a* and *b*). The macula of the utricle is oriented parallel to the base of the skull, and the macula of the saccule is perpendicular to the base of the skull.

The maculae resemble the spiral organ and consist of columnar supporting cells and hair cells. The "hairs" of these cells, which consist of numerous microvilli, called **stereocilia,** and one cilium, called a **kinocilium** (kī-nō-sil′ē-ŭm), are embedded in a **gelatinous mass**

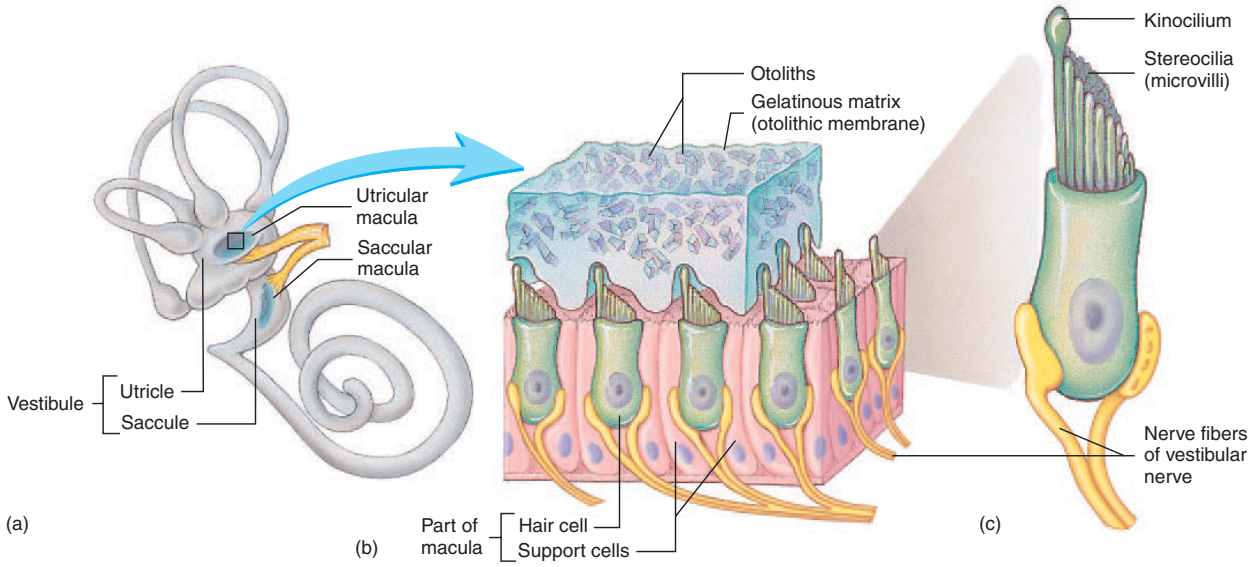


Figure 15.32 Structure of the Macula

(*a*) Vestibule showing the location of the utricular and saccular maculae. (*b*) Enlargement of the utricular macula, showing hair cells and otoliths in the macula. (*c*) An enlarged hair cell, showing the kinocilium and stereocilia.

weighted by the presence of **otoliths** (ō′tō-liths) composed of protein and calcium carbonate (figure 15.32*b*). The gelatinous mass moves in response to gravity, bending the hair cells and initiating action potentials in the associated neurons. Deflection of the hairs toward the kinocilium results in depolarization of the hair cell, whereas deflection of the hairs away from the kinocilium results in hyperpolarization of the hair cell. If the head is tipped, otoliths move in response to gravity and stimulate certain hair cells (figure 15.33). The hair cells are constantly being stimulated at a low level by the presence of the otolith-weighted covering of the macula; but as this covering moves in response to gravity, the pattern of intensity of hair cell stimulation changes. This pattern of stimulation and the subsequent pattern of action potentials from the numerous hair cells of the maculae can be translated by the brain into specific information about head position or acceleration. Much of this information is not perceived consciously but is dealt with subconsciously. The body responds by making subtle tone adjustments in muscles of the back and neck, which are intended to restore the head to its proper neutral, balanced position.

The kinetic labyrinth (figure 15.34) consists of three **semicircular canals** placed at nearly right angles to one another, one lying nearly in the transverse plane, one in the coronal plane, and one in the sagittal plane (see chapter 1). The arrangement of the semicircular canals enables a person to detect movement in all directions. The base of each semicircular canal is expanded into an **ampulla** (figure 15.34*a*). Within each ampulla, the epithelium is specialized to form a **crista ampullaris** (kris′tă am-pū-lar′ŭs). This specialized sensory epithelium is structurally and functionally very similar to that of the maculae. Each crista consists of a ridge or crest of epithelium with a curved gelatinous mass, the **cupula** (koo′poo-lă), suspended over the crest. The hairlike processes of the crista hair cells, similar to those in the maculae, are embedded in the cupula (figure 15.34*b*). The cupula contains no otoliths and therefore doesn't respond to gravitational pull. Instead, the cupula is a float that is displaced by fluid movements within the semicircular canals. Endolymph movement within each semicircular canal moves the cupula, bends the hairs, and initiates action potentials (figure 15.35).

As the head begins to move in a given direction, the endolymph does not move at the same rate as the semicircular canals (see figure 15.35). This difference causes displacement of the cupula in a direction opposite to that of the movement of the head, resulting in relative movement between the cupula and the endolymph. As movement continues, the fluid of the semicircular canals begins to move and "catches up" with the cupula, and stimulation is stopped. As movement of the head ceases, the endolymph continues to move because of its momentum, causing displacement of the cupula in the same direction as the head had been moving. Because displacement of the cupula is most intense when the rate of head movement changes, this system detects changes in the rate of movement rather than movement alone. As with the static labyrinth, the information obtained by the brain from the kinetic labyrinth is largely subconscious.

34. *What are the functions of the saccule and utricle? Describe the macula and its functions.*
35. *What is the function of the semicircular canals? Describe the crista ampullaris and its mode of operation.*

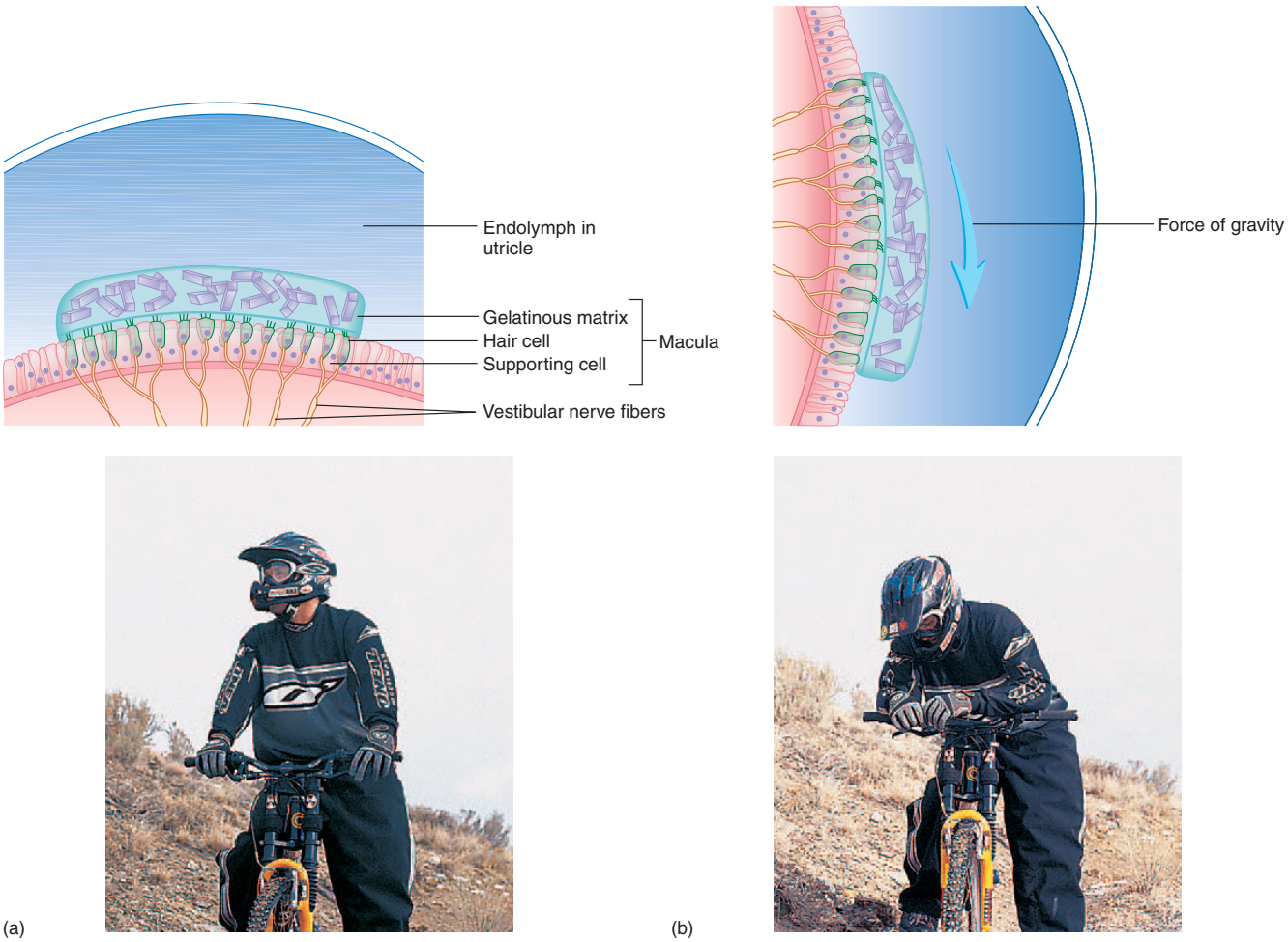


Figure 15.33 Function of the Vestibule in Maintaining Balance

(*a*) As the position of the head changes, such as when a person bends over, the maculae respond to changes in position of the head relative to gravity by moving in the direction of gravity. (*b*) In an upright position, the maculae don't move.

Space Sickness

Space sickness is a balance disorder occurring in zero gravity and resulting from unfamiliar sensory input to the brain. The brain must adjust to these unusual signals, or severe symptoms like headaches and dizziness may result. Space sickness is unlike motion sickness in that motion sickness results from an excessive stimulation of the brain, whereas space sickness results from too little stimulation as a result of weightlessness.

Neuronal Pathways for Balance

Neurons synapsing on the hair cells of the maculae and cristae ampullares converge into the **vestibular ganglion,** where their cell bodies are located (figure 15.36). Sensory fibers from these neurons join sensory fibers from the cochlear ganglion to form the vestibulocochlear nerve (VIII) and terminate in the **vestibular nucleus** within the medulla oblongata. Axons run from this nucleus to numerous areas of the CNS, such as the spinal cord, cerebellum, cerebral cortex, and the nuclei controlling extrinsic eye muscles.

Balance is a complex process not simply confined to one type of input. In addition to vestibular sensory input, the vestibular nucleus receives input from proprioceptive neurons throughout the body, and from the visual system. People are asked to close their eyes while balance is evaluated in a sobriety test because alcohol affects the proprioceptive and vestibular components of balance (cerebellar function) to a greater extent than it does the visual portion.

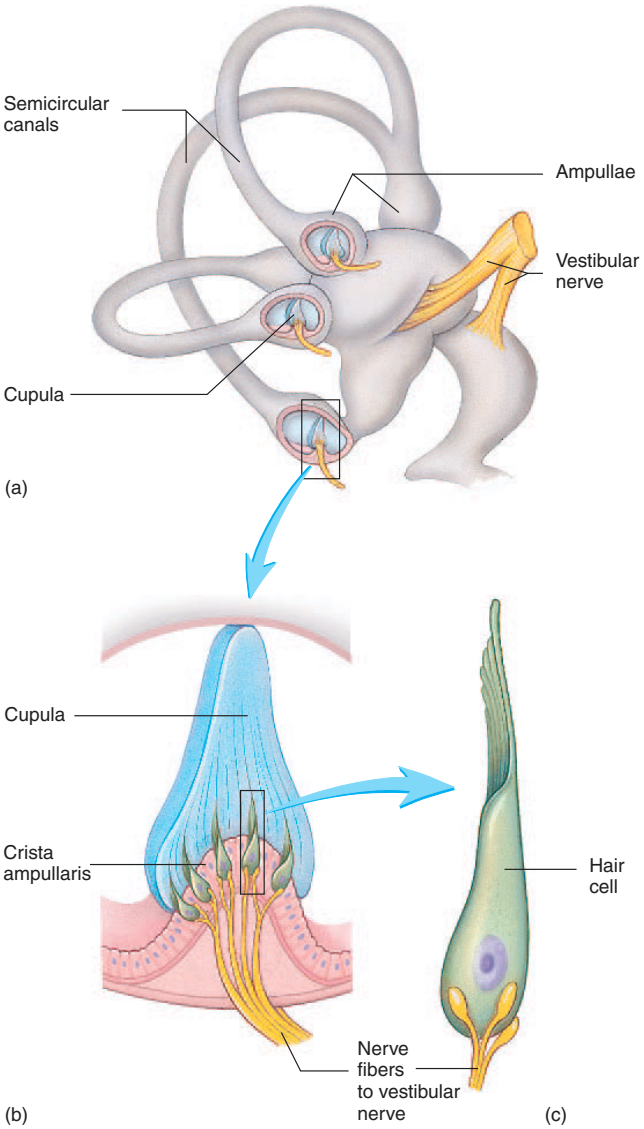


Figure 15.34 Semicircular Canals

(*a*) Semicircular canals showing location of the crista ampullaris in the ampullae of the semicircular canals. (*b*) Enlargement of the crista ampullaris, showing the cupula and hair cells. (*c*) Enlargement of a hair cell.

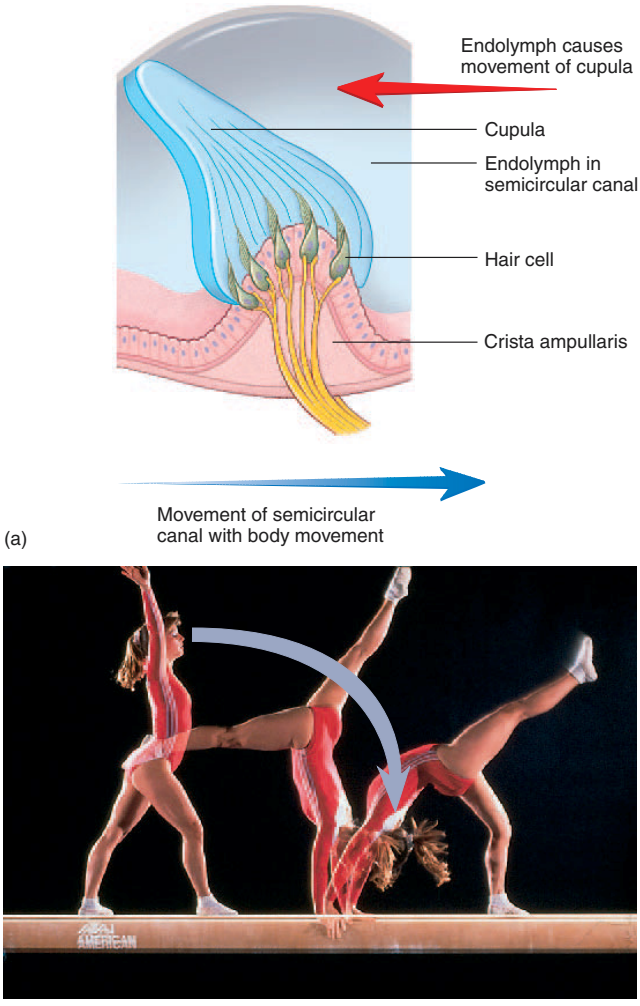
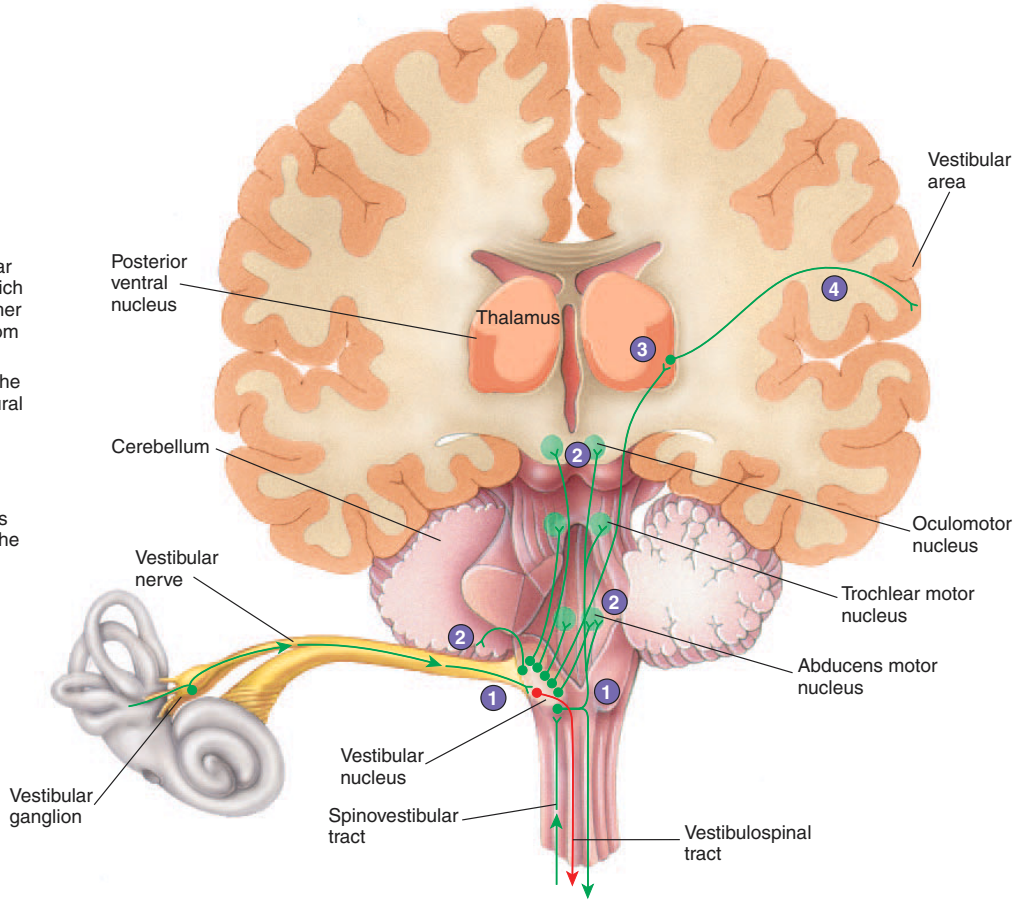


Figure 15.35 Function of the Semicircular Canals

The crista ampullaris responds to fluid movements within the semicircular canals. (*a*) When a person is at rest, the crista ampullaris does not move. (*b*) As a person begins to move in a given direction, the semicircular canals begin to move with the body (*blue arrow*), but the endolymph tends to remain stationary relative to the movement (momentum force: *red arrow* pointing in the opposite direction of body and semicircular canal movement), and the crista ampullaris is displaced by the endolymph in a direction opposite to the direction of movement.

Reflex pathways exist between the kinetic part of the vestibular system and the nuclei controlling the extrinsic eye muscles (oculomotor, trochlear, and abducens). A reflex pathway allows maintenance of visual fixation on an object while the head is in motion. This function can be demonstrated by spinning a person around about 10 times in 20 seconds, stopping him or her, and observing eye movements. The reaction is most pronounced if the individual's head is tilted forward about 30 degrees while spinning, thus bringing the lateral semicircular canals into the horizontal plane. A slight oscillatory movement of the eyes occurs. The eyes track in the direction of motion and return with a rapid recovery movement before repeating the tracking motion. This oscillation of the eyes is called

1. Sensory axons from the vestibular ganglion pass through the vestibular nerve to the vestibular nucleus, which also receives input from several other sources, such as proprioception from the legs.
2. Vestibular neurons send axons to the cerebellum, which influences postural muscles, and to the motor nuclei (oculomotor, trochlear, and abducens), which control extrinsic eye muscles.
3. Vestibular neurons also send axons to the posterior ventral nucleus of the thalamus.
4. Thalamic neurons project to the vestibular area of the cortex.



Process Figure 15.36 Central Nervous System Pathways for Balance

nystagmus (nis-tag′mŭs). If asked to walk in a straight line, the individual deviates in the direction of rotation, and if asked to point to an object, his or her finger deviates in the direction of rotation.

36. Describe the neuronal pathways for balance.

Effects of Aging on the Special Senses

Objective

- ***Describe changes that occur in the special senses with aging.***

Elderly people experience only a slight loss in the ability to detect odors. However, the ability to correctly identify specific odors is decreased, especially in men over age 70.

In general, the sense of taste decreases as people age. The number of sensory receptors decreases and the ability of the brain to interpret taste sensations declines.

Responses to taste change in some elderly people who are fighting cancer. One side effect of radiation treatment and chemotherapy is the gastrointestinal discomfort resulting from the treatments. The patients experience a loss of appetite because of conditioned taste aversions resulting from treatment.

The lenses of the eyes lose flexibility as a person ages because the connective tissue of the lenses becomes more rigid. Consequently there is first a reduction and then an eventual loss in the ability of the lenses to change shape. This condition, called presbyopia, is the most common age-related change in the eyes. It is discussed more fully in the Clinical Focus on "Eye Disorders" earlier in the chapter.

The most common visual problem in older people requiring medical treatment, such as surgery, is the development of cataracts. Macular degeneration is the second most common defect, glaucoma is third, and diabetic retinopathy is fourth. These defects are also described more fully in the Clinical Focus on "Eye Disorders."

The number of cones decreases, especially in the fovea centralis. These changes cause a gradual decline in visual acuity and color preception.

Clinical Focus Ear Disorders

Otosclerosis

Otosclerosis (ō′tō-sklē-rō′sis) is an ear disorder in which spongy bone grows over the oval window and immobilizes the stapes, leading to progressive loss of hearing. This disorder can be surgically corrected by breaking away the bony growth and the immobilized stapes. During surgery, the stapes is replaced by a small rod connected by a fat pad or a synthetic membrane to the oval window at one end and to the incus at the other end.

Tinnitus

Tinnitus (ti-nī′tŭs) consists of noises such as ringing, clicking, whistling, or booming in the ears. These noises may occur as a result of disorders in the middle or inner ear or along the central neuronal pathways.

Motion Sickness

Motion sickness consists of nausea, weakness, and other dysfunctions caused by stimulation of the semicircular canals during motion, such as in a boat, automobile, airplane, swing, or amusement park ride. It may progress to vomiting and incapacitation. Antiemetics such as anticholinergic or antihistamine medications can be taken to counter the nausea and vomiting associated with motion sickness. Scopolamine is an anticholinergic drug that reduces the excitability of vestibular receptors. Cyclizine (Marezine), dimenhydrinate (Dramamine), and diphenhydramine (Benadryl) are antihistamines that affect the neural pathways from the vestibule. Scopolamine can be administered transdermally in the form of a patch placed on the skin behind the ear (Transdermal-Scop). A patch lasts about 3 days.

Otitis Media

Infections of the middle ear, called **otitis media,** are quite common in young children. These infections usually result from the spread of infection from the mucous membrane of the pharynx through the auditory tube to the mucous lining of the middle ear. The symptoms of otitis media, consisting of low-grade fever, lethargy, and irritability, are often not easily recognized by the parent as signs of middle ear infection. The infection can also cause a temporary decrease or loss of hearing because fluid buildup has dampened the tympanic membrane or ossicles.

Earache

Earache can result from otitis media, otitis externa (inflammation of the external auditory meatus), dental abscesses, or temporomandibular joint pain.

As people age, the number of hair cells in the cochlea decreases. This decline doesn't occur equally in both ears. As a result, because direction is determined by comparing sounds coming into each ear, elderly people may experience a decreased ability to localize the origin of certain sounds. In some people, this may lead to a general sense of disorientation. In addition, CNS defects in the auditory pathways can result in difficulty understanding sounds with echoes or background noise. Such deficit makes it difficult for elderly people to understand rapid or broken speech.

With age, the number of hair cells in the saccule, utricle, and ampullae decrease. The number of otoliths also declines. As a result, elderly people experience a decreased sensitivity to gravity, acceleration, and rotation. Because of these decreases, elderly people experience dizziness (instability) and vertigo (a feeling of spinning). They often feel that they can't maintain posture and are prone to fall.

37. Explain the changes in taste, vision, hearing, and balance that occur with aging.

S U M M A R Y

Olfaction (p. 502)

Olfaction is the sense of smell.

Olfactory Epithelium and Bulb

1. Olfactory neurons in the olfactory epithelium are bipolar neurons. Their distal ends are enlarged as olfactory vesicles, which have long cilia. The cilia have receptors that respond to dissolved substances.
2. At least seven (perhaps 50) primary odors exist. The olfactory neurons have a very low threshold and accommodate rapidly.

Neuronal Pathways of Olfaction

1. Axons from the olfactory neurons extend as olfactory nerves to the olfactory bulb, where they synapse with mitral and tufted cells. Axons from these cells form the olfactory tracts. Association neurons in the olfactory bulbs can modulate output to the olfactory tracts.
2. The olfactory tracts terminate in the olfactory cortex. The lateral olfactory area is involved in the conscious perception of smell, the intermediate area with modulating smell, and the medial area with visceral and emotional responses to smell.

Taste (p. 504)

Taste buds usually are associated with circumvallate, fungiform, and foliate papillae. Filiform papillae do not have taste buds.

Histology of Taste Buds

1. Taste buds consist of support and gustatory cells.
2. The gustatory cells have gustatory hairs that extend into taste pores.

Function of Taste

1. Receptors on the hairs detect dissolved substances.
2. Five basic types of taste exist: sour, salty, bitter, sweet, and umami.

Neuronal Pathways for Taste

1. The facial nerve carries taste sensations from the anterior two-thirds of the tongue, the glossopharyngeal nerve from the posterior one-third of the tongue, and the vagus nerve from the epiglottis.
2. The neural pathways for taste extend from the medulla oblongata to the thalamus and to the cerebral cortex.

Visual System (p. 508)

Accessory Structures

1. The eyebrows prevent perspiration from entering the eyes and help shade the eyes.
2. The eyelids consist of five tissue layers. They protect the eyes from foreign objects and help lubricate the eyes by spreading tears over their surface.
3. The conjunctiva covers the inner eyelid and the anterior part of the eye.
4. Lacrimal glands produce tears that flow across the surface of the eye. Excess tears enter the lacrimal canaliculi and reach the nasal cavity through the nasolacrimal canal. Tears lubricate and protect the eye.
5. The extrinsic eye muscles move the eyeball.

Anatomy of the Eye

1. The fibrous tunic is the outer layer of the eye. It consists of the sclera and cornea.
   - The sclera is the posterior four-fifths of the eye. It is white connective tissue that maintains the shape of the eye and provides a site for muscle attachment.
   - The cornea is the anterior one-fifth of the eye. It is transparent and refracts light that enters the eye.
2. The vascular tunic is the middle layer of the eye.
   - The iris is smooth muscle regulated by the autonomic nervous system. It controls the amount of light entering the pupil.
   - The ciliary muscles control the shape of the lens. They are smooth muscles regulated by the autonomic nervous system. The ciliary process produces aqueous humor.
3. The retina is the inner layer of the eye and contains neurons sensitive to light.
   - The macula lutea (fovea centralis) is the area of greatest visual acuity.
   - The optic disc is the location through which nerves exit and blood vessels enter the eye. It has no photosensory cells and is therefore the blind spot of the eye.
4. The eye has two compartments.
   - The anterior compartment is filled with aqueous humor, which circulates and leaves by way of the canal of Schlemm.
   - The posterior compartment is filled with vitreous humor.
5. The lens is held in place by the suspensory ligaments, which are attached to the ciliary muscles.

Functions of the Complete Eye

1. Light is that portion of the electromagnetic spectrum that humans can see.
2. When light travels from one medium to another, it can bend or refract. Light striking a concave surface refracts outward (divergence). Light striking a convex surface refracts inward (convergence).
3. Converging light rays meet at the focal point and are said to be focused.
4. The cornea, aqueous humor, lens, and vitreous humor all refract light. The cornea is responsible for most of the convergence, whereas the lens can adjust the focal point by changing shape.
   - Relaxation of the ciliary muscles causes the lens to flatten, producing the emmetropic eye.
   - Contraction of the ciliary muscles causes the lens to become more spherical. This change in lens shape enables the eye to focus on objects that are less than 20 feet away, a process called accommodation.
5. The far point of vision is the distance at which the eye no longer has to change shape to focus on an object. The near point of vision is the closest an object can come to the eye and still be focused.
6. The pupil becomes smaller during accommodation, increasing the depth of focus.

Structure and Function of the Retina

1. The pigmented retina provides a black backdrop for increasing visual acuity.
2. Rods are responsible for vision in low illumination (night vision).
   - A pigment, rhodopsin, is split by light into retinal and opsin, producing hyperpolarization in the rod.
   - Light adaptation is caused by a reduction of rhodopsin; dark adaptation is caused by rhodopsin production.
3. Cones are responsible for color vision and visual acuity.
   - Cones are of three types, each with a different photopigment. The pigments are most sensitive to blue, red, and green lights.
   - Perception of many colors results from mixing the ratio of the different types of cones that are active at a given moment.
4. Most visual images are focused on the fovea centralis, which has a very high concentration of cones. Moving away from the fovea, fewer cones (the macula lutea) are present; mostly rods are in the periphery of the retina.
5. The rods and the cones synapse with bipolar cells that in turn synapse with ganglion cells, which form the optic nerves.
6. Association neurons in the retina can modify information sent to the brain.

Neuronal Pathways for Vision

1. Ganglia cell axons extend to the lateral geniculate ganglion of the thalamus, where they synapse. From there neurons form the optic radiations that project to the visual cortex.
2. Neurons from the nasal visual field (temporal retina) of one eye and the temporal visual field (nasal retina) of the opposite eye project to the same cerebral hemisphere. Axons from the nasal retina cross in the optic chiasm, and axons from the temporal retina remain uncrossed.
3. Depth perception is the ability to judge relative distances of an object from the eyes and is a property of binocular vision. Binocular vision results because a slightly different image is seen by each eye.

Hearing and Balance (p. 527)

The osseous labyrinth is a canal system within the temporal bone that contains perilymph and the membranous labyrinth. Endolymph is inside the membranous labyrinth.

Auditory Structures and Their Functions

1. The external ear consists of the auricle and external auditory meatus.
2. The middle ear connects the external and inner ears.
   - The tympanic membrane is stretched across the external auditory meatus.
   - The malleus, incus, and stapes connect the tympanic membrane to the oval window of the inner ear.
   - The auditory tube connects the middle ear to the pharynx and functions to equalize pressure.
   - The middle ear is connected to the mastoid air cells.
3. The inner ear has three parts: the semicircular canals; the vestibule, which contains the utricle and the saccule; and the cochlea.
4. The cochlea is a spiral-shaped canal within the temporal bone.
   - The cochlea is divided into three compartments by the vestibular and basilar membranes. The scala vestibuli and scala tympani contain perilymph. The cochlear duct contains endolymph and the spiral organ (organ of Corti).
   - The spiral organ consists of hair cells that attach to the tectorial membrane.

Auditory Function

1. Sound waves are funneled by the auricle down the external auditory meatus, causing the tympanic membrane to vibrate.
2. The tympanic membrane vibrations are passed along the auditory ossicles to the oval window of the inner ear.
3. Movement of the stapes in the oval window causes the perilymph, vestibular membrane, and endolymph to vibrate, producing movement of the basilar membrane. Movement of the basilar membrane causes displacement of the hair cells in the spiral organ and the generation of action potentials, which travel along the vestibulocochlear nerve.
4. Some vestibulocochlear nerve axons synapse in the superior olivary nucleus. Efferent neurons from this nucleus project back to the cochlea, where they regulate the perception of pitch.
5. The round window protects the inner ear from pressure buildup and dissipates waves.

Neuronal Pathways for Hearing

1. Axons from the vestibulocochlear nerve synapse in the medulla. Neurons from the medulla project axons to the inferior colliculi, where they synapse. Neurons from this point project to the thalamus and synapse. Thalamic neurons extend to the auditory cortex.
2. Efferent neurons project to cranial nerve nuclei responsible for controlling muscles that dampen sound in the middle ear.

Balance

1. Static balance evaluates the position of the head relative to gravity and detects linear acceleration and deceleration.
   - The utricle and saccule in the inner ear contain maculae. The maculae consist of hair cells with the hairs embedded in a gelatinous mass that contains otoliths.
   - The gelatinous mass moves in response to gravity.
2. Kinetic balance evaluates movements of the head.
   - Three semicircular canals at right angles to one another are present in the inner ear. The ampulla of each semicircular canal contains the crista ampullaris, which has hair cells with hairs embedded in a gelatinous mass, the cupula.
   - When the head moves, endolymph within the semicircular canal moves the cupula.

Neuronal Pathways for Balance

1. Axons from the maculae and the cristae ampullares extend to the vestibular nucleus of the medulla. Fibers from the medulla run to the spinal cord, cerebellum, cortex, and nuclei that control the extrinsic eye muscles.
2. Balance also depends on proprioception and visual input.

Effects of Aging on the Special Senses (p. 540)

Elderly people experience a decline in function of all special functions: olfaction, taste, vision, hearing, and balance. These declines can result in loss of appetite, visual impairment, disorientation, and risk of falling.

REVIEW AND COMPREHENSION

1. Olfactory neurons
   a. have projections called cilia.
   b. have axons that combine to form the olfactory nerves.
   c. connect to the olfactory bulb.
   d. have receptors that react with odorants dissolved in fluid.
   e. all of the above.
2. Which of these statements is *not* true with respect to olfaction?
   a. Olfactory sensation is relayed directly to the cerebral cortex without passing through the thalamus.
   b. Olfactory neurons are replaced about every two months.
   c. The lateral olfactory area of the cortex is involved in the conscious perception of smell.
   d. The medial olfactory area of the cortex is responsible for visceral and emotional reactions to odors.
   e. The olfactory cortex is in the occipital lobe of the cerebrum.
3. Gustatory (taste) cells
   a. are found only on the tongue.
   b. extend through tiny openings called taste buds.
   c. have no axons but release neurotransmitter when stimulated.
   d. have axons that extend directly to the taste area of the cerebral cortex.
4. Which of these is *not* one of the basic tastes?
   a. spicy
   b. salt
   c. bitter
   d. umami
   e. sour
5. Which of these types of papillae have no taste buds associated with them?
   a. circumvallate
   b. filiform
   c. foliate
   d. fungiform
6. Tears
   a. are released onto the surface of the eye near the medial corner of the eye.
   b. in excess are removed by the canal of Schlemm.
   c. in excess can cause a sty.
   d. can pass through the nasolacrimal duct into the oral cavity.
   e. contain water, salts, mucus, and lysozyme.
7. The fibrous tunic of the eye includes the
   a. conjunctiva.
   b. sclera.
   c. choroid.
   d. iris.
   e. retina.
8. The ciliary body
   a. contains smooth muscles that attach to the lens by suspensory ligaments.
   b. produces the vitreous humor.
   c. is part of the iris of the eye.
   d. is part of the sclera.
   e. all of the above.
9. The lens normally focuses light onto the
   a. optic disc.
   b. iris.
   c. macula lutea.
   d. cornea.
   e. ciliary body.
10. Given these structures:
    1. lens
    2. aqueous humor
    3. vitreous humor
    4. cornea

Choose the arrangement that lists the structures in the order that light entering the eye encounters them.
a. 1,2,3,4
b. 1,4,2,3
c. 4,1,2,3
d. 4,2,1,3
e. 4,3,2,1

11. Aqueous humor
a. is the pigment responsible for the black color of the choroid.
b. exits the eye through the canal of Schlemm.
c. is produced by the iris.
d. can cause cataracts if overproduced.
e. is composed of proteins called crystallines.

12. Contraction of the smooth muscle in the ciliary body causes the
a. lens to flatten.
b. lens to become more spherical.
c. pupil to constrict.
d. pupil to dilate.

13. Given these events:
1. medial rectus contracts
2. lateral rectus contracts
3. pupils dilate
4. pupils constrict
5. lens of the eye flattens
6. lens of the eye becomes more spherical

Assume you are looking at an object 30 feet away. If you suddenly look at an object that is 1 foot away, which events occur?
a. 1,3,6
b. 1,4,5
c. 1,4,6
d. 2,3,6
e. 2,4,5

14. Given these events:
1. bipolar cells depolarize
2. decrease in glutamate released from presynaptic terminals of photoreceptor cells
3. light strikes photoreceptor cells
4. photoreceptor cells depolarized
5. photoreceptor cells hyperpolarized

Choose the arrangement that lists the correct order of events, starting with the photoreceptor cells in the resting, nonactivated state.
a. 1,2,3,4,5
b. 2,4,3,5,1
c. 3,4,2,5,1
d. 4,3,5,2,1
e. 5,3,4,1,2

15. Given these neurons in the retina:
1. bipolar cells
2. ganglionic cells
3. photoreceptor cells

Choose the arrangement that lists the correct order of the cells encountered by light as it enters the eye and travels toward the pigmented retina.
a. 1,2,3
b. 1,3,2
c. 2,1,3
d. 2,3,1
e. 3,1,2

16. Which of these photoreceptor cells is *not* correctly matched with its function?
a. rods—vision in low light
b. rods—visual acuity
c. cones—color vision

17. Concerning dark adaptation,
a. the amount of rhodopsin increases.
b. the pupils constrict.
c. it occurs more rapidly than light adaptation.
d. all of the above.

18. In the retina there are cones that are most sensitive to a particular color. Given this list of colors:
1. red
2. yellow
3. green
4. blue

Indicate which colors correspond to specific types of cones.
a. 2,3
b. 3,4
c. 1,2,3
d. 1,3,4
e. 1,2,3,4

19. Given these areas of the retina:
1. macula lutea
2. fovea centralis
3. optic disc
4. periphery of the retina

Choose the arrangement that lists the areas according to the density of cones, starting with the area that has the highest density of cones.
a. 1,2,3,4
b. 1,3,2,4
c. 2,1,4,3
d. 2,4,1,3
e. 3,4,1,2

20. Concerning axons in the optic nerve from the right eye,
a. they all go to the right occipital lobe.
b. they all go to the left occipital lobe.
c. they all go to the thalamus.
d. some go to the right occipital lobe, and some go to the left occipital lobe.

21. A lesion that destroyed the left optic tract of a boy eliminates vision in his
a. left nasal visual field.
b. left temporal visual field.
c. right temporal visual field
d. both a and b.
e. both a and c.

22. A person with an abnormally long eyeball (anterior to posterior) is _____ and uses a _____ to correct his or her vision.
a. nearsighted, concave lens
b. nearsighted, convex lens
c. farsighted, concave lens
d. farsighted, convex lens

23. Which of these structures is found within or is a part of the external ear?
a. oval window
b. auditory tube
c. ossicles
d. auricle
e. cochlear duct

24. Given these ear bones:
1. incus
2. malleus
3. stapes

Choose the arrangement that lists the ear bones in order from the tympanic membrane to the ear.
a. 1,2,3
b. 1,3,2
c. 2,1,3
d. 2,3,1
e. 3,2,1

25. Given these structures:
1. perilymph
2. endolymph
3. vestibular membrane
4. basilar membrane

Choose the arrangement that lists the structures in the order sound waves coming from the outside encounter them in producing sound.
a. 1,3,2,4
b. 1,4,2,3
c. 2,3,1,4
d. 2,4,1,3
e. 3,4,2,1

26. The spiral organ is found within the
a. cochlear duct.
b. scala vestibuli.
c. scala tympani.
d. vestibule.
e. semicircular canals.

27. An increase in the loudness of sound occurs as a result of an increase in the _____ of the sound wave.
a. frequency
b. amplitude
c. resonance
d. both a and b

28. Interpretation of different sounds is possible because of the ability of the _____ to vibrate at different frequencies and stimulate the _____.
a. vestibular membrane, vestibular nerve
b. vestibular membrane, spiral organ
c. basilar membrane, vestibular nerve
d. basilar membrane, spiral organ

29. Which structure is a specialized receptor found within the utricle?
a. macula
b. crista ampullaris
c. spiral organ
d. cupula

30. Damage to the semicircular canals affects the ability to detect
a. linear acceleration.
b. the position of the head relative to the ground.
c. the movement of the head in all directions.
d. all of the above.

Answers in Appendix F

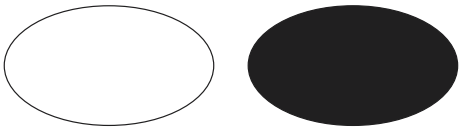
CRITICAL THINKING

1. Describe all the special sensations involved when a person picks up an apple and bites into it. What types of receptors are involved? Which aspects of the taste of the apple are actually taste and which are olfaction?
2. An elderly man with normal vision develops cataracts. He is surgically treated by removing the lenses of his eyes. What kind of glasses would you recommend he wear to compensate for the removal of his lenses?
3. Some animals have a reflective area in the choroid called the tapetum lucidum. Light entering the eye is reflected back instead of being absorbed by the choroid. What would be the advantage of this arrangement? The disadvantage?
4. Perhaps you have heard someone say that eating carrots is good for the eyes. What is the basis for this claim?
5. On a camping trip Jean Tights rips her pants. That evening she is going to repair the rip. As the sun goes down, the light becomes more and more dim. When she tries to thread the needle, it is obvious that she is not looking directly at the needle but is looking a few inches to the side. Why does she do this?
6. A man stares at a black clock on a white wall for several minutes. Then he shifts his view and looks at only the blank white wall. Although he is no longer looking at the clock, he sees a light clock against a dark background. Explain what happened.
7. Describe the results of a lesion of the optic chiasm.
8. Persistent exposure to loud noise can cause loss of hearing, especially for high-frequency sounds. What part of the ear is probably damaged? Be as specific as possible.
9. Professional divers are subject to increased pressure as they descend to the bottom of the ocean. Sometimes this pressure can lead to damage to the ear and loss of hearing. Describe the normal mechanisms that adjust for changes in pressure, suggest some conditions that might interfere with pressure adjustment, and explain how the increased pressure might cause loss of hearing.
10. If a vibrating tuning fork is placed against the mastoid process of the temporal bone, the vibrations are perceived as sound, even if the external auditory meatus is plugged. Explain how this could happen.

Answers in Appendix G

ANSWERS TO PREDICT QUESTIONS

1. Inhaling slowly and deeply allows a large amount of air to be drawn into the olfactory recess, whereas not as much air enters during normal breaths. Sniffing (rapid, repeated air intake) is effective for the same reason.
2. Adaptation can occur at several levels in the olfactory system. First, adaptation can occur at the receptor cell membrane, where receptor sites are filled or become less sensitive to a specific odor. Second, association neurons within the olfactory bulb can modify sensitivity to an odor by inhibiting mitral cells or tufted cells. Third, neurons from the intermediate olfactory area of the cerebrum can send action potentials to the association neurons in the olfactory bulb to inhibit further sensory action potentials.
3. Eyedrops placed into the eye tend to drain through the nasolacrimal duct into the nasal cavity. Recall that much of what is considered "taste" is actually smell. The medication is detected by the olfactory neurons and is interpreted by the brain as taste sensation. Crying produces extra tears, which are conducted to the nasal cavity, causing a "runny" nose.
4. Inflammation of the cornea involves edema, the accumulation of fluid. Fluid accumulation in the cornea increases its water content, and because water causes the proteoglycans to expand, the transparency of the lens decreases, interfering with normal vision.
5. Eye strain, or eye fatigue, occurs primarily in the ciliary muscles. It occurs because close vision requires accommodation. Accommodation occurs as the ciliary muscles contract, releasing the tension of the suspensory ligaments, and allowing the lens to become more rounded. Continued close vision requires maintenance of accommodation, which requires that the ciliary muscles remain contracted for a long time, resulting in their fatigue.
6. Rhodopsin breakdown is associated with adaptation to bright light and occurs rapidly, whereas rhodopsin production occurs slowly and is associated with adaptation to conditions of little light. Eyes adapt rather quickly to bright light but quite slowly to very dim light.
7. Rod cells distributed over most of the retina are involved in both peripheral vision (out of the corner of the eye) and vision under conditions of very dim light. When attempting to focus directly on an object, however, a person relies on the cones within the macula lutea; although the cones are involved in visual acuity, they don't function well in dim light; thus the object may not be seen at all.
8. A lesion in the right optic nerve at *B* results in loss of vision in the right visual field (see following illustration).



9. The stapedius muscle, attached to the stapes, is innervated by the facial nerve (VII). Loss of facial nerve function eliminates part of the sound attenuation reflex, although not all of it, because the tensor tympani muscle, innervated by the trigeminal nerve, is still functional. A reduction in the sound attenuation reflex results in sounds being excessively loud in the affected ear. A reduced reflex can also leave the ear more susceptible to damage by prolonged loud sounds.
10. "Perfect pitch" is the ability to precisely reproduce a pitch just by being told its name or reading it on a sheet of music, with no other musical support, such as from piano accompaniment. This remarkable talent as well as conditions such as tone deafness (the complete inability to recognize or reproduce musical pitches) or a decreased ability to perceive tone differences could occur at a number of locations. The structure of the basilar membrane may be such that tones are not adequately spaced along the cochlear duct in some people to facilitate clear separation of tones. The reflex from the superior olive to the spiral organ may have a very narrow "window of function" for people with perfect pitch but may not be functioning in some other people. The auditory cortex may not be able to translate as accurately in some people to distinguish differences in tones.
11. It is much easier to perceive subtle musical tones when music is played somewhat softly as opposed to very loudly because loud sounds have sound waves with a greater amplitude, which causes the basilar membrane to vibrate more violently over a wider range. The spreading of the wave in the basilar membrane to some extent counteracts the reflex from the superior olive that is responsible for enabling a person to hear subtle tone differences.