Sensory Organs

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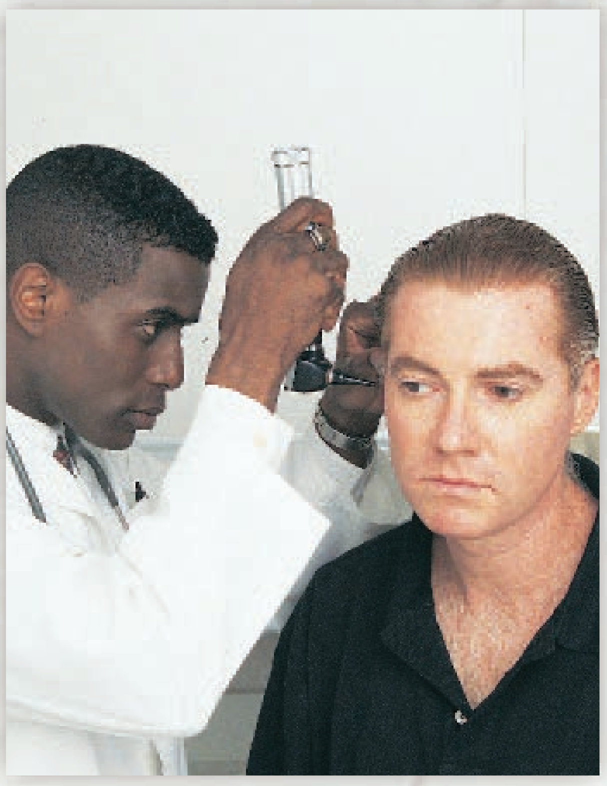


Clinical Case Study

A 50-year-old man complained to his family doctor of progressive hearing loss in his right ear. In order to rule out visible abnormalities or wax buildup, the physician performed an otoscopic examination, which revealed no abnormalities. The physician then struck a tuning fork and placed it on the skin over the mastoid process of the patient's right temporal bone. The patient immediately exclaimed, "I can hear that really well, even in my bad ear!" After a moment or so the patient noted that the tone had nearly died out. The doctor then moved the instrument 2 centimeters away from the same ear. At that location, the patient was unable to hear anything. The doctor explained that although someone with normal hearing will hear a vibrating fork when it is held against the mastoid process, the person will hear it better when it is held just outside the external acoustic canal.

What components of the patient's hearing mechanism were bypassed when the handle of the tuning fork was placed on his mastoid process? Describe the type of hearing problem this patient has. Is it a conduction problem or a perception problem?

Hints: The hearing organs of the inner ear can receive and effectively process sound waves directly from the bone in which they are encased. List in order the structures bypassed by sound waves being processed through the mastoid process. Carefully read the section on the structure of the ear and the one on sound waves and neural pathways for hearing. Also review the Clinical Considerations section on functional impairments of the ear.

FIGURE: Hearing loss may be congenital (occurring prenatally) or acquired (occurring postnatally), and there are a number of factors that may cause each. Scenescent (age-related) hearing loss afflicts all elderly people to one degree or another.

OVERVIEW OF SENSORY PERCEPTION

Sensory organs are highly specialized extensions of the nervous system. They contain sensory neurons adapted to respond to specific stimuli and conduct nerve impulses to the brain.

Objective 1 State the conditions necessary for perceiving a sensation.

Objective 2 Discuss the selectivity of sensory receptors for specific stimuli.

The sense organs are actually extensions of the nervous system that respond to changes in the internal and external environment and transmit action potentials (nerve impulses) to the brain. It is through the sense organs that we achieve awareness of the environment, and for this reason they have been described as "windows for the brain." A stimulus must first be received before the sensation can be interpreted in the brain and the necessary body adjustments made. Not only do we depend on our sense organs to experience pleasure, they also ensure our very survival. For example, they enable us to hear warning sounds, see dangers, avoid toxic substances, and perceive sensations of pain, hunger, and thirst.

A *sensation* is an awareness of a bodily state or condition that occurs whenever a sensory impulse is transmitted to the brain. The interpretation of a sensation is referred to as *perception*. Perceptions are the creations of our brain; in other words, we see, hear, taste, and smell with our brain. In order to perceive a sensation, the following conditions are necessary.

- A *stimulus* sufficient to initiate a response in the nervous system must be present.
- A *receptor* must convert the stimulus to a nerve impulse. A receptor is a specialized peripheral dendritic ending of a sensory nerve fiber or the specialized receptor cells associated with it.
- The *conduction of the nerve impulse* must occur from the receptor to the brain along a nervous pathway.
- The *interpretation of the impulse* in the form of a perception must occur within a specific portion of the brain.

Only those impulses that reach the cerebral cortex of the brain are consciously interpreted. If impulses terminate in the spinal cord or brain stem, they may initiate a reflexive motor response but not a conscious awareness. Impulses reaching the cerebral cortex travel through nerve fibers composing sensory, or ascending, tracts. Clusters of neuron cell bodies, called *nuclei*, are synaptic sites along sensory tracts within the CNS. The nuclei that sensory impulses pass through before reaching the cerebral cortex are located in the spinal cord, medulla oblongata, pons, and thalamus.

Through the use of scientific instruments, it is known that the senses act as energy filters that allow perception of only a narrow range of energy. Vision, for example, is limited to light rays in the visible spectrum. Other types of rays of the same type of energy as visible light, such as X rays, radio waves, and ultraviolet and infrared light, cannot normally excite the sensory receptors in the eyes. Although filtered and distorted by the limitations of sensory function, our perceptions allow us to interact effectively with our environment and are of obvious survival value.

Knowledge Check

1. Distinguish between stimulus, sensation, and perception.
2. List the four conditions necessary for perception and identify which of the four must always involve consciousness in order for perception to occur.
3. Use examples to explain the statement that each of the senses acts as a filter.

CLASSIFICATION OF THE SENSES

The senses are classified as general or special according to the degree of complexity of the receptors and neural pathways. They are also classified as somatic or visceral according to the location of the receptors.

Objective 3 Compare and contrast somatic, visceral, and special senses.

Objective 4 Describe the three basic kinds of receptors and give examples of each.

Structurally, the sensory receptor can be the dendrites of sensory neurons, which are either free (such as those in the skin that respond to pain and temperature) or encapsuled within nonneural structures (such as lamellated corpuscles or pressure receptors in the skin) (see table 15.1). Other receptors form from epithelial cells that synapse with sensory dendrites. These include taste buds on the tongue, photoreceptors in the eyes, and hair cells in the inner ears.

Although we usually speak of five senses, in reality we possess many more. The senses of the body can be classified as general or special according to the degree of complexity of their receptors and sensory pathways. **General senses** are widespread through the body and are structurally simple. Examples are touch, pressure, cold-heat, and pain. **Special senses** are localized in complex receptor organs and have extensive neural pathways (tracts) in the brain. The special senses are taste, smell, sight, hearing, and balance.

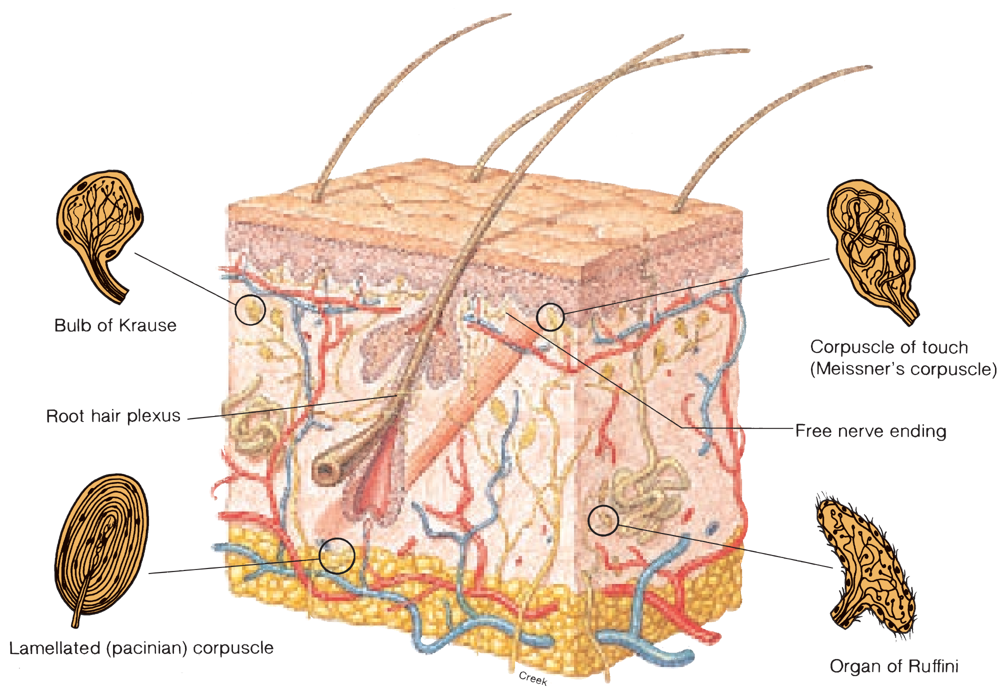
The senses can also be classified as somatic or visceral according to the location of the receptors. **Somatic senses** are those in which the receptors are localized within the body wall. These include the cutaneous (skin) receptors and those within

somatic: Gk. *somatikos*, body

CHAPTER 15

TABLE 15.1 Cutaneous Receptors

Type	Location	Function
Corpuscles of touch (Meissner's corpuscles) (mechanoreceptors)	Papillae of dermis; numerous in hairless portions of body (eyelids, fingertips, lips, nipples, external genitalia)	Detect light motion against surface of skin
Free nerve endings (tactile receptors; thermoreceptors; pain receptors)	Lower layers of epidermis	Detect touch and pressure, changes in temperature, and tissue damage
Root hair plexuses (tactile receptors)	Surrounding hair follicles	Detect movement of hair
Lamellated (pacinian) corpuscles (mechanoreceptors)	Hypodermis; synovial membranes; perimysium; certain visceral organs	Detect deep pressure and high-frequency vibration
Organs of Ruffini (mechanoreceptors)	Lower layers of dermis	Detect deep pressure and stretch
Bulbs of Krause (mechanoreceptors)	Dermis; lips; mouth; conjunctiva of eye	Detect light pressure and low-frequency vibration



muscles, tendons, and joints. **Visceral senses** are those in which the receptors are located within visceral organs. Both classification schemes may be used in describing some senses; for example, hearing (a special somatic sense) or pain from the gastrointestinal tract (a general visceral sense).

Senses are also classified according to the location of the receptors and the types of stimuli to which they respond. There are three basic kinds of receptors: *exteroceptors*, *visceroceptors (enteroceptors)*, and *proprioceptors*.

visceral: L. *viscera*, body organs

Exteroceptors

Exteroceptors (*ek''ster-o-sep'torz*) are located near the surface of the body, where they respond to stimuli from the external environment. They include the following:

- rod and cone cells in the retina of the eye—photoreceptors;
- hair cells in the spiral organ (organ of Corti) within the inner ear—mechanoreceptors;
- olfactory receptors in the nasal epithelium of the nasal cavity—chemoreceptors;

- taste receptors on the tongue—chemoreceptors; and
- skin receptors within the dermis—*tactile receptors* for touch, *mechanoreceptors* for pressure, *thermoreceptors* for temperature, and *nociceptors (no''sĭ-sep'torz)* for pain.

Pain receptors are stimulated by chemicals released from damaged tissue cells, and thus are a type of chemoreceptor. Although there are specific pain receptors, nearly all types of receptors transmit impulses that are perceived as pain if they are stimulated excessively. For example, even extremely loud sounds may be perceived as pain. Pain receptors are located throughout the body, but only those located within the skin are classified as exteroceptors.

Visceroceptors

As the name implies, visceroceptors *(vis''er-o-sep'torz)* are sensory nerve cells that produce sensations arising from the viscera, such as internal pain, hunger, thirst, fatigue, or nausea. Specialized visceroceptors located within the circulatory system are sensitive to changes in blood pressure; these are called *baroreceptors*. The circulatory system also contains *chemoreceptors* that monitor respiratory gases.

Proprioceptors

Proprioceptors are sensory nerve cells that relay information about body position, equilibrium, and movement. They are located in the inner ear, in and around joints, and between tendons and muscles.

Proprioceptors are especially abundant in postural muscles such as the trapezius, which maintains the vertical position of your head on the atlas vertebra. When your head starts to nod forward, such as when you are falling asleep during a boring lecture, proprioceptors are activated in the stretched muscles, and impulses are immediately sent to the cerebellum where motor units involving the trapezius muscles are activated. This homeostatic feedback mechanism causes your head to suddenly jerk back before your nodding head hits the desk. It also awakens you so that you are conscious of your body position relative to your surroundings.

Receptors may also be classified on the basis of sensory adaptation (accommodation). Some receptors respond with a burst of activity when a stimulus is first applied, but then quickly decrease their firing rate—adapt to the stimulus—when the stimulus is maintained. Receptors with this response pattern are called **phasic receptors.** Receptors that produce a relatively constant rate of firing as long as the stimulus is maintained are known as **tonic receptors.**

Phasic receptors alert us to changes in sensory stimuli and are in part responsible for the fact that we can cease paying attention to constant stimuli. This ability is called *sensory adaptation.* Odor and touch, for example, adapt rapidly; bathwater feels hotter when we first enter it. Sensations of pain, by contrast, adapt little if at all.

Knowledge Check

4. Using examples, explain how sensory receptors can be classified according to complexity, location, structure, and the type of stimuli to which they respond.
5. Distinguish between phasic and tonic receptors.

SOMATIC SENSES

The somatic senses arise in cutaneous receptors and proprioceptors. The perception of somatic sensations is determined by the density of the receptors in the stimulated receptive field and the intensity of the sensation.

Objective 5 Describe the structure, function, and location of the various tactile and pressure receptors.

Objective 6 Explain the purpose of pain and describe the receptors that respond to pain and the neural pathways for pain sensation.

Objective 7 Explain what is meant by referred pain and phantom pain and give examples of each.

The **somatic senses,** or **somesthetic senses,** arise in cutaneous receptors and proprioceptors. Cutaneous sensations include touch, tickle, pressure, cold, heat, and pain. The proprioceptors located in the inner ears, joints, tendons, and muscles relay information about body position, equilibrium, and movement.

Tactile and Pressure Receptors

Both tactile receptors and pressure receptors are sensitive to mechanical forces that distort or displace the tissue in which they are located. **Tactile receptors** respond to fine, or light, touch and are located primarily in the dermis and hypodermis of the skin. **Pressure receptors** respond to pressure, vibration, and stretch and are commonly found in the hypodermis of the skin and in the tendons and ligaments of joints. The tactile and pressure receptors are summarized in table 15.1.

Corpuscles of Touch

A corpuscle of touch *(Meissner's corpuscle)* is an oval receptor composed of a mass of dendritic endings from two or three nerve fibers enclosed by connective tissue sheaths. These corpuscles are numerous in the hairless portions of the body, such as the eyelids, lips, tip of the tongue, fingertips, palms of the hands, soles of the feet, nipples, and external genitalia. Corpuscles of touch lie within the papillary layer of the dermis, where they are especially sensitive to the movement of objects that barely contact the skin

nociceptor: L. *nocco,* to injure; *ceptus,* taken
proprioceptor: L. *proprius,* one's own; *ceptus,* taken

corpuscle: L. *corpusculum,* diminutive of *corpus,* body
Meissner's corpuscle: from George Meissner, German histologist, 1829–1905

(see chapter 5). Sensations of fine or light touch are perceived as these receptors are stimulated. They also function when a person touches an object to determine its texture.

The highly sensitive fingertips are used in reading braille. Braille symbols consist of dots that are raised 1 mm from the surface of the page and separated from each other by 2.5 mm. Experienced braille readers can scan words at about the same speed that a sighted person can read aloud—a rate of about 100 words per minute.

Free Nerve Endings

Free nerve endings are the least modified and the most superficial of the tactile receptors. These receptors extend into the lower layers of the epidermis, where they end as knobs between the epithelial cells. Free nerve endings respond chiefly to pain and temperature (discussed shortly), but they also detect touch and pressure, for example from clothing. Some free nerve endings are particularly sensitive to tickle and itch.

Root Hair Plexuses

Root hair plexuses are a specialized type of free nerve ending. They are coiled around hair follicles, where they respond to movement of the hair.

Lamellated Corpuscles

Lamellated *(pacinian)* corpuscles are large, onion-shaped receptors composed of the dendritic endings of several sensory nerve fibers enclosed by connective tissue layers. They are commonly found within the synovial membranes of synovial joints, in the perimysium of skeletal muscle tissue, and in certain visceral organs. Lamellated corpuscles are also abundant in the skin of the palms and fingers of the hand, soles of the feet, external genitalia, and breasts. They respond to heavy pressures, generally those that are constantly applied. They can also detect deep vibrations in tissues and organs.

Organs of Ruffini

The organs of Ruffini are encapsulated nerve endings that are found in the deep layers of the dermis and in subcutaneous tissue, where they respond to deep continuous pressure and to stretch. They are also present in joint capsules and function in the detection of joint movement.

Bulbs of Krause

The bulbs of Krause are thought to be a variation of Meissner's corpuscles. They are most abundant in the mucous membranes, and therefore are sometimes called *mucocutaneous corpuscles*.

Historically, both the organs of Ruffini and the bulbs of Krause have been considered to be thermoreceptors—the former heat receptors and the latter cold receptors. However, both are actually mechanoreceptors. The bulbs of Krause respond to light pressure and low-frequency vibration.

Any mother can attest to the calming effect that holding and patting have on a crying baby. It has been known that the touch of massage can relieve pain and improve concentration. There is now evidence that touching and caressing newborns actually enhance their development. Massaged infants gain weight nearly 50% faster than unmassaged infants. They are also more active, alert, and responsive. Even premature infants grow and mature faster if they are regularly held and touched.

Experiments with rats have shown that licking and grooming by the mother stimulate the secretion of growth hormones in her pups (young). The amount of growth hormone is significantly reduced in isolated pups that are not licked or groomed. Isolated pups that are stroked periodically with a paintbrush, however, have normal secretion of growth hormone.

Receptors for Heat, Cold, and Pain

The principal receptors for heat and cold (thermoreceptors) and for pain (nociceptors) are the free nerve endings. Several million of them are distributed throughout the skin and internal tissues. The free nerve endings responsible for cold sensations are closer to the surface of the skin and are 10 to 15 times more abundant in any given area of skin than those responsible for sensations of heat.

Pain receptors respond to damage to tissues and are activated by all types of stimuli. They are sparse in most visceral organs and absent entirely within the nervous tissue of the brain. Although the free nerve endings are specialized to respond to tissue damage, all of the cutaneous receptors will relay impulses that are interpreted as pain if stimulated excessively.

The protective value of pain receptors is obvious. Unlike other cutaneous receptors, free nerve endings exhibit little accommodation, so impulses are relayed continuously to the CNS as long as the irritating stimulus is present. Pain receptors are particularly sensitive to chemical stimulation. Muscle spasms, muscle fatigue, or an inadequate supply of blood to an organ may also cause pain.

Impulses for pain are conducted to the spinal cord through sensory neurons. The pain sensations are then conducted to the thalamus along the *lateral spinothalamic tract* of the spinal cord, and from there to the somatesthetic area of the cerebral cortex. Although an awareness of pain occurs in the thalamus, the type and intensity of pain is interpreted in specialized areas of the cerebral cortex.

The sensation of pain can be clinically classified as **somatic pain** or **visceral pain.** Stimulation of the cutaneous pain receptors results in the perception of superficial somatic pain. Deep somatic pain comes from stimulation of receptors in skeletal muscles, joints, and tendons.

Stimulation of the receptors within the viscera causes the perception of visceral pain. Through precise neural pathways, the brain is able to perceive the area of stimulation and project the pain sensation back to that area. The sensation of pain from certain visceral organs, however, may not be perceived as arising from those organs but from other somatic locations. This phenomenon is known as **referred pain** (fig. 15.1). The sensation of referred pain is relatively consistent from one person to another and is clinically important in diagnosing organ

braille: from Louis Braille, French teacher of the blind, 1809–52.
pacinian corpuscle: from Filippo Pacini, Italian anatomist, 1812–83
organs of Ruffini: from Angelo Ruffini, Italian anatomist, 1864–1929
bulbs of Krause: from Wilhelm J. F. Krause, German anatomist, 1833–1910

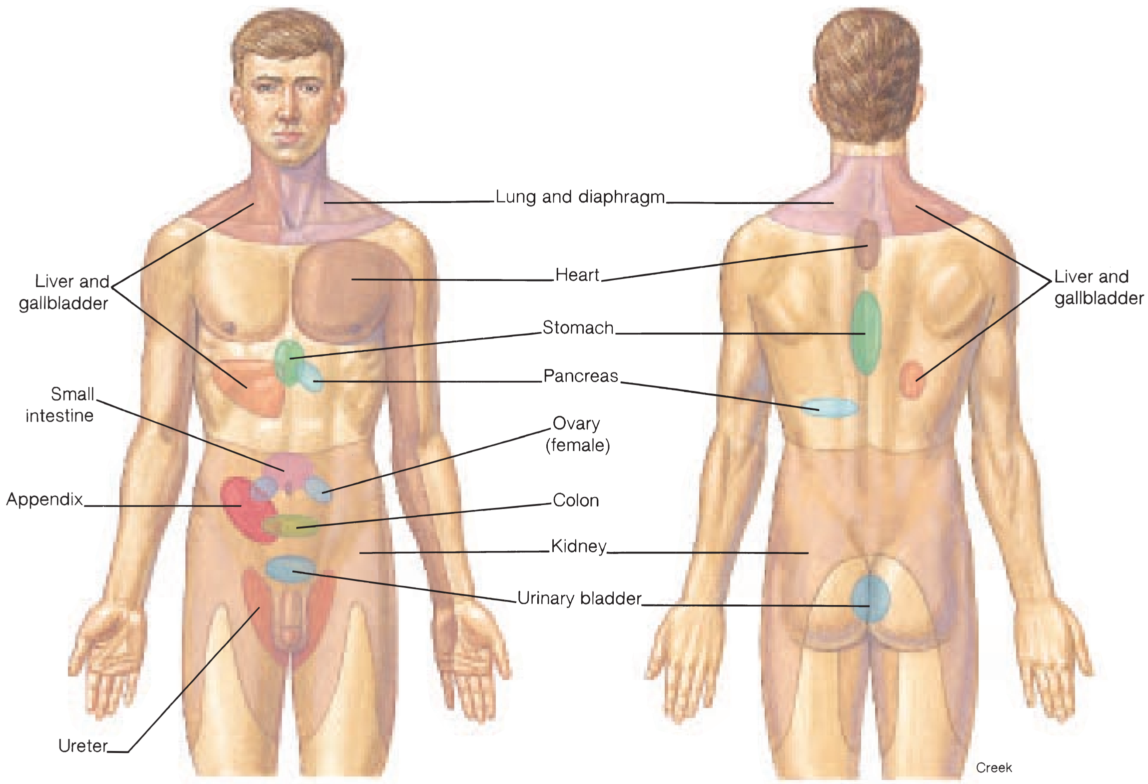


FIGURE 15.1 Sites of referred pain are perceived cutaneously but actually originate from specific visceral organs.

dysfunctions. The pain of a heart attack, for example, may be perceived subcutaneously over the heart and down the medial side of the left arm. Ulcers of the stomach may cause pain that is perceived as coming from the upper central (epigastric) region of the trunk. Pain from problems of the liver or gallbladder may be perceived as localized visceral pain or as referred pain arising from the right neck and shoulder regions.

Referred pain is not totally understood but seems to be related to the development of the tracts within the spinal cord. There are thought to be some *common nerve pathways* that are used by sensory impulses coming from both the cutaneous areas and from visceral organs (fig. 15.2). Consequently, impulses along these pathways may be incorrectly interpreted as arising cutaneously rather than from within a visceral organ.

The perception of pain is of survival value because it alerts the body to an injury, disease, or organ dysfunction. *Acute pain* is sudden, usually short term, and can generally be endured and attributed to a known cause. *Chronic pain,* however, is long term and tends to weaken a person as it interferes with the ability to function effectively. Certain diseases, such as arthritis, are characterized by chronic pain. In these patients, relief of pain is of paramount concern. Treatment of chronic pain often requires the use of moderate pain-reducing drugs (analgesics) or intense narcotic drugs. Treatment in severely tormented chronic pain patients may include severing sensory nerves or implanting stimulating electrodes in appropriate nerve tracts.

Phantom pain is frequently experienced by an amputee who continues to feel pain from the body part that was amputated, as if it were still there. After amputation, the severed sensory neurons heal and function in the remaining portion of the appendage. Although it is not known why impulses that are interpreted as pain are sent periodically through these neurons, the sensations evoked in the brain are projected to the region of the amputation, resulting in phantom pain.

Proprioceptors

Proprioceptors monitor our own movements (*proprius* means "one's own") by responding to changes in stretch and tension, and by transmitting action potentials to the cerebellum. Proprioceptor information is then used to adjust the strength and timing of muscle contractions to produce coordinated movements. Some of the sensory impulses from proprioceptors reach the level of consciousness as the **kinesthetic sense,** by which the position of the body parts is perceived. With the kinesthetic sense, the position and movement of the limbs can be determined without visual sensations, such as when dressing or walking in the dark. The kinesthetic sense, along with hearing, becomes keenly developed in a blind person.

High-speed transmission is a vital characteristic of the kinesthetic sense because rapid feedback to various body parts is essential for quick, smooth, coordinated body movements.

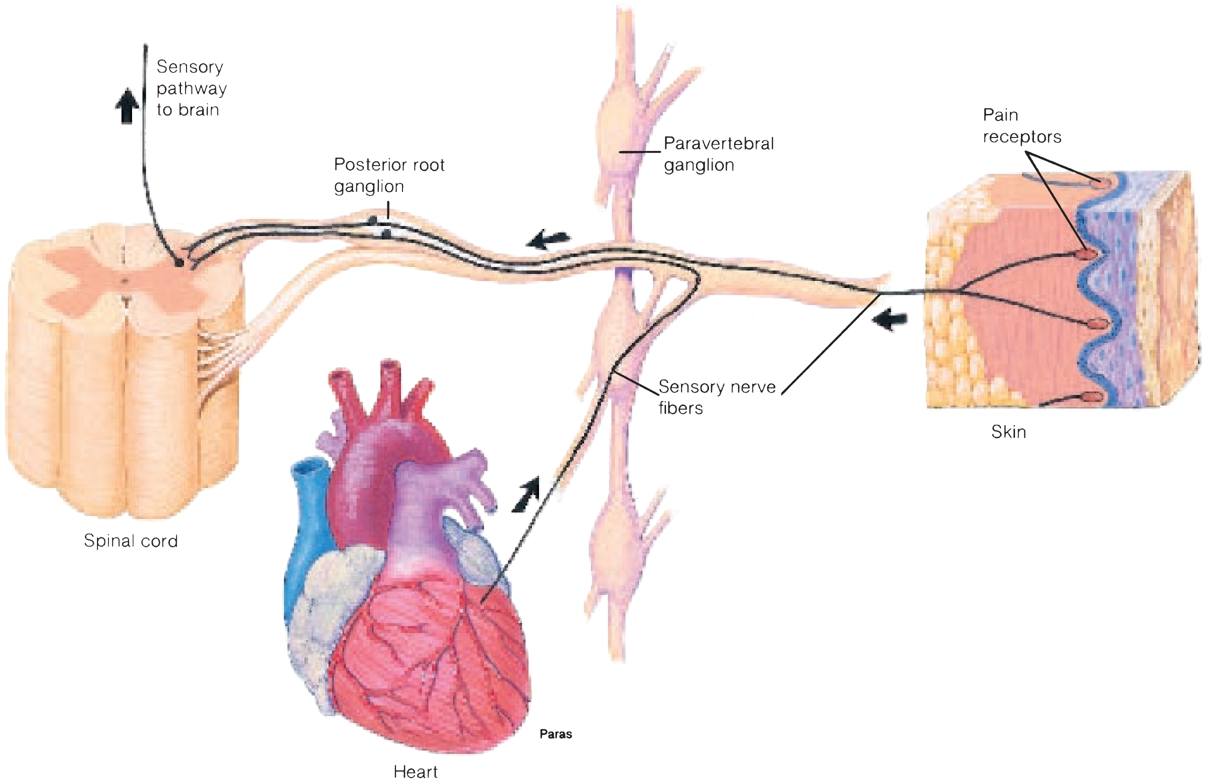


FIGURE 15.2 An explanation of referred pain. Pain originating from the myocardium of the heart may be perceived as coming from the skin of the left arm because sensory impulses from these two organs are conducted through common nerve pathways to the brain.

Proprioceptors are located in and around synovial joints, in skeletal muscle, between tendons and muscles, and in the inner ear. They are of four types: joint kinesthetic receptors, neuromuscular spindles, neurotendinous receptors, and sensory hair cells.

- **Joint kinesthetic receptors** are located in synovial joint capsules, where they are stimulated by changes in body position as the joints are moved.
- **Neuromuscular spindles** are located in skeletal muscle, particularly in the muscles of the limbs. They consist of the endings of sensory neurons that are spiraled around specialized individual muscle fibers (fig. 15.3). Neuromuscular spindles are stimulated by an increase in muscle tension caused by the lengthening or stretching of the individual fibers, and thus provide information about the length of the muscle and the speed of muscle contraction.
- **Neurotendinous receptors** (*Golgi tendon organs*) are located where a muscle attaches to a tendon (fig. 15.3). They are stimulated by the tension produced in a tendon when the attached muscle is either stretched or contracted.
- **Sensory hair cells** of the inner ear are located in a fluid-filled, ductule structure called the membranous labyrinth. Their function in equilibrium is discussed later in this chapter in connection with the mechanics of equilibrium.

Neural Pathways for Somatic Sensation

The conduction pathways for the somatic senses are shown in figure 15.4. Sensations of proprioception and of touch and pressure are carried by large, myelinated nerve fibers that ascend in the posterior columns of the spinal cord on the ipsilateral (same) side. These fibers do not synapse until they reach the medulla oblongata of the brain stem; hence, fibers that carry these sensations from the feet are incredibly long. After synapsing in the medulla oblongata with second-order sensory neurons, information in the latter neurons crosses over to the contralateral (opposite) side as it ascends via a fiber tract called the **medial lemniscus** (*lem-nis'kus*) to the thalamus. Third-order sensory neurons in the thalamus that receive this input in turn project to the **postcentral gyrus** in the cerebral cortex.

Sensations of heat, cold, and pain are carried by thin, unmyelinated sensory neurons into the spinal cord. These synapse within the spinal cord with second-order association neurons that cross over to the contralateral side and ascend to the brain in the **lateral spinothalamic tract.** Fibers that mediate touch and pressure ascend in the **ventral spinothalamic tract.** Fibers of both spinothalamic tracts synapse in the thalamus with third-order neurons, which in turn project to the postcentral gyrus. Note that, in all cases, somatic information is carried to the postcentral

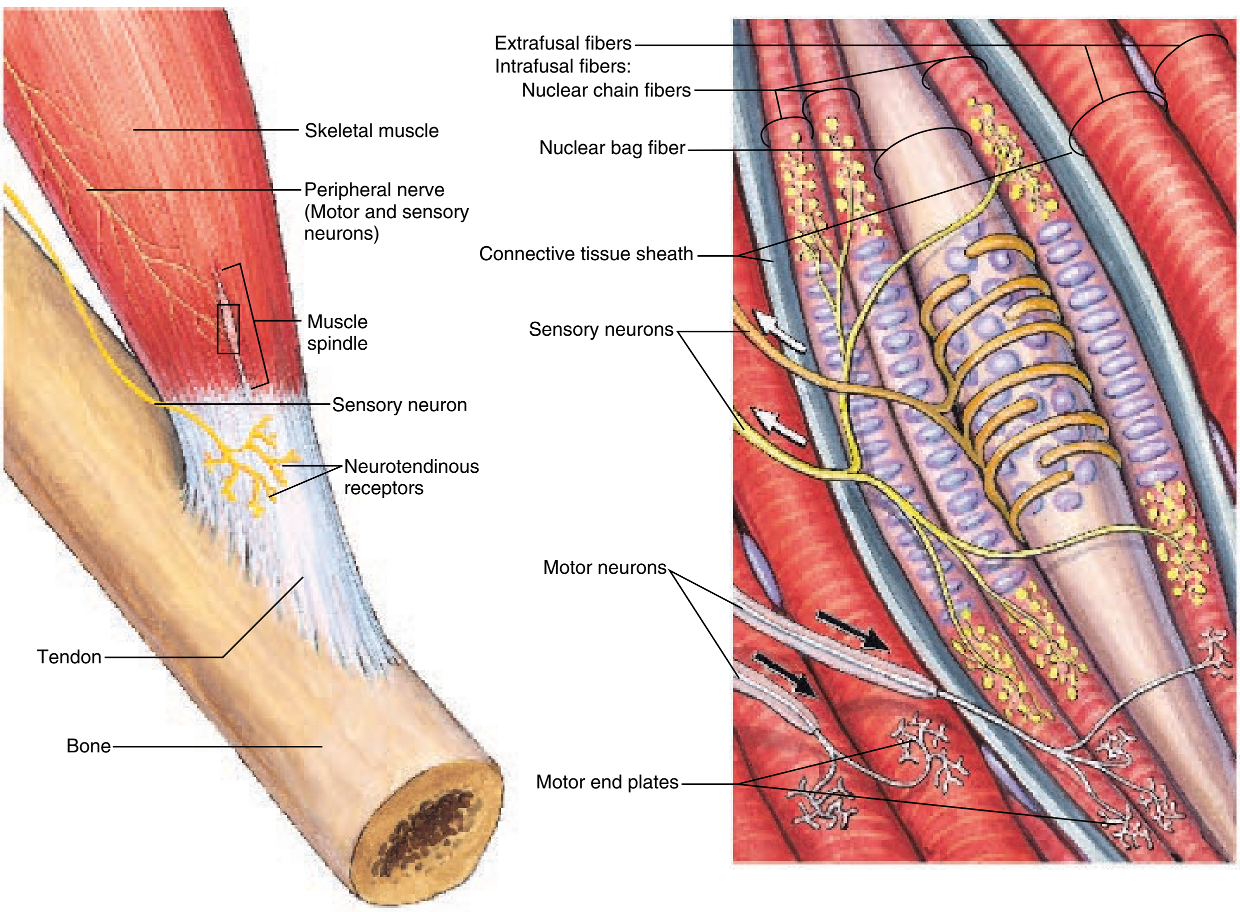


FIGURE 15.3 Proprioceptors are located within skeletal muscle tissue, tendons, and joint membranes. (*a*) The location of muscle spindles and neurotendinous receptors. (*b*) A magnification of the structure and innervation of muscle spindles.

gyrus in third-order neurons. Also, because of decussation (crossing-over), somatic information from each side of the body is projected to the postcentral gyrus of the contralateral cerebral hemisphere.

All somatic information from the same area of the body projects to the same area of the postcentral gyrus. It is therefore possible to map out areas of the postcentral gyrus that receive sensory information from different parts of the body (see fig. 11.22). Such a map is greatly distorted, however, because it shows larger areas of cerebral cortex devoted to sensation in the face and hands than in other areas of the body. The disproportionately large areas of the caricature-like *sensory homunculus (ho-mung'kyoo-lus)* drawn on the gyrus reflect the fact that there is a higher density of sensory receptors in the face and hands than in other parts of the body.

homunculus: L. *homunculus*, diminutive of *homp*, man ("little man")

Knowledge Check

6. List the different types of cutaneous receptors and state where they are located. What portion of the brain interprets tactile sensations?
7. Discuss the importance of pain. List the receptors that respond to pain and the structures of the brain that are particularly important in the perception of pain sensation.
8. Using examples, distinguish between referred pain and phantom pain. Discuss why it is important for a physician to know the referred pain sites.
9. Using a flow chart, describe the neural pathways leading from cutaneous pain and pressure receptors to the postcentral gyrus. Indicate where decussation occurs.

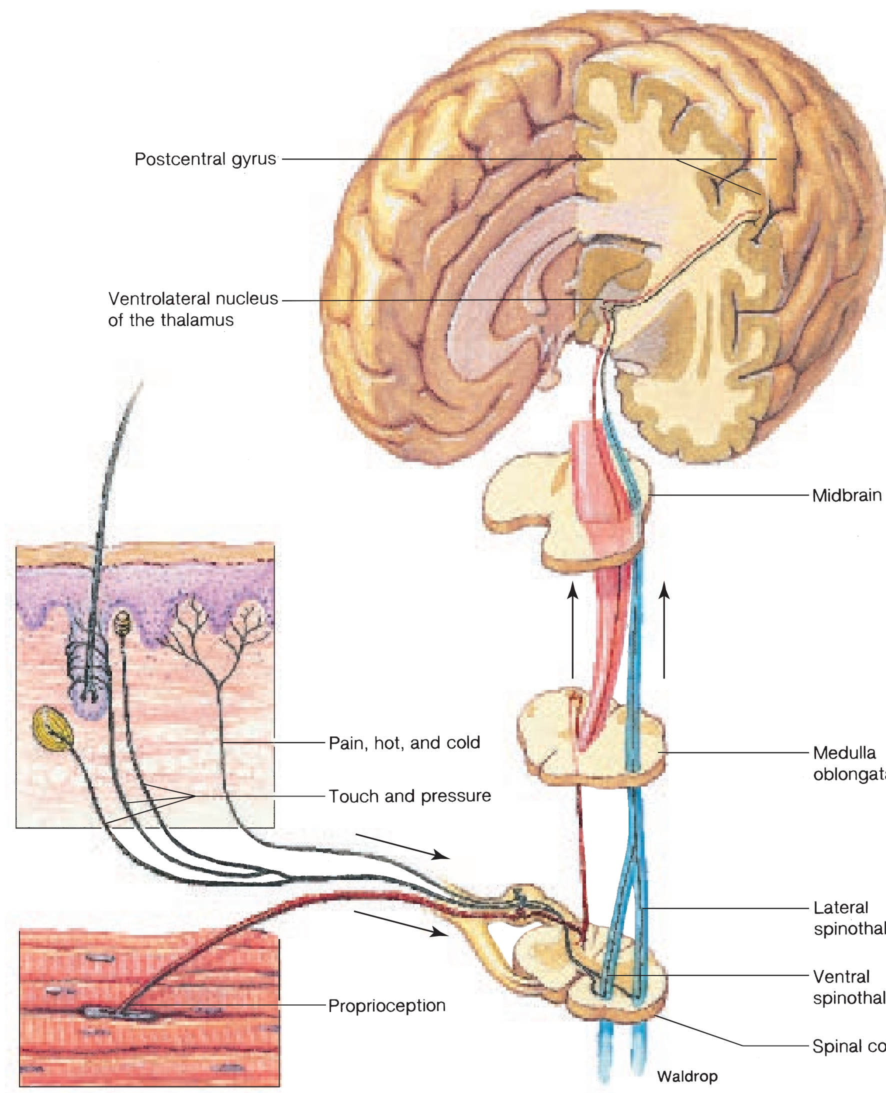


FIGURE 15.4 Pathways that lead from the cutaneous receptors and proprioreceptors into the postcentral gyrus in the cerebral cortex. (Arrows indicate the direction that action potentials travel.)

OLFACTORY SENSE

Olfactory receptors are the dendritic endings of the olfactory nerve (I) that respond to chemical stimuli and transmit the sensation of olfaction directly to the olfactory portion of the cerebral cortex.

Objective 8 Describe the sensory pathway for olfaction.

Olfactory reception in humans is not highly developed compared to that of certain other vertebrates. Because we do not rely on smell for communicating or for finding food, the olfactory sense is probably the least important of our senses. It is more important in detecting the presence of an odor rather than its intensity. Accommodation occurs relatively rapidly with this sense. Olfaction functions closely with gustation (taste) in that the receptors for both are *chemoreceptors*, which require dissolved substances for stimuli.

Olfactory receptor cells are located in the nasal mucosa within the roof of the nasal cavity on both sides of the nasal septum (fig. 15.5). Olfactory cells are moistened by the surrounding glandular goblet cells. The cell bodies of the bipolar olfactory cells lie between the supporting columnar cells. The free end of each olfactory cell contains several dendritic endings, called **olfactory hairs** that constitute the sensitive portion of the receptor cell. These unmyelinated dendritic endings respond to airborne molecules that enter the nasal cavity.

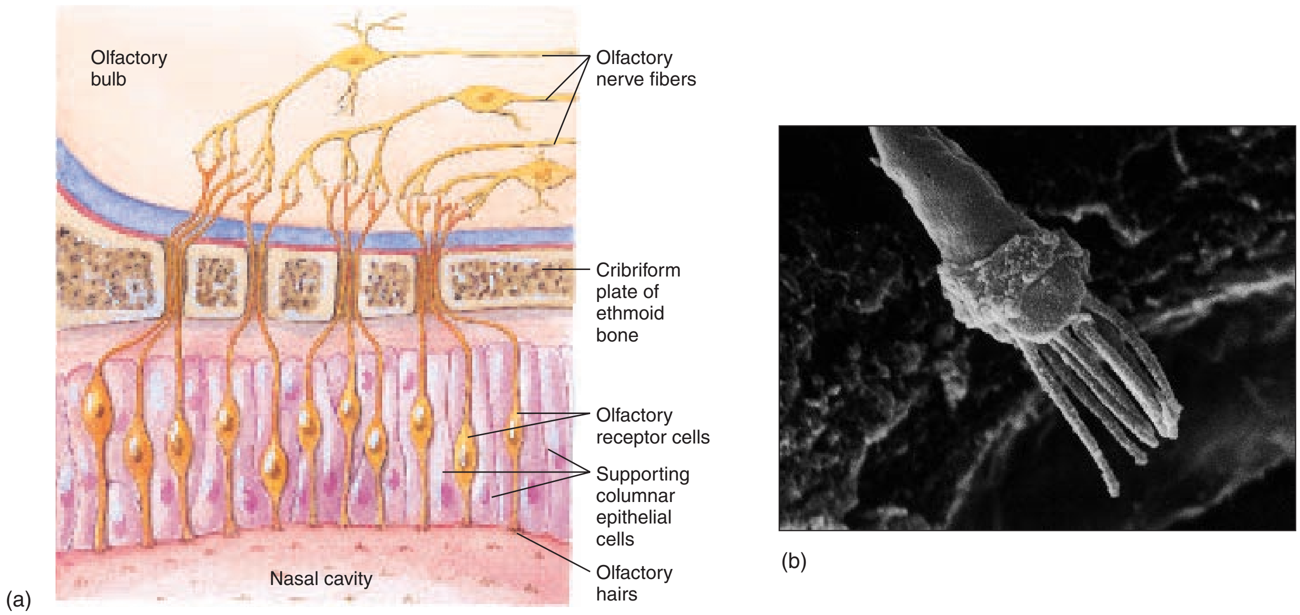


FIGURE 15.5 Olfaction. (*a*) The olfactory receptor area within the roof of the nasal cavity. (*b*) A scanning electron micrograph of olfactory hairs extending from an olfactory receptor cell.

The sensory pathway for olfaction consists of several neural segments. The unmyelinated axons of the olfactory cells unite to form the **olfactory nerves,** which traverse the foramina of the cribriform plate and terminate in the paired masses of gray and white matter called the **olfactory bulbs.** The olfactory bulbs lie on both sides of the crista galli of the ethmoid bone, beneath the frontal lobes of the cerebrum. Within the olfactory bulb, neurons of the olfactory nerves synapse with dendrites of neurons forming the **olfactory tract.** Sensory impulses are conveyed along the olfactory tract and into the olfactory portion of the cerebral cortex, where they are interpreted as odor and cause the perception of smell.

Unlike taste, which is divisible into only four modalities, thousands of distinct odors can be distinguished by people who are trained in this capacity (as in the perfume industry). The molecular basis of olfaction is not understood, but it is known that a single odorant molecule is sufficient to excite an olfactory receptor.

Only about 2% of inhaled air comes in contact with the olfactory receptors, which are positioned in the nasal mucosa above the mainstream of airflow. Olfactory sensitivity can be increased by forceful sniffing, which draws the air into contact with the receptors.

Certain chemicals activate the trigeminal nerves (V) as well as the olfactory nerves (I) and cause reactions. Pepper, for example, may cause sneezing; onions cause the eyes to water; and smelling salts (ammonium salts) initiate respiratory reflexes and are used to revive unconscious persons. However, because of the caustic nature of smelling salts and the irreparable damage it may cause to the unmyelinated olfactory hairs, it is seldom used in first aid treatment of an unconscious person.

Knowledge Check

10. What are olfactory hairs? Where are they located?
11. Trace the pathway of an olfactory stimulus from the olfactory hairs to the cerebral cortex, where interpretation occurs.

GUSTATORY SENSE

Taste receptors are specialized epithelial cells, clustered together in taste buds, that respond to chemical stimuli and transmit the sense of taste through the glossopharyngeal nerve (IX) or the facial nerve (VII) to the taste area in the parietal lobe of the cerebral cortex for interpretation.

Objective 9 List the three principal types of papillae and explain how they function in the perception of taste.

Objective 10 Identify the cranial nerves and the sensory pathways of gustation.

The *gustatory* (taste) *receptors* are located in the **taste buds.** Taste buds are specialized sensory organs that are most numerous on the surface of the tongue, but they are also present on the soft palate and on the walls of the oropharynx. The cylindrical taste bud is composed of numerous sensory **gustatory cells** that are encapsu-

gustatory: L. *gustare*, to taste

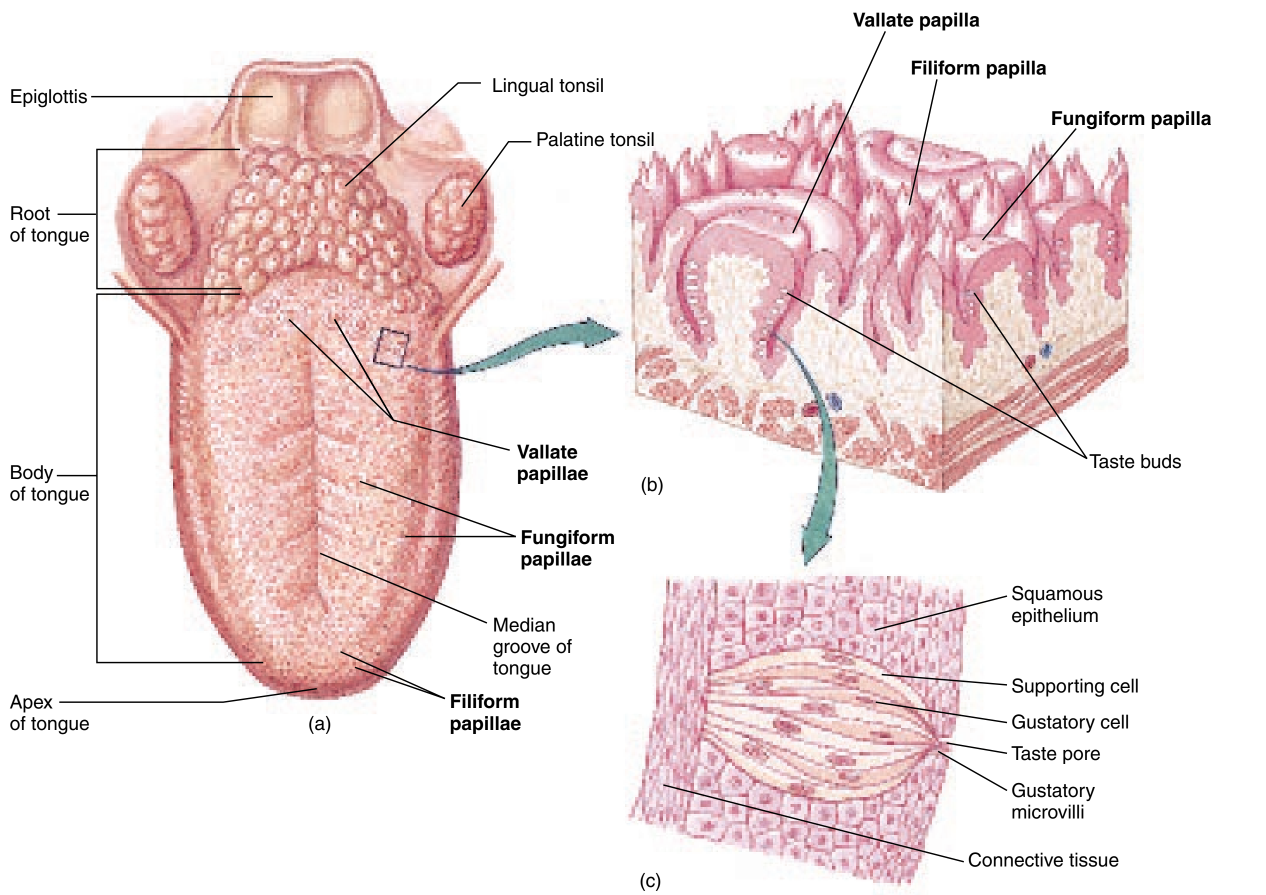


FIGURE 15.6 Papillae of the tongue and associated taste buds. (*a*) The surface of the tongue. (*b*) Numerous taste buds are positioned within the vallate and fungiform papillae. (*c*) Each gustatory cell and its associated gustatory microvillus are encapsuled by supporting cells.

lated by **supporting cells** (fig. 15.6). Each gustatory cell contains a dendritic ending called a **gustatory microvillus** that projects to the surface through an opening in the taste bud called the **taste pore.** The gustatory microvilli are the sensitive portion of the receptor cells. Saliva provides the moistened environment necessary for a chemical stimulus to activate the gustatory microvilli.

Taste buds are elevated by surrounding connective tissue and epithelium to form *papillae* (*pă-pil'e*) (fig. 15.6). Three principal types of papillae can be identified:

- **Vallate papillae.** The largest but least numerous are the vallate (*val'āt*) papillae, which are arranged in an inverted V-shape pattern on the back of the tongue.
- **Fungiform papillae.** Knoblike fungiform (*fun'gĭ-form*) papillae are present on the tip and sides of the tongue.
- **Filiform papillae.** Short, thickened, threadlike filiform (*fil'ĭ-form*) papillae are located on the anterior two-thirds of the tongue.

papillae: L. *papilla,* nipple

Taste buds are found only in the vallate and fungiform papillae. The filiform papillae, although the most numerous of the human tongue papillae, are not involved in the perception of taste. Their outer cell layers are continuously converted into scalelike projections, which give the tongue surface its somewhat abrasive feel.

There are only four basic tastes, which are sensed most acutely on particular parts of the tongue (fig. 15.7). These are *sweet* (tip of tongue), *sour* (sides of tongue), *bitter* (back of tongue), and *salty* (over most of the tongue, but concentrated on the sides). A combination of these taste modalities allows for impressive taste discrimination. Wine tasters, for example, can consistently recognize subtle differences in hundreds of varieties of wine.

Sour taste is produced by hydrogen ions (H^+); all acids therefore taste sour. Most organic molecules, particularly sugars, taste sweet to varying degrees. Only pure table salt (NaCl) has a pure salty taste. Other salts, such as KCl (commonly used in place of NaCl by people with hypertension), taste salty but have bitter overtones. Bitter taste is evoked by quinine and seemingly unrelated molecules.

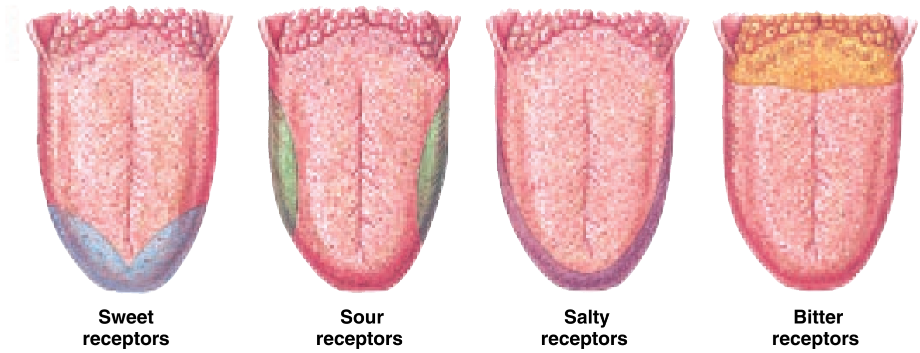


FIGURE 15.7 Patterns of taste receptor distribution on the surface of the tongue. This diagram indicates the tongue regions that are maximally sensitive to different tastes.

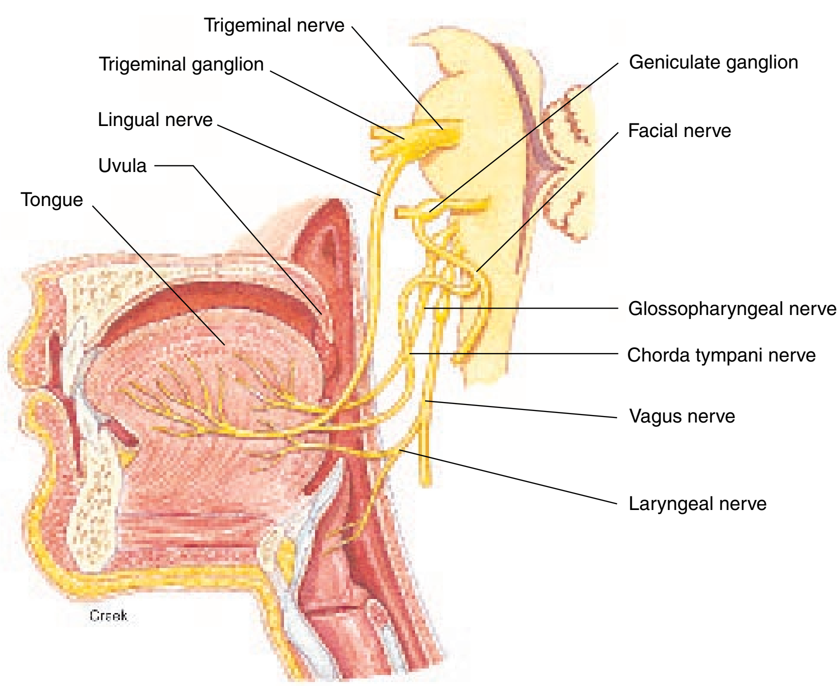


FIGURE 15.8 The gustatory pathway that conveys taste sensations to the brain involves the paired facial (seventh cranial) nerves and the glossopharyngeal (ninth cranial) nerves. The chorda tympani nerve is the sensory branch of the facial nerve innervating the tongue. Branches from the paired vagus (tenth cranial) nerves and the trigeminal (fifth cranial) nerves also provide some sensory innervation. The hypoglossal (twelfth cranial) nerve (not shown) provides motor innervation to the tongue. The lingual nerve transmits general sensory information from the tongue (hot, cold, pressure, and pain).

The sensory pathway that relays taste sensations to the brain mainly involves two paired cranial nerves (fig. 15.8). Taste buds on the posterior third of the tongue have a sensory pathway through the *glossopharyngeal nerves,* whereas the anterior two-thirds of the tongue is served by the *chorda tympani branch of the facial nerves.* Taste sensations passing through the nerves just mentioned are conveyed through the medulla oblongata and thalamus to the parietal lobe of the cerebral cortex, where they are interpreted.

Because taste and smell are both chemoreceptors, they complement each other. We often confuse a substance's smell with its taste; and if we have a head cold or hold our nose while eating, food seems to lose its flavor.

Knowledge Check

12. Distinguish between papillae, taste buds, and gustatory microvilli. Discuss the function of each as it relates to taste.
13. Describe the three principal types of papillae.
14. Which cranial nerves have sensory innervation associated with taste? What are the sensory pathways to the brain where the perception of taste occurs?

TABLE 15.2 Structures of the Eye and Analogous Structures of a Camera

Eye Structures and Principal Functions	Camera Structures and Principal Functions
Eyelid: protection	Lens cap: protection
Conjunctiva: protection	Lens filter: protection
Cornea and lens: focus incoming light waves	Lens system: focuses incoming light waves
Iris and pupil: regulate amount of incoming light	Variable aperture system: regulates amount of incoming light
Sclera: contains and protects internal eye structures	Camera frame: contains and protects internal camera structures
Pigment epithelium: maintains consistently dark environment within the posterior cavity of eyeball	Black interior of camera: maintains dark environment within the back of the camera
Retina: contains photosensitive cones and rods that respond to light waves	Film: material coated on one side with photosensitive emulsion that records an image from light waves

VISUAL SENSE

Rod and cone cells are the photoreceptors within the eyeball that are sensitive to light energy. They are stimulated to transmit nerve impulses through the optic nerve and optic tract to the visual cortex of the occipital lobes, where the interpretation of vision occurs. Formation of the sensory components of the eye is complete at 20 weeks, and the accessory structures have been formed by 32 weeks.

Objective 11 Describe the accessory structures of the eye and the structure of the eyeball.

Objective 12 Trace the path of light rays through the eye and explain how they are focused on distant and near objects.

Objective 13 Describe the neural pathway of a visual impulse and discuss the neural processing of visual information.

The eyes are organs that refract (bend) and focus incoming light rays onto the sensitive photoreceptors at the back of each eye. Nerve impulses from the stimulated photoreceptors are conveyed through visual pathways within the brain to the occipital lobes of the cerebrum, where the sense of vision is perceived. The specialized photoreceptor cells can respond to an incredible 1 billion different stimuli each second. Further, these cells are sensitive to about 10 million gradations of light intensity and 7 million different shades of color.

The eyes are anteriorly positioned on the skull and set just far enough apart to achieve *binocular (stereoscopic) vision* when focusing on an object. This three-dimensional perspective allows a person to assess depth. Often likened to a camera (table 15.2), the eyes are responsible for approximately 80% of all knowledge that is assimilated.

The eyes of other vertebrates are basically similar to ours. Certain species, however, have adaptive modifications. Consider, for example, the extremely keen eyesight of a hawk, which soars high in the sky searching for food, or the eyesight of the owl, which feeds only at night. Note how the location of the eyes on the head corresponds to behavior. Predatory species, such as cats, have eyes that are directed forward, allowing depth perception. Prey species, such as deer, have eyes positioned high on the sides of their heads, allowing panoramic vision to detect distant threatening movements, even while grazing.

Accessory Structures of the Eye

Accessory structures of the eye either protect the eyeball or enable eye movement. Protective structures include the bony orbit, eyebrow, facial muscles, eyelids, eyelashes, conjunctiva, and the lacrimal apparatus that produces tears. Eyeball movements depend on the actions of the extrinsic ocular muscles that arise from the orbit and insert on the outer layer of the eyeball.

Orbit

Each eyeball is positioned in a bony depression in the skull called the orbit (see fig. 6.21 and table 6.5). Seven bones of the skull (frontal, lacrimal, ethmoid, zygomatic, maxilla, sphenoid, and palatine) form the walls of the orbit that support and protect the eye.

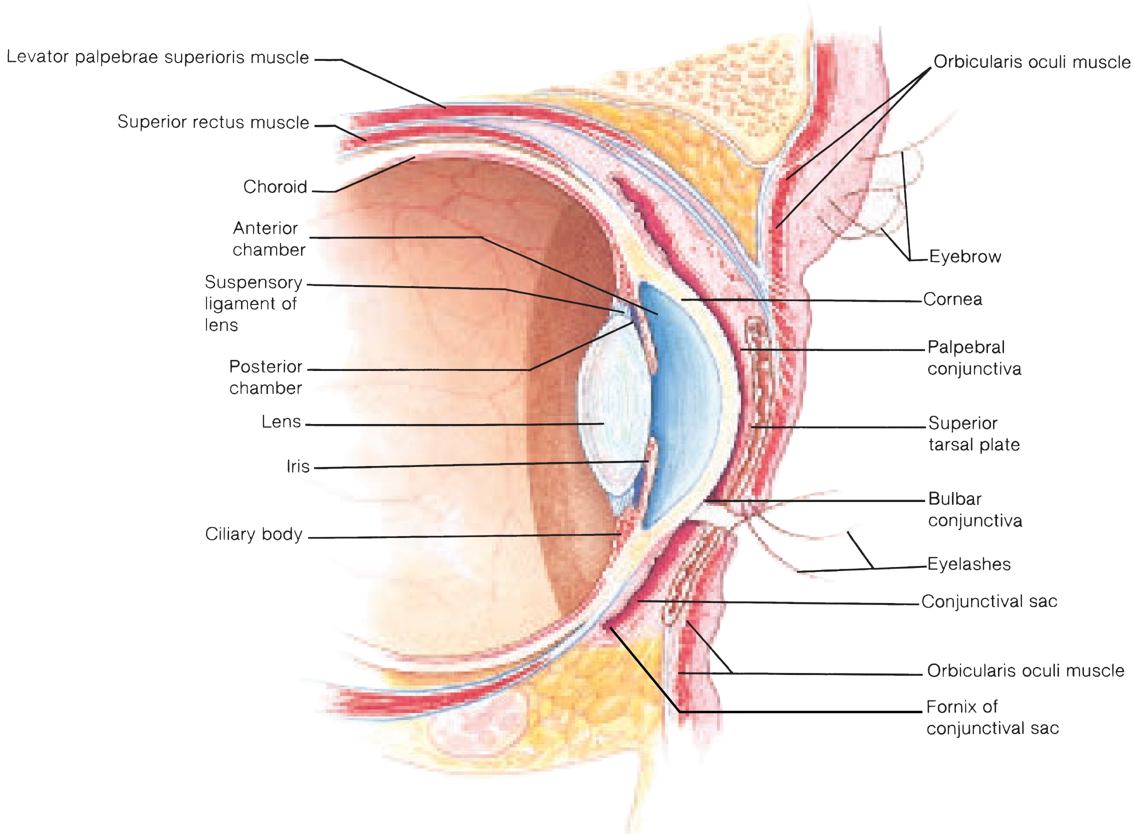


FIGURE 15.9 The eyeball and associated structures in sagittal section.

Eyebrows

Eyebrows consist of short, thick hairs positioned transversely above both eyes along the superior orbital ridges (figs. 15.9 and 15.10). Eyebrows shade the eyes from the sun and prevent perspiration or falling particles from getting into the eyes. Underneath the skin of each eyebrow is the orbital portion of the orbicularis oculi muscle and a portion of the corrugator supercilli muscle (see fig. 9.13). Contraction of either of these muscles causes the eyebrow to move, often reflexively, to protect the eye.

Eyelids and Eyelashes

Eyelids, or **palpebrae** (*pal'pĕ-bre*), develop as reinforced folds of skin with attached skeletal muscle that make them movable. In addition to the orbicularis oculi muscle attached to the skin that surrounds the front of the eye, the levator palpebrae superioris muscle attaches along the upper eyelid and provides it with greater movability than the lower eyelid. Contraction of the orbicularis oculi muscle closes the eyelids over the eye, and contraction of the levator palpebrae superioris muscle elevates the upper eyelid to expose the eye.

The eyelids protect the eyeball from desiccation by reflexively blinking about every 7 seconds and moving fluid across the anterior surface of the eyeball. Reflexively blinking as a moving object approaches the eye is obviously of great protective value. To avoid a blurred image, the eyelid will generally blink when the eyeball moves to a new position of fixation.

The **palpebral fissure** (fig. 15.10) is the space between the upper and lower eyelids. The shape of the palpebral fissure is elliptical when the eyes are open. The **commissures** (*canthi*) of the eye are the medial and lateral angles where the eyelids come together. The **medial commissure,** which is broader than the **lateral commissure,** is characterized by a small, reddish, fleshy elevation called the **lacrimal caruncle** (*kar'ung-kul*) (fig. 15.11). The lacrimal caruncle contains sebaceous and sudoriferous glands; it produces the whitish secretion, commonly called "sleep dust" that sometimes collects during sleep.

palpebra: L. *palpebra*, eyelid (related to *palpare*, to part gently)

commissure: L. *commissura*, a joining

caruncle: L. *caruncula*, diminutive of *caro*, flesh

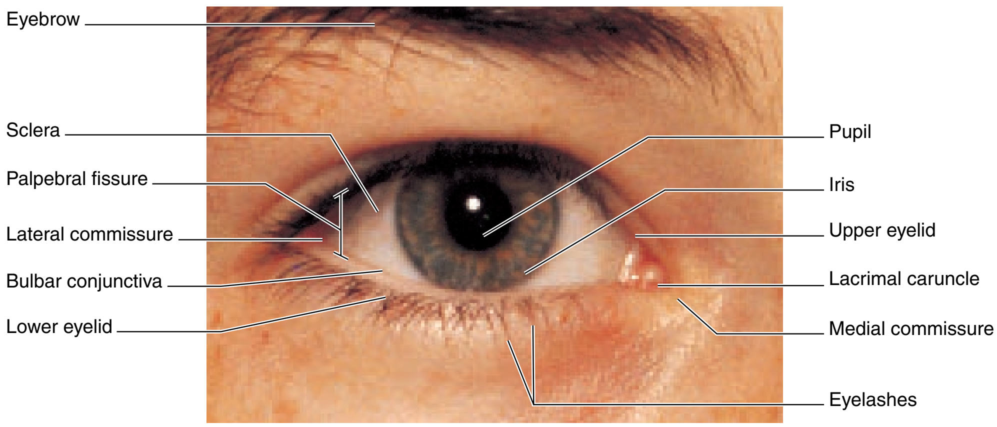


FIGURE 15.10 The surface anatomy of the eye.

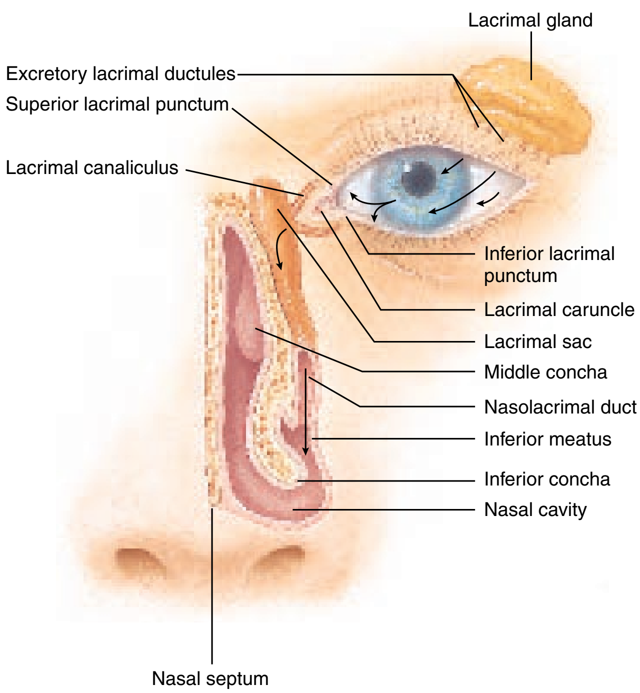


FIGURE 15.11 The lacrimal apparatus consists of the lacrimal gland, which produces lacrimal fluid (tears), and a series of ducts through which the lacrimal fluid drains into the nasal cavity. Lacrimal fluid moistens and cleanses the conjunctiva that lines the interior surface of the eyelids and covers the exposed anterior surface of the eyeball.

In people of Asian descent, a fold of skin of the upper eyelid, called the *epicanthic fold*, may normally cover part of the medial commissure. An epicanthic fold may also be present in some infants with Down syndrome.

Each eyelid supports a row of **eyelashes** that protects the eye from airborne particles. The shaft of each eyelash is surrounded by a root hair plexus that makes the hair sensitive enough to cause a reflexive closure of the lids. Eyelashes of the upper lid are long and turn upward, whereas those of the lower lid are short and turn downward.

In addition to the layers of the skin and the underlying connective tissue and orbicularis oculi muscle fibers, each eyelid contains a tarsal plate, tarsal glands, and conjunctiva. The **tarsal plates,** composed of dense regular connective tissue, are important in maintaining the shape of the eyelids (fig. 15.9). Specialized sebaceous glands called **tarsal glands** are embedded in the tarsal plates along the exposed inner surfaces of the eyelids. The ducts of the tarsal glands open onto the edges of the eyelids, and their oily secretions help keep the eyelids from sticking to each other. Modified sweat glands called **ciliary glands** are also located within the eyelids, along with additional sebaceous glands at the bases of the hair follicles of the eyelashes. An infection of these sebaceous glands is referred to as a *sty* (also spelled *stye*).

Conjunctiva

The conjunctiva *(con''jungk-ti'vă)* is a thin mucus-secreting epithelial membrane that lines the interior surface of each eyelid and exposed anterior surface of the eyeball (see fig. 15.9). It consists of stratified squamous epithelium that varies in thickness in different regions. The **palpebral conjunctiva** is thick and adheres to the tarsal plates of the eyelids. Where the conjunctiva reflects onto the anterior surface of the eyeball, it is known as the **bulbar conjunctiva.** This portion is transparent and especially thin where it covers the cornea. Because the conjunctiva is continuous from the eyelids to the anterior surface of the eyeball, a space called the **conjunctival sac** is present when the eyelids are closed. The conjunctival sac protects the eyeball by preventing foreign objects from passing beyond the confines of the sac. The conjunctiva heals rapidly if scratched.

tarsal: Gk. *tarsos*, flat basket

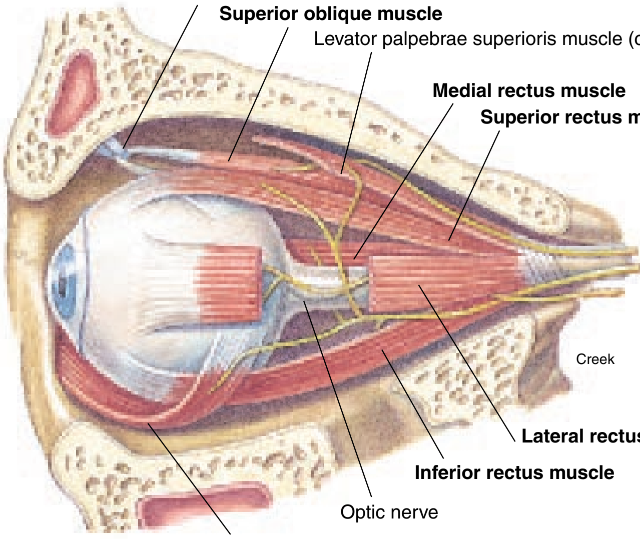


FIGURE 15.12 The extrinsic ocular muscles of the right eyeball. (The extrinsic ocular muscles are labeled in boldface type.)

Lacrimal Apparatus

The lacrimal apparatus consists of the lacrimal gland, which secretes the *lacrimal fluid* (tears), and a series of ducts that drain the lacrimal fluid into the nasal cavity (fig. 15.11). The **lacrimal gland,** which is about the size and shape of an almond, is located in the superolateral portion of the orbit. It is a compound tubuloacinar gland that secretes lacrimal fluid through several excretory lacrimal ductules into the conjunctival sac of the upper eyelid. With each blink of the eyelids, lacrimal fluid is spread over the surface of the eye—much like windshield wipers spread windshield washing fluid. Lacrimal fluid drains into two small openings, called **lacrimal puncta,** on both sides of the lacrimal caruncle. From here, the lacrimal fluid drains through the **superior** and **inferior lacrimal canaliculi** *(kan''ă-lik'yŭ-li)* into the **lacrimal sac** and continues through the **nasolacrimal duct** to the inferior meatus of the nasal cavity (fig. 15.11).

Lacrimal fluid is a lubricating mucus secretion that contains a bactericidal substance called *lysozyme*. Lysozyme reduces the likelihood of infections. Normally, about 1 milliliter of lacrimal fluid is produced each day by the lacrimal gland of each eye. If irritating substances, such as particles of sand or chemicals from onions, make contact with the conjunctiva, the lacrimal glands secrete greater volumes. The extra lacrimal fluid protects the eye by diluting and washing away the irritating substance.

Humans are the only animals known to weep in response to emotional stress. While crying, the volume of lacrimal secretion is so great that the tears may spill over the edges of the eyelids and the nasal cavity fill with fluid. The crying response is an effective means of communicating one's emotions and results from stimulation of the lacrimal glands by parasympathetic motor neurons of the facial nerves.

Extrinsic Ocular Muscles

The movements of the eyeball are controlled by six extrinsic eye muscles called the **extrinsic ocular muscles** (figs. 15.12 and 15.13). Each extrinsic ocular muscle originates from the bony orbit and inserts by a tendinous attachment to the tough outer tunic of the eyeball. Four *recti muscles* (singular, *rectus*) maneuver the eyeball in the direction indicated by their names **(superior, inferior, lateral,** and **medial),** and two **oblique muscles (superior** and **inferior)** rotate the eyeball on its axis (see also fig. 9.17). One of the extrinsic ocular muscles, the superior oblique, passes through a pulleylike cartilaginous loop called the **trochlea** *(trok'le-ă)* before attaching to the eyeball. Although stimulation of each muscle causes a precise movement of the eyeball, most of the movements involve the combined contraction of usually two or more muscles.

The motor units of the extrinsic ocular muscles are the smallest in the body. This means that a single motor neuron serves about 10 muscle fibers, resulting in precise movements. The eyes move in synchrony by contracting synergistic muscles while relaxing antagonistic muscles.

The extrinsic ocular muscles are innervated by three cranial nerves (table 15.3). Innervation of the other skeletal and smooth muscles that serve the eye is also indicated in table 15.3.

trochlea: Gk. *trochos*, a wheel

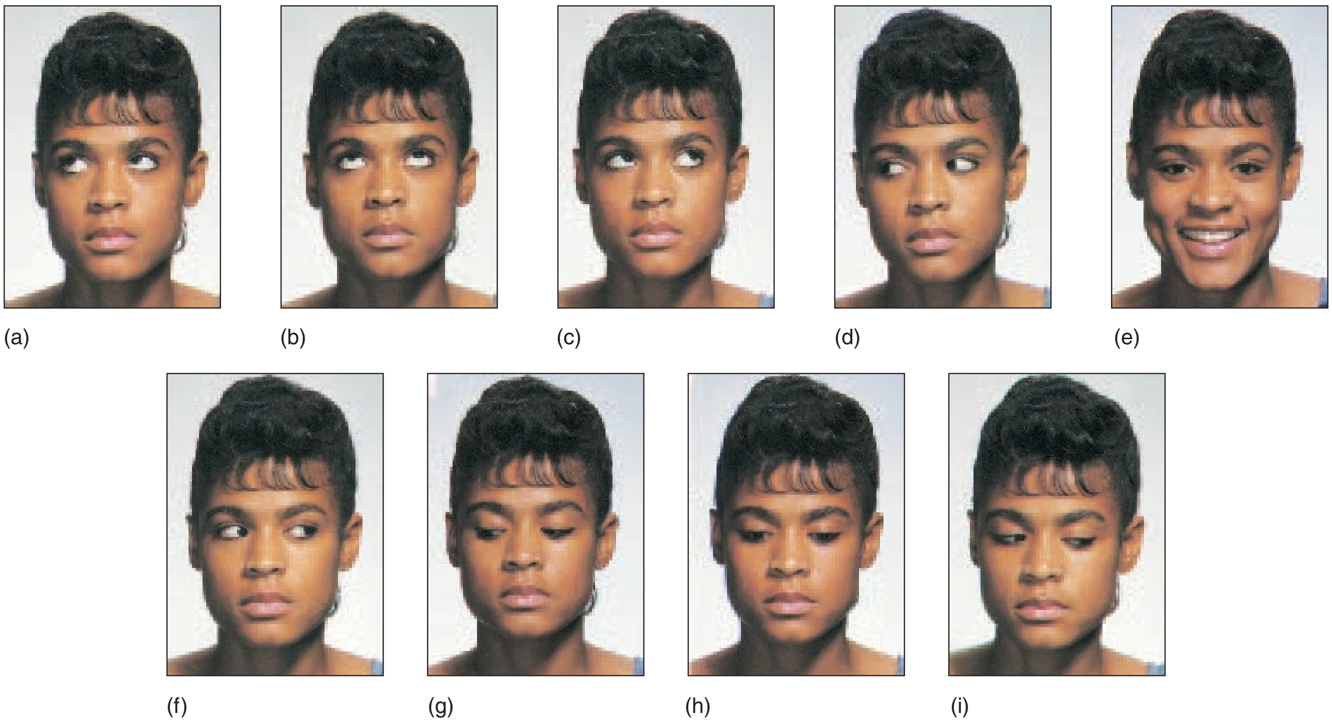


FIGURE 15.13 The positions of the eyes as the extrinsic ocular muscles are contracted. (*a*) Right eye, inferior oblique muscle; left eye, superior and medial recti muscles. (*b*) Both eyes, superior recti and inferior oblique muscles. (*c*) Right eye, superior and medial recti muscles; left eye, inferior oblique muscle. (*d*) Right eye, lateral rectus muscle; left eye, medial rectus muscle. (*e*) Primary position with the eyes fixed on a distant fixation point. (*f*) Right eye, medial rectus muscle; left eye, lateral rectus muscle. (*g*) Right eye, superior oblique muscle; left eye, inferior and medial recti muscles. (*h*) Both eyes, inferior recti and superior oblique muscles. (*i*) Right eye, inferior and medial recti muscles; left eye, superior oblique muscle.

TABLE 15.3 Muscles of the Eye

Muscle	Innervation	Action
Extrinsic Ocular Muscles (skeletal muscles)		
Superior rectus	Oculomotor nerve (III)	Rotates eye upward and toward midline
Inferior rectus	Oculomotor nerve (III)	Rotates eye downward and toward midline
Medial rectus	Oculomotor nerve (III)	Rotates eye toward midline
Lateral rectus	Abducens nerve (VI)	Rotates eye away from midline
Superior oblique	Trochlear nerve (IV)	Rotates eye downward and away from midline
Inferior oblique	Oculomotor nerve (III)	Rotates eye upward and away from midline
Intrinsic Ocular Muscles (smooth muscles)		
Ciliary muscle	Oculomotor nerve (III) parasympathetic fibers	Causes suspensory ligament to relax
Pupillary constrictor muscle	Oculomotor nerve (III) parasympathetic fibers	Causes pupil to constrict
Pupillary dilator muscle	Sympathetic fibers	Causes pupil to dilate

A physical examination may include an eye movement test. As the patient's eyes follow the movement of a physician's finger, the physician can assess weaknesses in specific muscles or dysfunctions of specific cranial nerves. The patient experiencing *double vision (diplopia)* when moving his eyes may be suffering from muscle weakness. Looking laterally tests the abducens nerve; looking inferiorly and laterally tests the trochlear nerve; and crossing the eyes tests the oculomotor nerves of both eyes.

Structure of the Eyeball

The eyeball of an adult is essentially spherical, approximately 25 mm (1 in.) in diameter. About four-fifths of the eyeball lies within the orbit of the skull. The eyeball consists of three basic layers: the *fibrous tunic*, the *vascular tunic*, and the *internal tunic* (fig. 15.14).

Fibrous Tunic

The fibrous tunic is the outer layer of the eyeball. It is divided into two regions: the posterior five-sixths is the opaque *sclera* and the anterior one-sixth is the transparent *cornea* (fig. 15.15).

The toughened **sclera** *(skler'ă)* is the white of the eye. It is composed of tightly bound elastic and collagenous fibers that give shape to the eyeball and protect its inner structures. It also provides a site for attachment of the extrinsic ocular muscles. The sclera is avascular but does contain sensory receptors for pain. The large **optic nerve** exits through the sclera at the back of the eyeball.

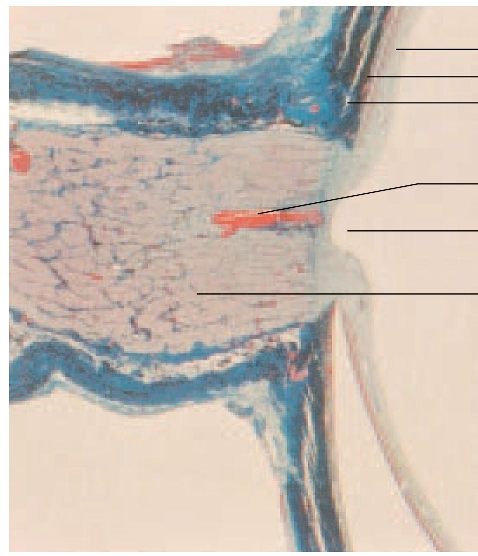
The transparent **cornea** is convex, so that it refracts (bends in a converging pattern) incoming light rays. The transparency of the cornea is due to tightly packed, avascular dense connective tissue. Also, the relatively few cells that are present in the cornea are arranged in unusually regular patterns. The circumferential edge of the cornea is continuous structurally with the sclera. The outer surface of the cornea is covered with a thin, nonkeratinized stratified squamous epithelial layer called the **anterior corneal epithelium,** which is actually a continuation of the bulbar conjunctiva of the sclera (see fig. 15.9).

A defective cornea can be replaced with a donor cornea in a surgical procedure called a *corneal transplant (keratoplasty).* A defective cornea is one that does not transmit or refract light effectively because of its shape, scars, or disease. During a corneal transplant, the defective cornea is excised and replaced with a transplanted cornea that is sutured into place. It is considered to be the most successful type of homotransplant (between individuals of the same species).

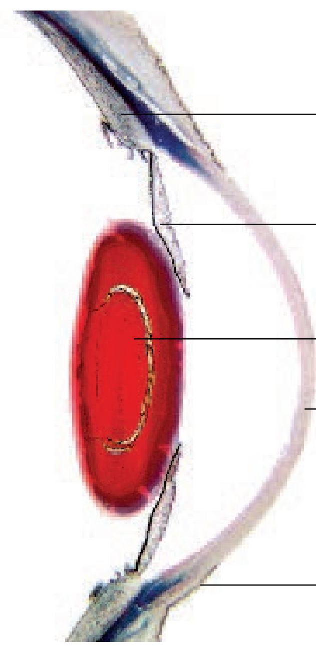
Vascular Tunic

The vascular tunic, or **uvea** *(yoo've-ă)* of the eyeball, consists of the *choroid*, the *ciliary body*, and the *iris* (fig. 15.15).

The **choroid** (*kor'oid*) is a thin, highly vascular layer that lines most of the internal surface of the sclera. The choroid



(a)



(b)

FIGURE 15.14 Photomicrographs of the eyeball. (*a*) A posterior portion showing the tunics of the eye, the optic disc, and the optic nerve (7×) and (*b*) an anterior portion showing the cornea ciliary body, iris, and the lens (7×).

sclera: Gk. *skleros*, hard
optic: L. *optica*, see
cornea: L. *cornu*, horn
uvea: L. *uva*, grape
choroid: Gk. *chorion*, membrane

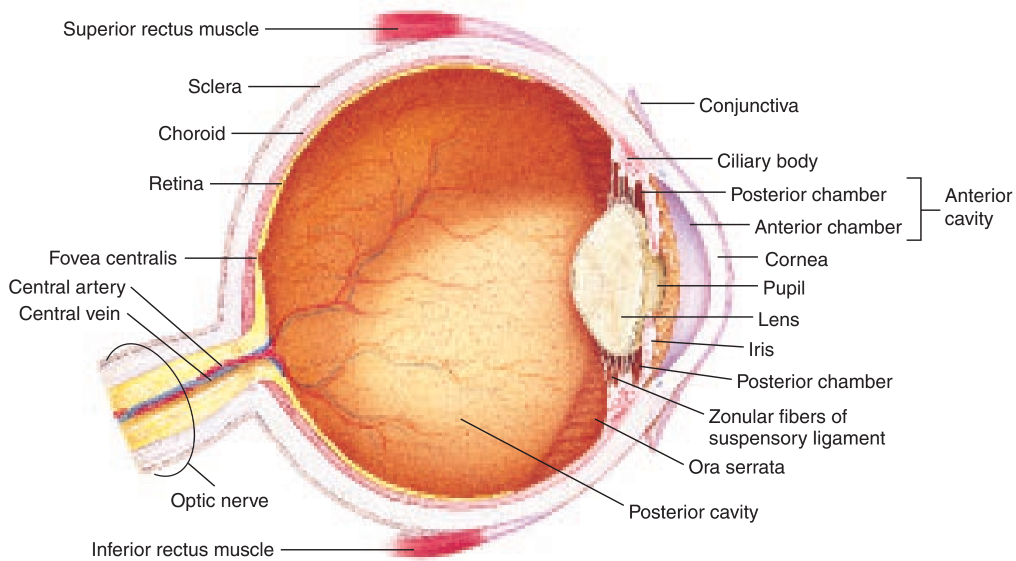


FIGURE 15.15 A sagittal section of the eyeball.

contains numerous pigment-producing melanocytes, which give it a brownish color that prevents light rays from being reflected out of the eyeball. There is an opening in the choroid at the back of the eyeball where the optic nerve is located.

The **ciliary body** is the thickened anterior portion of the vascular tunic that forms an internal muscular ring toward the front of the eyeball (fig. 15.16). Bands of smooth muscle fibers, collectively called the **ciliary muscles** are found within the ciliary body. Numerous extensions of the ciliary body called **ciliary processes** attach to the **zonular fibers,** which in turn attach to the *lens capsule*. Collectively, the zonular fibers constitute the **suspensory ligament.** The transparent **lens** consists of tight layers of protein fibers arranged like the layers of an onion. A thin, clear **lens capsule** encloses the lens and provides attachment for the suspensory ligament (see figs. 15.16 and 15.24).

The shape of the lens determines the degree to which the light rays that pass through will be refracted. Constant tension of the suspensory ligament, when the ciliary muscles are relaxed, flattens the lens somewhat (fig. 15.17). Contraction of the ciliary muscles relaxes the suspensory ligament and makes the lens more spherical. The constant tension within the lens capsule causes the surface of the lens to become more convex when the suspensory ligament is not taut. A flattened lens permits viewing of a distant object, whereas a rounded lens permits viewing of a close object.

The **iris** is the anterior portion of the vascular tunic and is continuous with the choroid. The iris is viewed from the outside as the colored portion of the eyeball (figs. 15.15 and 15.16). It consists of smooth muscle fibers arranged in a circular and a radial pattern. Autonomic contraction of the smooth muscle fibers regulates the diameter of the **pupil** (table 15.4 and fig. 15.18), an opening in the center of the iris. Contraction of the pupillary constrictor muscle of the iris, stimulated by bright light, constricts the pupil and diminishes the amount of light entering the eyeball (see fig. 13.8). Contraction of the pupillary dilator muscle, in response to dim light, enlarges the pupil and permits more light to enter.

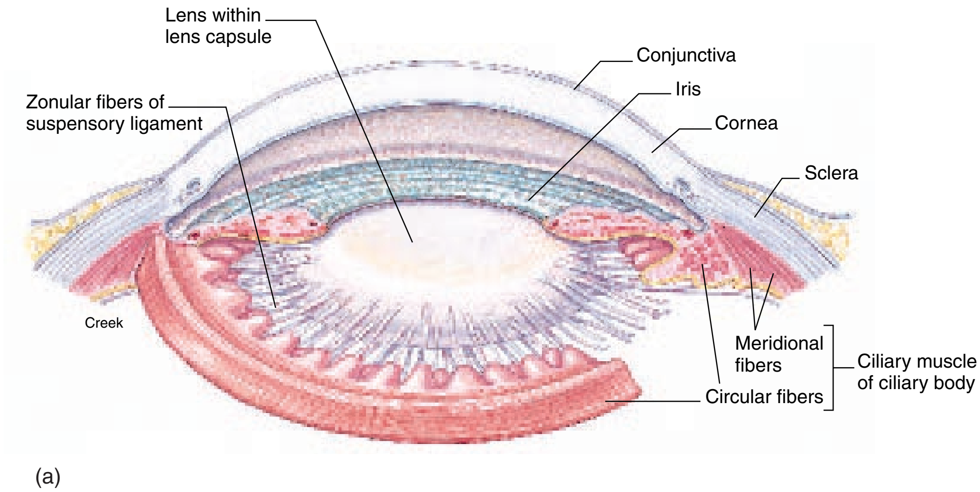
The amount of dark pigment, melanin, in the iris is what determines its color. In newborns, melanin is concentrated in the folds of the iris, so that all newborn babies have blue eyes. After a few months, the melanin moves to the surface of the iris and gives the baby his or her permanent eye color, ranging from steel blue to dark brown.

The arrangement of smooth muscle fibers of the iris presents a unique pattern for each person that is a thousand times more distinctive than the whorls on a fingerprint.

Internal Tunic (Retina)

The **retina** (*ret'ĭ-nă*) covers the choroid as the innermost layer of the eye (fig. 15.15). It consists of an outer **pigmented layer,** in contact with the choroid, and an inner **nervous layer,** or *visual portion* (see fig. 15.15). The thick nervous layer of the retina terminates in a jagged margin near the ciliary body called the **ora serrata** (*o'ră ser-ra'tă*). The thin pigmented layer extends anteriorly over the back of the ciliary body and iris.

zonular: L. *zona*, a girdle
iris: Gk. *irid*, rainbow
ora serrata: L. *ora*, margin; *serra*, saw



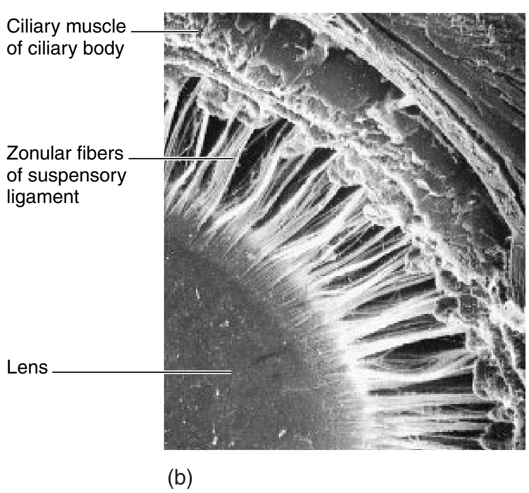


FIGURE 15.16 The structure of the anterior portion of the eyeball. (*a*) The relationship between the lens, zonular fibers, and ciliary muscles of the eye and (*b*) a scanning electron micrograph in anterior view showing that same relationship.

The pigmented layer and nervous layer of the retina are not attached to each other, except where they surround the optic nerve and at the ora serrata. Because of this loose connection, the two layers may become separated as a *detached retina.* Such a separation can be corrected by fusing the layers with a laser.

The nervous layer of the retina is composed of three principal layers of neurons. Listing them in the order in which they conduct impulses, they are the *rod* and *cone cells*, *bipolar neurons*, and *ganglion neurons* (fig. 15.19). In terms of the passage of light, however, the order is reversed. Light must first pass through the layer of ganglion cells and then the layer of bipolar cells before reaching and stimulating the rod and cone cells.

Rod and **cone cells** are photoreceptors. Rod cells number over 100 million per eye and are more slender and elongated than cone cells (fig. 15.20). Rod cells are positioned on the peripheral parts of the retina, where they respond to dim light for black-and-white vision. They also respond to form and movement but provide poor visual acuity. Cone cells, which number about 7 million per eye, provide daylight color vision and greater visual acuity. The photoreceptors synapse with **bipolar neurons,** which in turn synapse with the **ganglion neurons.** The axons of ganglion neurons leave the eye as the optic nerve.

Cone cells are concentrated in a depression near the center of the retina called the **fovea centralis,** which is the area of keenest vision (figs. 15.15 and 15.21). Surrounding the fovea centralis is the yellowish **macula lutea** (*mak′yŭ-lă loo′te-ă*), which

fovea: L. *fovea*, small pit

macula lutea: L. *macula*, spot; *luteus*, yellow

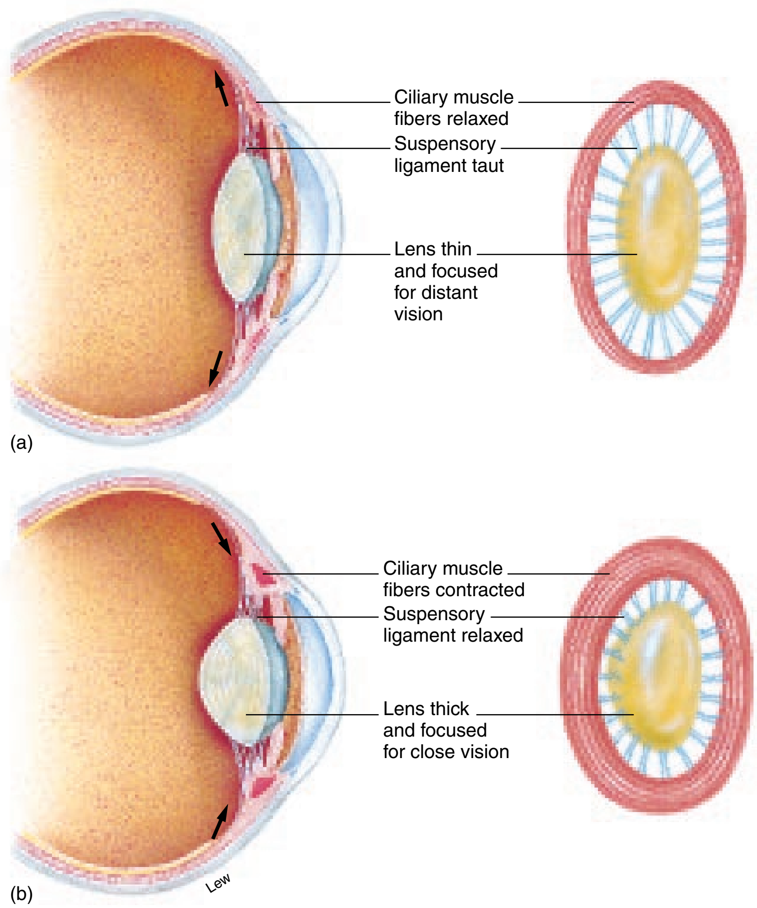


FIGURE 15.17 Changes in the shape of the lens to bring light rays into sharp focus on the retina. (*a*) The lens is flattened for distant vision when the ciliary muscle fibers are relaxed and the suspensory ligament is taut. (*b*) The lens is more spherical for close-up vision when the ciliary muscle fibers are contracted and the suspensory ligament is relaxed.

also has an abundance of cone cells (fig. 15.21). There are no photoreceptors in the area where the optic nerve is attached to the eyeball. This area is a *blind spot* and is referred to as the **optic disc** (figs. 15.21 and 15.22). A person is normally unaware of the blind spot because (1) the eyes continually move about, (2) an object is viewed from a different angle with each eye, and (3) the image of an object that falls on the blind spot of one retina will fall on receptors of the other retina. The blind spot can easily be demonstrated as described in figure 15.23.

Blood Supply to the Eyeball

Both the choroid and the retina are richly supplied with blood. Two **ciliary arteries** pierce the sclera at the posterior aspect of the eyeball and traverse the choroid to the ciliary body and base of the iris. Although the ciliary arteries enter the eyeball independently, they anastomose (connect) extensively throughout the choroid.

The **central artery** (central retinal artery) branches from the ophthalmic artery and enters the eyeball in contact with the optic nerve. As the central artery passes through the optic disc, it divides into superior and inferior branches, each of which then divides into temporal and nasal branches to serve the inner layers of the retina (see fig. 15.15). The **central vein** drains blood from the eyeball through the optic disc. The branches of the central artery can be observed within the eyeball through an ophthalmoscope (fig. 15.21).

An examination of the internal eyeball with an ophthalmoscope is frequently part of a routine physical examination. Arterioles can be seen within the eyeball. If they appear abnormal (for example, constricted, dilated, or hemorrhaged), they may be symptomatic of certain diseases or body dysfunctions. Diseases such as arteriosclerosis, diabetes, cataracts, or glaucoma can be detected by examining the internal eyeball.

TABLE 15.4 Summary of Structures of the Eyeball

Tunic and Structure	Location	Composition	Function
Fibrous Tunic	Outer layer of eyeball	Avascular connective tissue	Gives shape to eyeball
Sclera	Posterior outer layer; white of eye	Tightly bound classic and collagen fibers	Supports and protects eyeball
Cornea	Anterior surface of eyeball	Tightly packed dense connective tissue—transparent and convex	Transmits and refracts light
Vascular Tunic (Uvea)	Middle layer of eyeball	Highly vascular pigmented tissue	Supplies blood; prevents reflection
Choroid	Middle layer in posterior portion of eyeball	Vascular layer	Supplies blood to eyeball
Ciliary body	Anterior portion of vascular tunic	Smooth muscle fibers and glandular epithelium	Supports the lens through suspensory ligament and determines its thickness; secretes aqueous humor
Iris	Anterior portion of vascular tunic; continuous with ciliary body	Smooth muscle fibers, and pigment cells	Regulates the diameter of pupil, and hence the amount of light entering the posterior cavity
Internal Tunic	Inner layer of eyeball	Tightly packed photoreceptors, neurons, blood vessels, and connective tissue	Provides location and support for rod and cone cells
Retina	Principal portion of internal tunica in contact with vitreous humor	Photoreceptor neurons (rod and cone cells), bipolar neurons, ganglion neurons	Photoreception; transmits impulses
Lens (not part of any tunic)	Between anterior and posterior chambers within lens capsule; supported by suspensory ligament of ciliary body	Tightly arranged protein fibers; transparent	Refracts light and focuses onto fovea centralis

Cavities and Chambers of the Eyeball

The interior of the eyeball is separated by the lens and its associated lens capsule into an **anterior cavity** and a **posterior cavity** (see fig. 15.15). The anterior cavity is subdivided by the iris into an **anterior chamber** and a **posterior chamber** (see fig. 15.15). The anterior chamber is located between the cornea and the iris. The posterior chamber is located between the iris and the suspensory ligament and lens. The anterior and posterior chambers connect through the pupil and are filled with a watery fluid called **aqueous humor.** The constant production of aqueous humor maintains an *intraocular pressure* of about 12 mmHg within the anterior and posterior chambers. Aqueous humor also provides nutrients and oxygen to the avascular lens and cornea. An estimated 5.5 ml of aqueous humor is secreted each day from the vascular epithelium of the ciliary body (fig. 15.24). From its site of secretion within the posterior chamber, the aqueous humor passes through the pupil into the anterior chamber. From here, it drains from the eyeball through the **scleral venous sinus** (canal of Schlemm) into the bloodstream. The scleral venous sinus is located at the junction of the cornea and iris.

The large posterior cavity is filled with a transparent jelly-like **vitreous humor.** Vitreous humor contributes to the intraocular pressure that maintains the shape of the eyeball and holds the retina against the choroid. Unlike aqueous humor, vitreous humor is not continuously produced; rather, it is formed prenatally. Additional vitreous humor forms as a person's eyes become larger through normal body growth.

The structures within the eyeball are summarized in table 15.4.

Puncture wounds to the eyeball are especially dangerous and frequently cause blindness. Protective equipment such as goggles, shields, and shatterproof lenses should be used in hazardous occupations and certain sports. If the eye is punctured, the main thing to remember is to *leave the object in place* if it is still impaling the eyeball. Removal may allow the fluids to drain from the eyeball, causing loss of intraocular pressure, a detached retina, and possibly blindness.

canal of Schlemm: from Friedrich S. Schlemm, German anatomist, 1795–1858

vitreous: L. *vitreus*, glassy

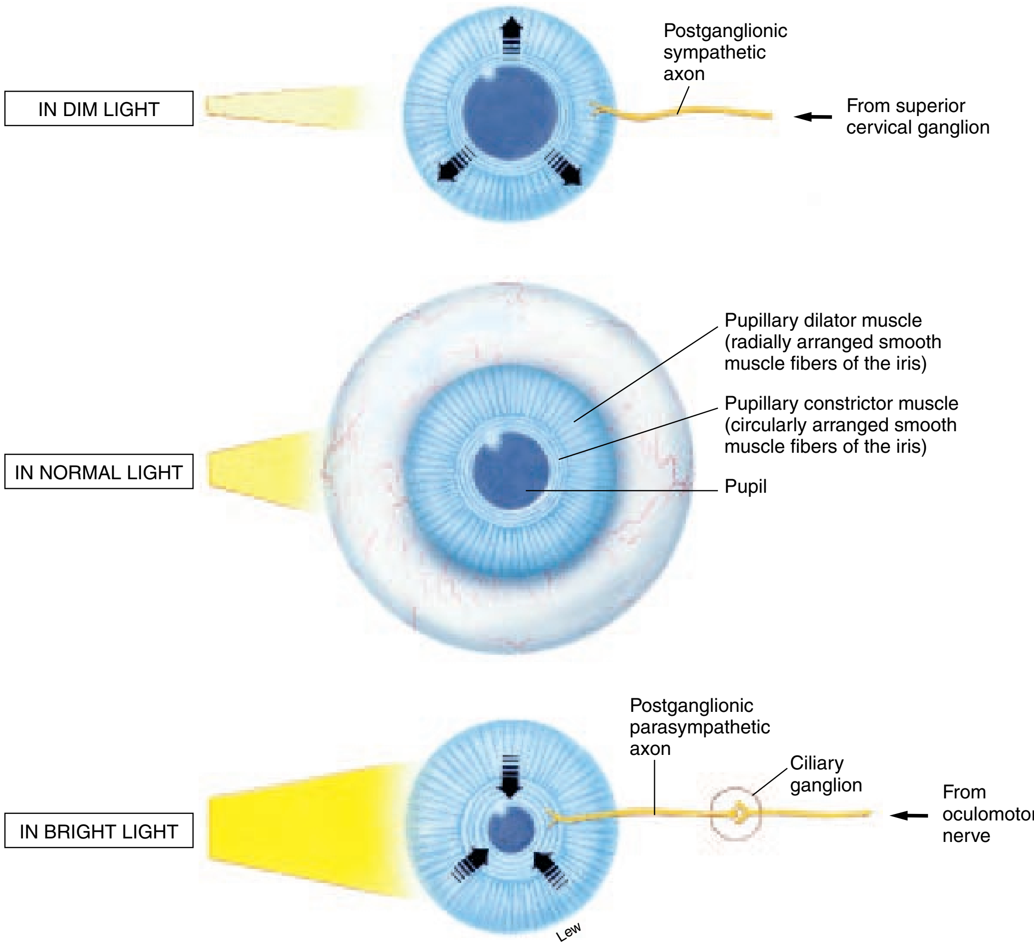


FIGURE 15.18 Dilation and constriction of the pupil. In dim light, the radially arranged smooth muscle fibers are stimulated to contract by sympathetic stimulation, dilating the pupil. In bright light, the circularly arranged smooth muscle fibers are stimulated to contract by parasympathetic stimulation, constricting the pupil.

Function of the Eyeball

The focusing of light rays and stimulation of photoreceptors of the retina require five basic processes:

1. *transmission of light rays* through transparent media of the eyeball;
2. *refraction of light rays* through media of different densities;
3. *accommodation of the lens* to focus the light rays;
4. *constriction of the pupil* by the iris to regulate the amount of light entering the posterior cavity; and
5. *convergence of the eyeballs*, so that visual acuity is maintained.

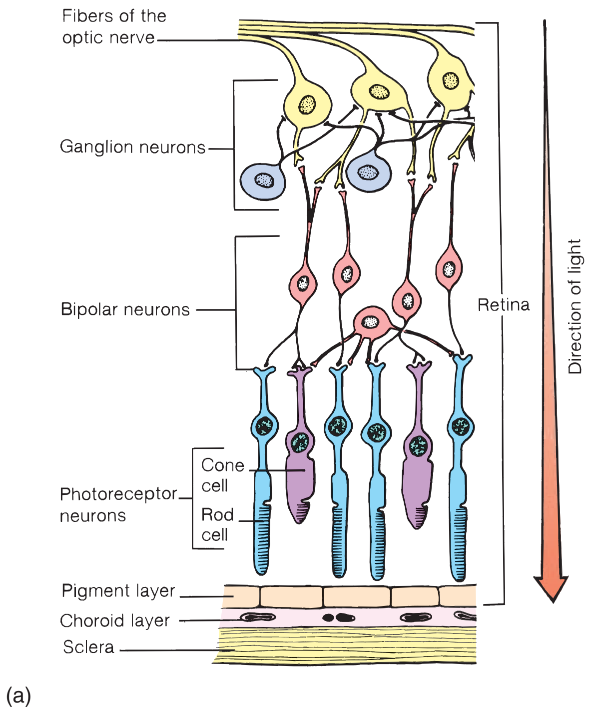
Visual impairment may result if one or more of these processes does not function properly (see Clinical Considerations).

Transmission of Light Rays

Light rays entering the eyeball pass through four transparent media before they stimulate the photoreceptors. In sequence, the media through which light rays pass are the cornea, aqueous humor, lens, and vitreous humor. The cornea and lens are solid media composed of tightly packed, avascular protein fibers. An additional thin, transparent membranous continuation of the conjunctiva covers the outer surface of the cornea. The aqueous humor is a low-viscosity fluid, whereas the vitreous humor is jellylike in consistency.

Refraction of Light Rays

Refraction is the bending of light rays. Refraction occurs as light rays pass at an oblique angle from a medium of one optical density to a medium of a different optical density. The convex



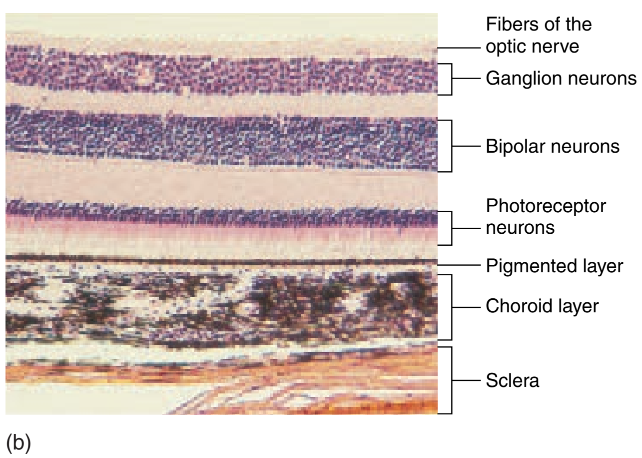


FIGURE 15.19 The layers of the retina. The retina is inverted, so that light must pass through various layers of nerve cells before reaching the photoreceptors (rod cells and cone cells). (*a*) A schematic diagram and (*b*) a light micrograph.

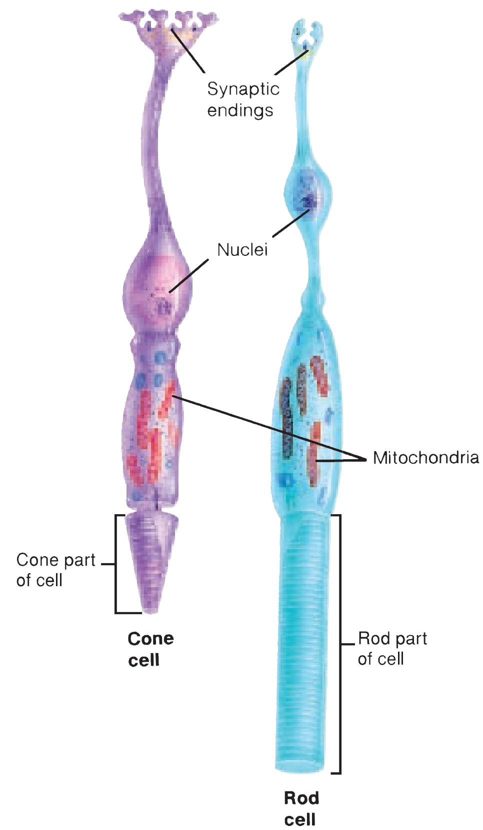


FIGURE 15.20 Photoreceptor cells of the retina.

cornea is the principal refractive medium; the aqueous and vitreous humors produce minimal refraction. The lens is particularly important for refining and altering refraction. Of the refractive media, only the lens can be altered in shape to achieve precise refraction.

The refraction of light rays is so extensive that the visual image is formed upside down on the retina (fig. 15.25). Nerve impulses of the image in this position are relayed to the visual cortex of the occipital lobe, where the inverted image is interpreted as right side up.

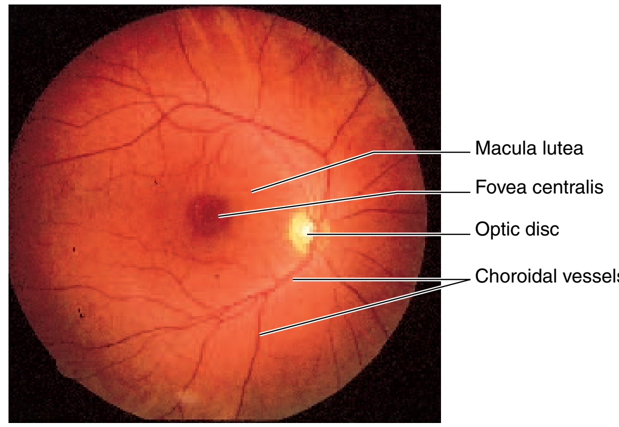
Accommodation of the Lens

Accommodation is the automatic adjustment of the curvature of the lens by contraction of ciliary muscles to bring light rays into sharp focus on the retina. The lens of the eyeball is biconvex. When an object is viewed from a distance of less than about 20 feet, the lens must make an adjustment, or accommodation, for clear focus on the retina. Contraction of the smooth muscle fibers of the ciliary body causes the suspensory ligament to relax and the lens to become thicker (see fig. 15.17). A thicker, more convex lens causes the greater refraction of light required for viewing close objects.

Constriction of the Pupil

Constriction of the pupil occurs through parasympathetic stimulation that causes the pupillary constrictor muscles of the iris to contract (see fig. 15.18). Pupillary constriction is important for two reasons. One is that it reduces the amount of light that enters the posterior cavity. A reflexive constriction of the pupil protects the retina from sudden or intense bright light. More important, a re-

(a)



(b)

FIGURE 15.21 (*a*) A physician viewing the internal anatomy of the eyeball. (*b*) The appearance of the retina as viewed with an ophthalmoscope. Optic nerve fibers leave the eyeball at the optic disc to form the optic nerve. (Note the blood vessels that can be seen entering the eyeball at the optic disc.)

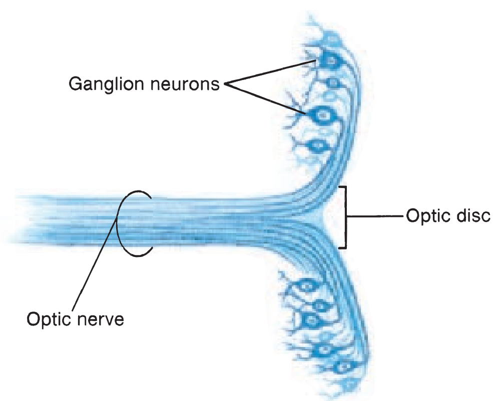


FIGURE 15.22 The optic disc is a small area of the retina where the fibers of the ganglion neurons emerge to form the optic nerve. The optic disc is frequently called the blind spot because it is devoid of rod and cone cells.

FIGURE 15.23 The blind spot. Hold the drawing about 20 inches from your face with your left eye closed and your right eye focused on the circle. Slowly move the drawing closer to your face, and at a certain point the cross will disappear. This occurs because the image of the cross is focused on the optic disc, where photoreceptors are absent.

Amblyopia (am''ble-o pe-ă) ex anopsia, commonly called "lazy eye," is a condition of extrinsic ocular muscle weakness. This causes a deviation of one eye, so that there is not a concurrent convergence of both eyeballs. With this condition, two images are received by the optic portion of the cerebral cortex—one of which is suppressed to avoid *diplopia (double vision),* or images of unequal clarity. A person who has amblyopia will experience dimness of vision and partial loss of sight. Amblyopia is frequently tested for in young children; if it is not treated before the age of 6, little can be done to strengthen the afflicted muscle.

duced pupil diameter prevents light rays from entering the posterior cavity through the periphery of the lens. Light rays refracted from the periphery would not be brought into focus on the retina and would cause blurred vision. Autonomic constriction of the pupil and accommodation of the lens occur simultaneously.

Convergence of the Eyeballs

Convergence refers to the medial rotation of the eyeballs when fixating on a close object. In fact, focusing on an object close to the tip of the nose causes a person to appear cross-eyed. The eyeballs must converge when viewing close objects because only then can the light rays focus on the same portions in both retinas.

Visual Spectrum

The eyes transduce the energy of the *electromagnetic spectrum* (fig. 15.26) into nerve impulses. Only a limited part of this spectrum can excite the photoreceptors. Electromagnetic energy with wavelengths between 400 and 700 nanometers (nm) constitute *visible light*. Light of longer wavelengths, which are in the infrared regions of the spectrum, does not have sufficient energy to excite photoreceptors but is perceived as heat. Ultraviolet light, which has shorter wavelengths and more energy than visible light, is filtered out by the yellow color of the eye's lens. Certain insects, such as honeybees, and people who have had their lenses removed and not replaced with prostheses, can see light in the ultraviolet range.

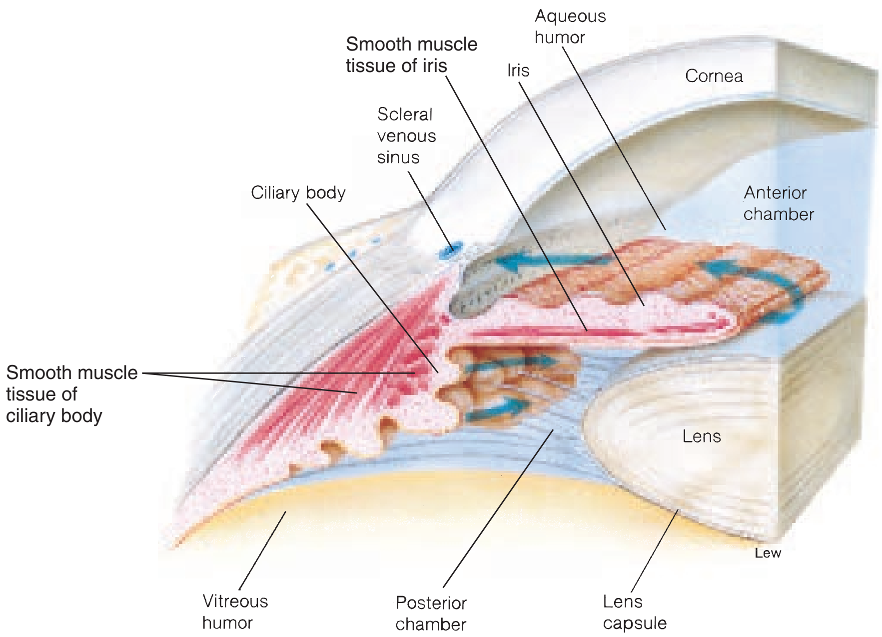


FIGURE 15.24 Aqueous humor maintains the intraocular pressure within the anterior and posterior chambers of the anterior cavity of the eyeball. It is secreted into the posterior chamber, flows through the pupil into the anterior chamber, and drains from the eyeball through the scleral venous sinus.

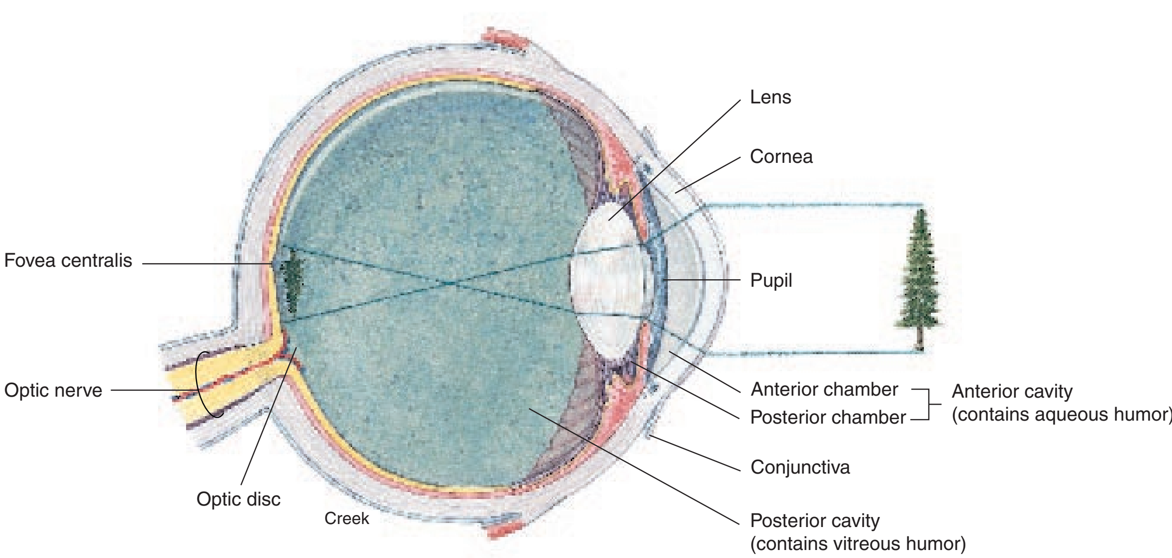


FIGURE 15.25 The refraction of light waves within the eyeball causes the image of an object to be inverted on the retina.

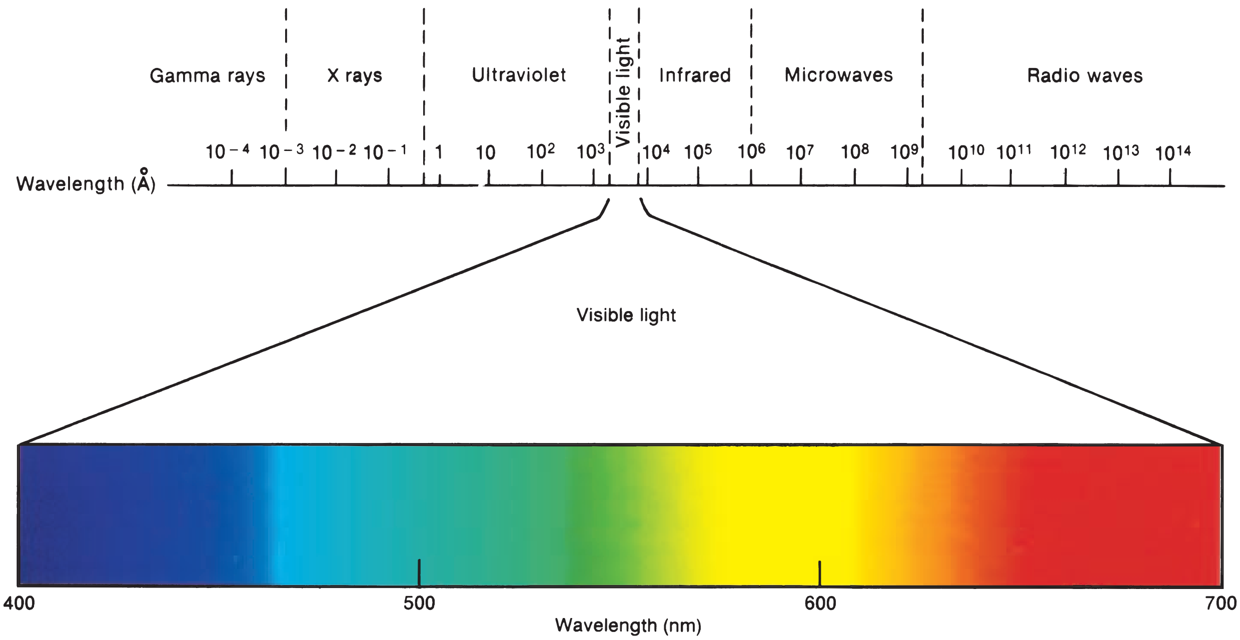


FIGURE 15.26 The electromagnetic spectrum (top) is shown in Angstrom units (1 Å = 10^{-10} meter). The visible spectrum (bottom) constitutes only a small range of this spectrum and is shown in nanometer units (1 nm = 10^{-9} meter).

Three distinct and specialized types of cone cells within the retina permit color vision (fig. 15.26). Different photosensitive pigments enable each type to absorb light rays primarily in the blue, green, or red portion of the color spectrum. Blue cone cells are stimulated by wavelengths between 400 and 550 nm; green cone cells are stimulated by wavelengths between 450 and 550 nm; and red cone cells are stimulated by wavelengths between 500 and 700 nm. *Color blindness* is the inability to distinguish colors, particularly reds and greens. Red-green color blindness is a sex-linked recessive trait that occurs in about 8% of U.S. males and 0.5% of females. Color blindness for the majority of these people is a misnomer, however, because in nearly all cases there is a deficiency in the number of specific cone cells, not a total lack of them. Hence, there is some ability to distinguish color.

A driver with red-green color blindness—the most common type—is able to distinguish traffic signals without difficulty because yellow has been added to the red light, and blue has been added to the green.

Neural Pathways for Vision, Eye Movements, and Processing Visual Information

The photoreceptor neurons, rod and cone cells, are the functional units of sight in that they respond to light rays and produce nerve impulses. Nerve impulses from the rod and cone cells pass through bipolar neurons to ganglion neurons (see fig. 15.19). The optic nerve consists of axons of aggregated ganglion neurons that emerge through the posterior aspect of the eyeball. The two optic nerves (one from each eyeball) converge at the **optic chiasma** (*ki-as'mă*) (fig. 15.27). At this point, all of the fibers arising from the medial (nasal) half of each retina cross to the opposite side. Those fibers of the optic nerve that arise from the lateral (temporal) half of the retina do not cross, however. The **optic tract** is a continuation of optic nerve fibers from the optic chiasma. It is composed of fibers arising from the retinas of both eyeballs.

As the optic tracts enter the brain, some of the fibers in the tracts terminate in the **superior colliculi** (*ko-lik'yoo-li*) These fibers and the motor pathways they activate constitute the **tectal system,** which is responsible for body-eye coordination.

Approximately 70% to 80% of the fibers in the optic tract pass to the **lateral geniculate** (*jĕ-nik'yŭ-lit*) **body** of the thalamus (fig. 15.27). Here the fibers synapse with neurons whose axons constitute a pathway called the **optic radiation.** The optic radiation transmits impulses to the **striate cortex** area of the occipital lobe of the cerebrum. This arrangement of visual fibers, known as the **geniculostriate system,** is responsible for perception of the visual field.

The nerve fibers that cross at the optic chiasma arise from the retinas in the medial portions of both eyes. The photoreceptors of these fibers are stimulated by light entering the eyeball from the periphery. If the optic chiasma is cut longitudinally, peripheral vision will be lost, leaving only "tunnel vision." If an optic tract is cut, both eyes will be partially blind, the lateral field of vision will be lost for one eye, and the medial field of vision lost for the other.

Superior Colliculi and Eye Movements

Neural pathways from the superior colliculi to motor neurons in the spinal cord help mediate the startle response to the sight, for example, of an unexpected intruder. Other nerve fibers from the

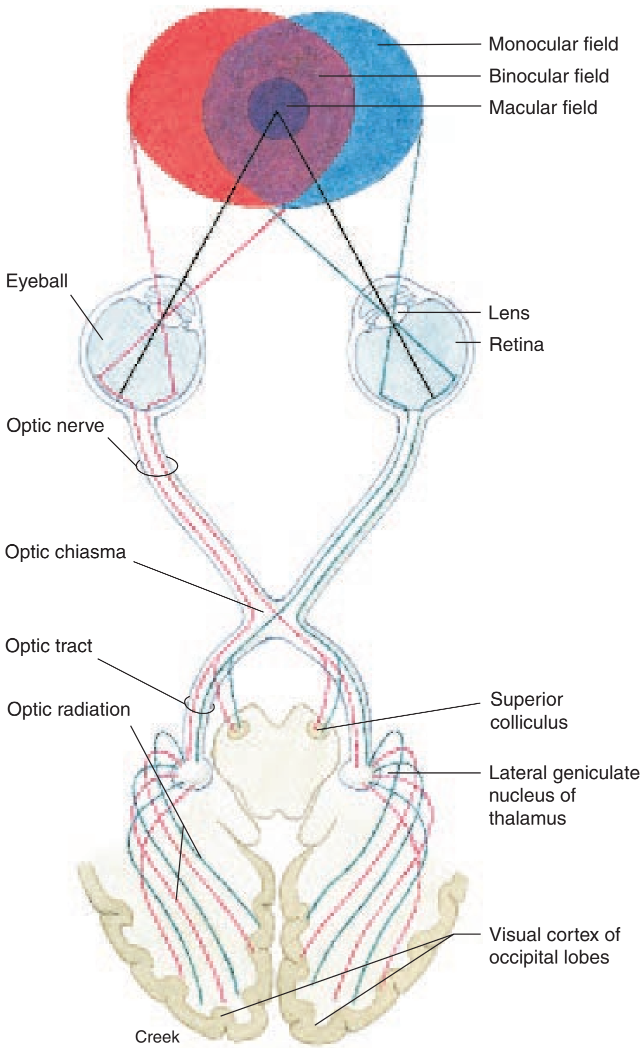


FIGURE 15.27 Visual fields of the eyes and neural pathways for vision. An overlapping of the visual field of each eye provides binocular vision—the ability to perceive depth.

superior colliculi stimulate the **extrinsic ocular muscles** (see table 15.3), which are the skeletal muscles that move the eyes.

Two types of eye movements are coordinated by the superior colliculi. *Smooth pursuit movements* track moving objects and keep the image focused on the fovea centralis. *Saccadic (să-kad′ik) eye movements* are quick (lasting 20–50 msec), jerky movements that occur while the eyes appear to be still. These saccadic movements are believed to be important in maintaining visual acuity.

The tectal system is also involved in the control of the **intrinsic ocular muscles**—the smooth muscles of the iris and of the ciliary body. Shining a light into one eye stimulates the *pupillary reflex* in which both pupils constrict. This is caused by activation of parasympathetic neurons by fibers from the superior colliculi. Postganglionic neurons in the ciliary ganglia behind the eyes, in turn, stimulate constrictor fibers in the iris. Contraction of the ciliary body during *accommodation* also involves stimulation of the superior colliculi.

Processing of Visual Information

For visual information to have meaning, it must be associated with past experience and integrated with information from other senses. Some of this higher processing occurs in the inferior temporal lobes of the cerebral cortex. Experimental removal of these areas from monkeys impairs their ability to remember visual tasks that they previously learned and hinders their ability to associate visual images with the significance of the objects viewed. Monkeys with their inferior temporal lobes removed, for example, will fearlessly handle a snake. The symptoms produced by loss of the inferior temporal lobes are known as *Klüver–Bucy syndrome*.

In an attempt to reduce the symptoms of severe epilepsy, surgeons at one time would cut the corpus callosum in some patients. This fiber tract, as previously described, transmits impulses between the right and left cerebral hemispheres. The right cerebral hemisphere of patients with such *split brains* would therefore, receive sensory information only from the left half of the external world. The left hemisphere, similarly cut off from communication with the right hemisphere, would receive sensory information only from the right half of the external world. In some situations, these patients would behave as if they had two separate minds.

Experiments with split-brain patients have revealed that the two hemispheres have separate abilities. This is true even though each hemisphere normally receives input from both halves of the external world through the corpus callosum. If the sensory image of an object, such as a key, is delivered only to the left hemisphere (by showing it only to the right visual field), the object can be named. If the object is presented to the right cerebral cortex, the person knows what the object is but cannot name it. Experiments such as this suggest that (in right-handed people) the left hemisphere is needed for language and the right hemisphere is responsible for pattern recognition.

Knowledge Check

15. List the accessory structures of the eye that either cause the eye to move or protect it within the orbit.
16. Diagram the structure of the eye and label the following: sclera, cornea, choroid, retina, fovea centralis, iris, pupil, lens, and ciliary body. What are the principal cells or tissues in each of the three layers of the eye?
17. Trace the path of light through the two cavities of the eye and explain the mechanism of light refraction. Describe how the eye is focused for viewing distant and near objects.
18. List the different layers of the retina and describe the path of light and of nerve activity through these layers. Continue tracing the path of a visual impulse to the cerebral cortex, and list in order the structures traversed.

Klüver–Bucy syndrome: from Heinrich Klüver, German neurologist, 1897–1979 and Paul C. Bucy, American neurologist, b. 1904

Developmental Exposition

The Eye

EXPLANATION

The development of the eye is a complex process that involves the precise interaction of neuroectoderm, surface ectoderm, and mesoderm. It begins early in the fourth week, as the neuroectoderm forms a lateral diverticulum on each side of the prosencephalon (forebrain). As the diverticulum increases in size, the distal portion dilates to become the **optic vesicle** and the proximal portion constricts to become the **optic stalk** (exhibit I). Once the optic vesicle has formed, the overlying surface ectoderm thickens and invaginates. The thickened portion is the **lens placode** (*plak'ōd*) and the invagination is the **lens fovea.**

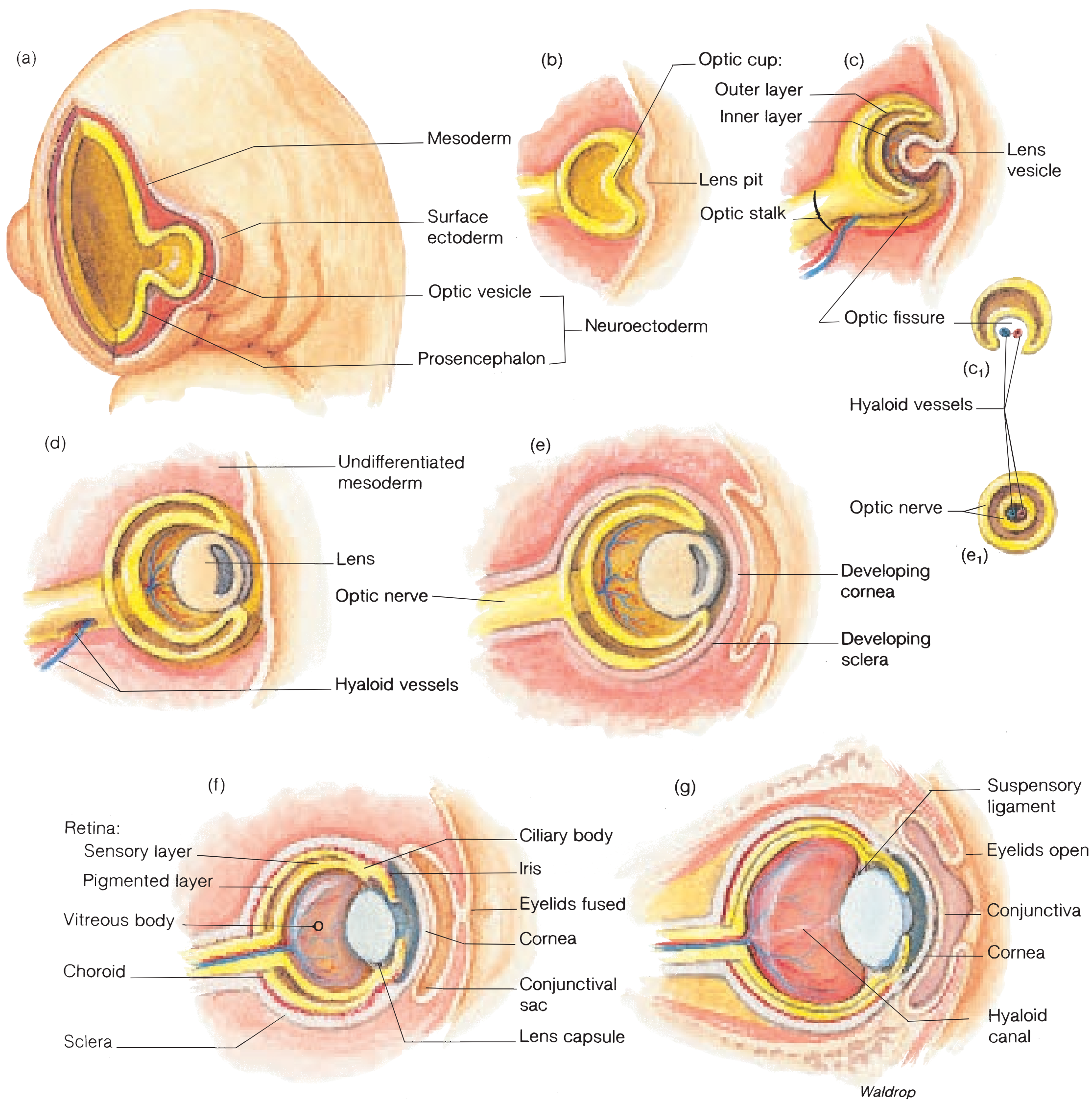


EXHIBIT I The development of the eye. (*a*) An anterior view of the developing head of a 22-day-old embryo and the formation of the optic vesicle from the neuroectoderm of the prosencephalon (forebrain). (*b*) The development of the optic cup. The lens vesicle is formed (*c*) as the ectodermal lens placode invaginates during the fourth week. The hyaloid vessels become enclosed within the optic nerve (c_1 and e_1) as there is fusion of the optic fissure. (*d*) The basic shape of the eyeball and the position of its internal structures are established during the fifth week. The successive development of the eye is shown at 6 weeks (*e*) and at 20 weeks (*f*), respectively. (*g*) The eye of the newborn.

(continued)

(concluded)

During the fifth week, the lens placode is depressed and eventually cut off from the surface ectoderm, causing the formation of the **lens vesicle.** Simultaneously, the optic vesicle invaginates and differentiates into the two-layered **optic cup.** Along the inferior surface of the optic cup, a groove called the **optic fissure** allows for passage of the **hyaloid artery** and **hyaloid vein** that serve the developing eyeball. The walls of the optic fissure eventually close, so that the hyaloid vessels are within the tissue of the optic stalk. They become the **central vessels of the retina** of the mature eye. The optic stalk eventually becomes the **optic nerve,** composed of sensory axons from the retina.

By the early part of the seventh week, the optic cup has differentiated into two sheets of epithelial tissue that become the sensory and pigmented layers of the **retina.** Both of these layers also line the entire vascular coat, including the **ciliary body, iris,** and the **choroid.** A proliferation of cells in the lens vesicle leads to the formation of the lens. The **lens capsule** forms from the mesoderm surrounding the lens, as does the **vitreous humor.** Mesoderm surrounding the optic cup differentiates into two distinct layers of the developing eyeball. The inner layer of mesoderm becomes the vascular **choroid,** and the outer layer becomes the toughened **sclera** posteriorly and the transparent **cornea** anteriorly. Once the cornea has formed, additional surface ectoderm gives rise to the thin **conjunctiva** covering the anterior surface of the eyeball. Epithelium of the **eyelids** and the **lacrimal glands** and **duct** develop from surface ectoderm, whereas the **extrinsic ocular muscles** and all connective tissues associated with the eye develop from mesoderm. These accessory structures of the eye develop gradually during the embryonic period and continue to develop into the fetal period as late as the fifth month.

hyaloid: Gk. *hyalos*, glass; *eiodos*, form

SENSES OF HEARING AND BALANCE

Structures of the outer, middle, and inner ear are involved in the sense of hearing. The inner ear also contains structures that provide a sense of balance, or equilibrium. The development of the ear begins during the fourth week and is complete by week 32.

Objective 14 List the structures of the ear that relate to hearing and describe their locations and functions.

Objective 15 Trace the path of sound waves as they travel through the ear and explain how they are transmitted and converted to nerve impulses.

Objective 16 Explain the mechanisms by which equilibrium is maintained.

The ear is the organ of hearing and equilibrium. It contains receptors that convert sound waves into nerve impulses and receptors that respond to movements of the head. Impulses from both receptor types are transmitted through the vestibulocochlear nerve (VIII) to the brain for interpretation. The ear consists of three principal regions: the *outer ear*, the *middle ear*, and the *inner ear* (fig. 15.28).

Outer Ear

The **outer ear** consists of the auricle, or pinna, and the external acoustic canal. The external acoustic canal is the fleshy tube that is fitted into the bony tube called the *external acoustic meatus (me-a'tus)*. The **auricle** (*or'ĭ-kul*) is the visible fleshy appendage attached to the side of the head. It consists of a cartilaginous framework of elastic connective tissue covered with skin. The rim of the auricle is the **helix,** and the inferior fleshy portion is the **earlobe** (fig. 15.29). The earlobe is the only portion of the auricle that is not supported with cartilage. The auricle has a ligamentous attachment to the skull and poorly developed auricular muscles that insert within it anteriorly, superiorly, and posteriorly. The blood supply to the auricle is from the posterior auricular and occipital arteries, which branch from the external carotid and superficial temporal arteries, respectively. The structure of the auricle directs sound waves into the external acoustic canal.

The **external acoustic canal** is a slightly S-shaped tube, about 2.5 cm (1 in.) long, that extends slightly upward from the auricle to the *tympanic membrane* (fig. 15.28). The skin that lines the canal contains fine hairs and sebaceous glands near the entrance. Deep within the canal, the skin contains specialized wax-secreting glands, called **ceruminous** *(se-roo'mĭ-nus)* **glands.** The *cerumen* (earwax) secreted from these glands keeps the tympanic membrane soft and waterproof. The cerumen and hairs also help to prevent small foreign objects from reaching the tympanic membrane. The bitter cerumen is probably an insect repellent as well.

The **tympanic** *(tim-pan'ik)* **membrane** ("eardrum") is a thin, double-layered, epithelial partition, approximately 1 cm in diameter, between the external acoustic canal and the middle ear. It is composed of an outer concave layer of stratified squamous epithelium and an inner convex layer of low columnar epithelium. Between the epithelial layers is a layer of connective tissue. The tympanic membrane is extremely sensitive to pain and is innervated by the auriculotemporal nerve (a branch of the mandibular nerve of the trigeminal nerve) and the auricular nerve (a branch of the vagus nerve). Small sensory branches from the facial nerve (VII) and the glosopharyngeal nerve (IX) also innervate the tympanic membrane.

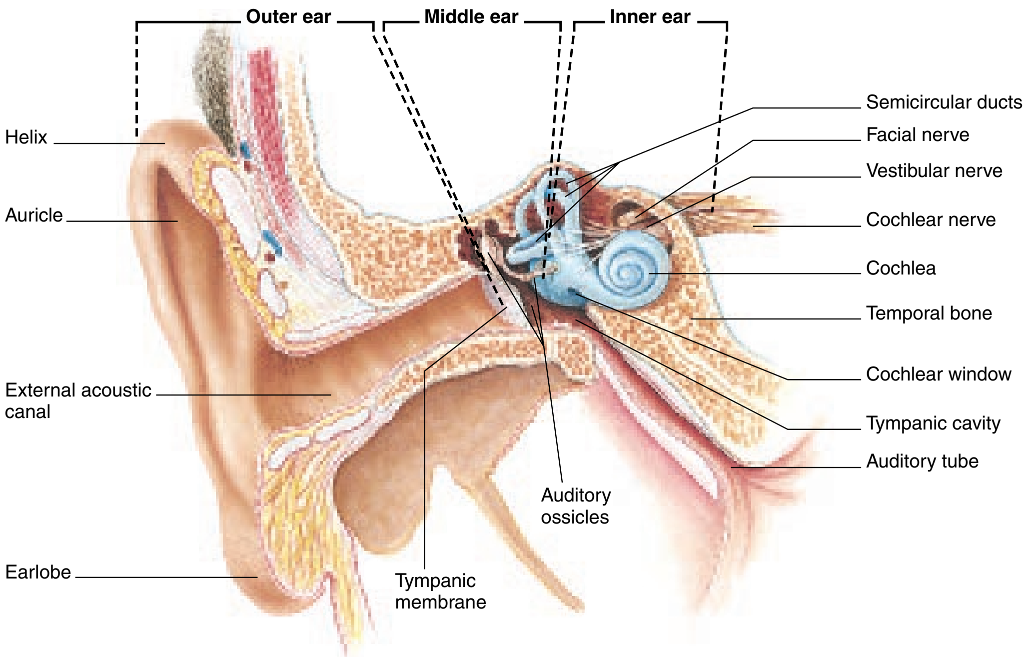


FIGURE 15.28 The ear. (Note the outer, middle, and inner regions indicated by dashed lines.)

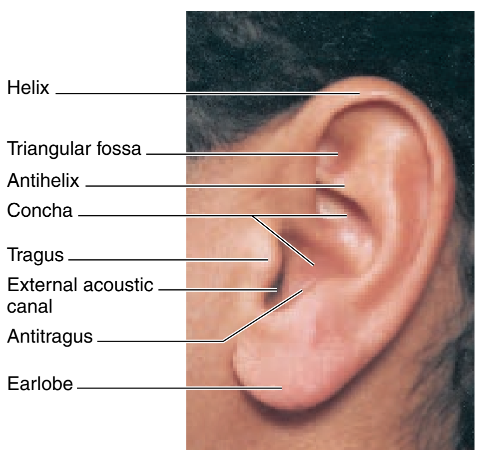


FIGURE 15.29 The surface anatomy of the auricle of the ear.

Inspecting the tympanic membrane with an otoscope during a physical examination provides clinical information about the condition of the middle ear (fig. 15.30). The color of the membrane, its curvature, the presence of lesions, and the position of the malleus of the middle ear are features of particular importance. If ruptured, the tympanic membrane will generally regenerate, healing itself within days.

otoscope: Gk. *otikos*, ear; *skopein*, to examine

Middle Ear

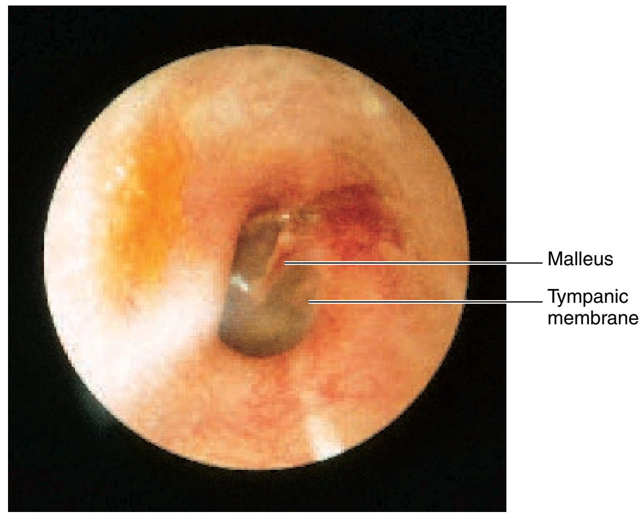
The laterally compressed **middle ear** is an air-filled chamber called the **tympanic cavity** in the petrous part of the temporal bone (see figs. 15.28 and 15.31). The tympanic membrane separates the middle ear from the external acoustic canal of the outer ear. A bony partition containing the **vestibular window** (*oval window*) and the **cochlear window** (*round window*) separates the middle ear from the inner ear.

There are two openings into the tympanic cavity. The **epitympanic recess** in the posterior wall connects the tympanic cavity to the **mastoidal air cells** within the mastoid process of the temporal bone. The **auditory** (eustachian) **tube** connects the tympanic cavity anteriorly with the nasopharynx and equalizes air pressure on both sides of the tympanic membrane.

Three **auditory ossicles** extend across the tympanic cavity from the tympanic membrane to the vestibular window (fig. 15.31). These tiny bones (the smallest in the body), from outer to inner, are the **malleus** *(mal′e-us)* (hammer), **incus** *(ing′kus)* (anvil), and **stapes** *(sta′pēz)* (stirrup). The auditory ossicles are attached to the wall of the tympanic cavity by ligaments. Vibrations of the tympanic membrane cause the auditory

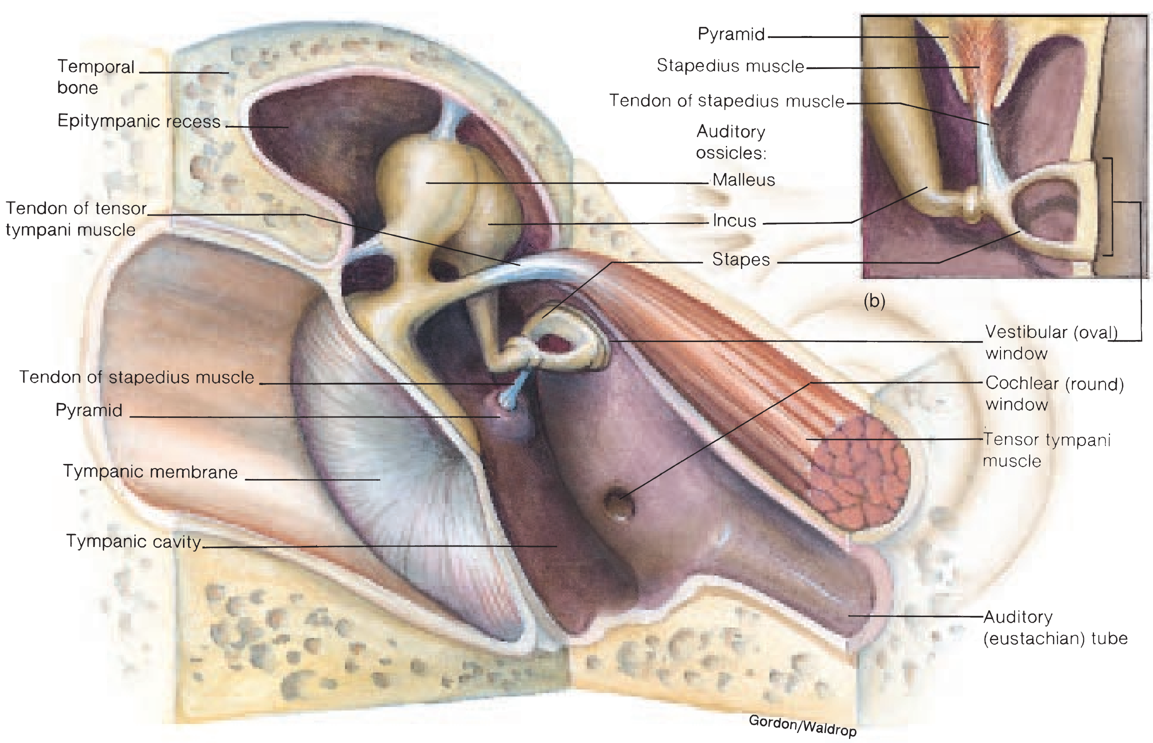
eustachian tube: from Bartolommeo E. Eustachio, Italian anatomist, 1520–74
malleus: L. *malleus*, hammer
incus: L. *incus*, anvil
stapes: L. *stapes*, stirrup

(a)



(b)

FIGURE 15.30 (*a*) A physician viewing the anatomy of the outer ear. (*b*) The appearance of the tympanic membrane as viewed with an otoscope.



(a)

FIGURE 15.31 (*a*) The auditory ossicles and associated structures within the tympanic cavity. (*b*) A rotated view of the stapes positioned against the vestibular window.

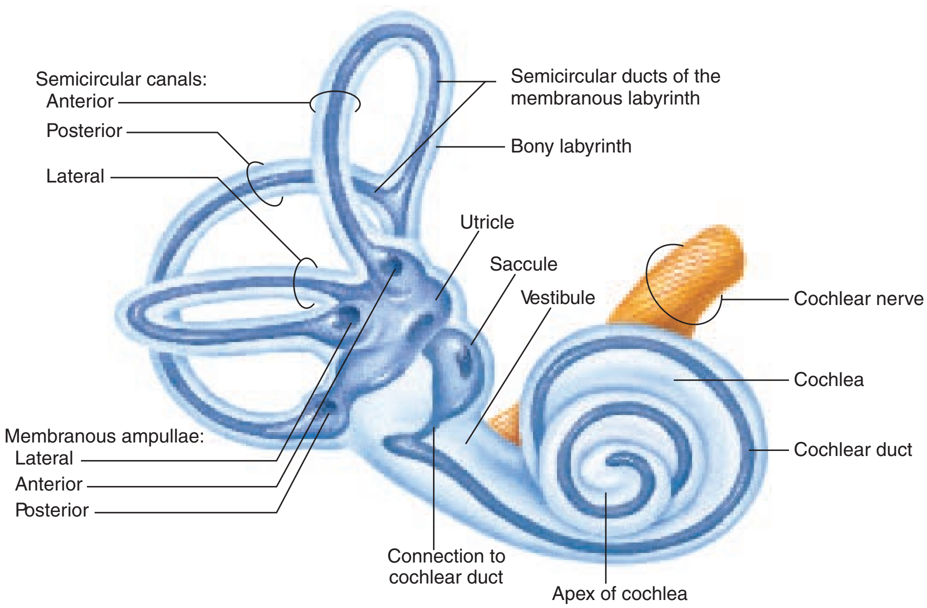


FIGURE 15.32 The labyrinths of the inner ear. The membranous labyrinth (darker color) is contained within the bony labyrinth. The principal structures of the inner ear are the cochlea for hearing and the vestibular organs (semicircular canals, utricle, and saccule) for balance and equilibrium.

ossicles to move and transmit sound waves across the tympanic cavity to the vestibular window. Vibration of the vestibular window moves a fluid within the inner ear and stimulates the receptors of hearing.

As the auditory ossicles transmit vibrations from the tympanic membrane, they act as a lever system to amplify sound waves. In addition, the sound waves are intensified as they are transmitted from the relatively large surface of the tympanic membrane to the smaller surface area of the vestibular window. The combined effect increases sound amplification about 20 times.

Two small skeletal muscles, the **tensor tympani** muscle and the **stapedius** muscle (fig. 15.31), attach to the malleus and stapes, respectively, and contract reflexively to protect the inner ear against loud noises. When contracted, the tensor tympani muscle pulls the malleus inward, and the stapedius muscle pulls the stapes outward. This combined action reduces the force of vibration of the auditory ossicles.

The mucous membranes that line the tympanic cavity, the mastoidal air cells, and the auditory tube are continuous with those of the nasopharynx. For this reason, infections that spread to the nose or throat may spread to the tympanic cavity and cause a middle-ear infection. They may also spread to the mastoidal air cells and cause *mastoiditis.* Forcefully blowing the nose advances the spread of the infection.

An equalization of air pressure on both sides of the tympanic membrane is important in hearing. When atmospheric pressure is reduced, as occurs when traveling to higher altitudes, the tympanic membrane bulges outward in response to the greater air pressure within the tympanic cavity. The bulging is painful and may impair hearing by reducing flexibility. The auditory tube, which is collapsed most of the time in adults, opens during swallowing or yawning and allows the air pressure on the two sides of the tympanic membrane to equalize.

Inner Ear

The entire structure of the **inner ear** is referred to as the **labyrinth** (*lab'ĭ-rinth*) The labyrinth consists of an outer shell of dense bone called the **bony labyrinth** that surrounds and protects a **membranous labyrinth** (fig. 15.32). The space between the bony labyrinth and the membranous labyrinth is filled with a fluid called *perilymph,* which is secreted by cells lining the bony canals. Within the tubular chambers of the membranous labyrinth is yet another fluid called *endolymph.* These two fluids provide a liquid-conducting medium for the vibrations involved in hearing and the maintenance of equilibrium.

The bony labyrinth is structurally and functionally divided into three areas: the *vestibule*, *semicircular canals*, and *cochlea*. The functional organs for hearing and equilibrium are located in these areas.

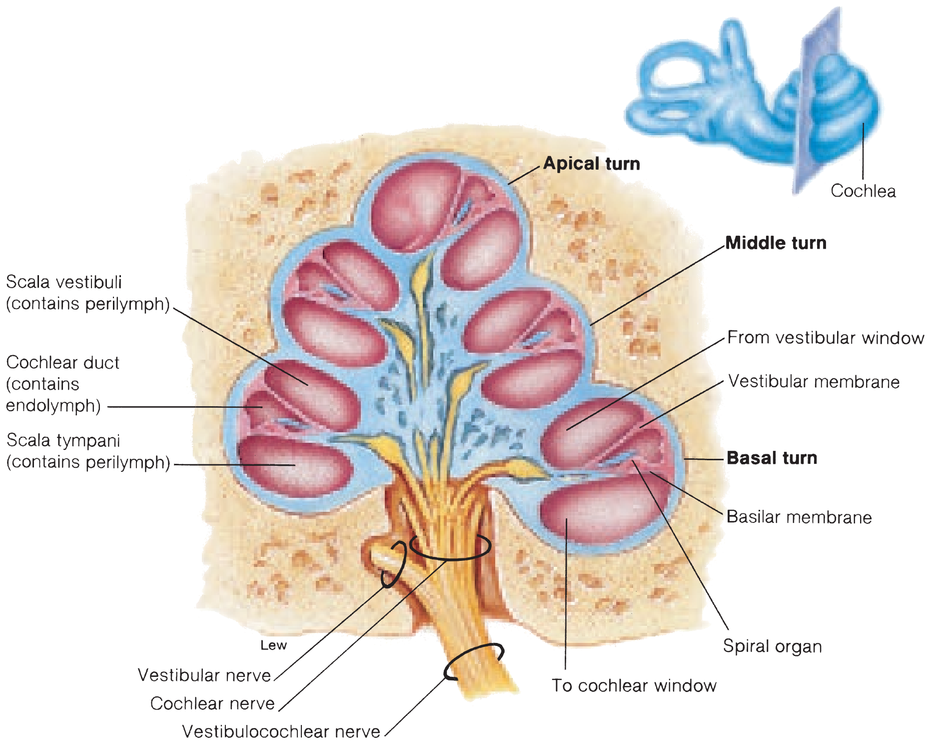


FIGURE 15.33 A coronal section of the cochlea showing its three turns (indicated in boldface type) and its three compartments—the scala vestibuli, cochlear duct, and scala tympani.

Vestibule

The vestibule is the central portion of the bony labyrinth. It contains the **vestibular** (oval) **window,** into which the stapes fits, and the **cochlear** (round) **window** on the opposite end (fig. 15.32).

The membranous labyrinth within the vestibule consists of two connected sacs called the **utricle** *(yoo'trĭ-kul)* and the **saccule** *(sak'yool)* The utricle is larger than the saccule and lies in the upper back portion of the vestibule. Both the utricle and saccule contain receptors that are sensitive to gravity and linear movement (acceleration) of the head.

Semicircular Canals

Posterior to the vestibule are the three bony semicircular canals, positioned at nearly right angles to each other. The thinner **semicircular ducts** form the membranous labyrinth within the semicircular canals (fig. 15.32). Each of the three semicircular ducts has a **membranous ampulla** *(am-pool'ă)* at one end and connects with the upper back part of the utricle. Receptors within the semicircular ducts are sensitive to angular acceleration and deceleration of the head, as in rotational movement.

Cochlea

The snail-shaped cochlea is coiled two and a half times around a central core of bone (fig. 15.33). There are three chambers in the cochlea (fig. 15.34). The upper chamber, the **scala** (*ska'lă*) **vestibuli,** begins at the vestibular window and extends to the apex (end) of the coiled cochlea. The lower chamber, the **scala tympani,** begins at the apex and terminates at the cochlear window. Both the scala vestibuli and the scala tympani are filled with perilymph. They are completely separated, except at the narrow apex of the cochlea, called the **helicotrema** (*hel''ĭ-kŏ-tre'mă*) where they are continuous (see fig. 15.36). Between the scala vestibuli and the scala tympani is the **cochlear duct,** the triangular middle chamber of the cochlea. The roof of the cochlear duct is called the **vestibular membrane,** and the floor is called the **basilar membrane.** The cochlear duct, which is filled with endolymph, ends at the helicotrema.

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cochlea: L. *cochlea*, snail shell

scala: Gk. *scala*, staircase

helicotrema: Gk. *helix*, a spiral; *crema*, a hole

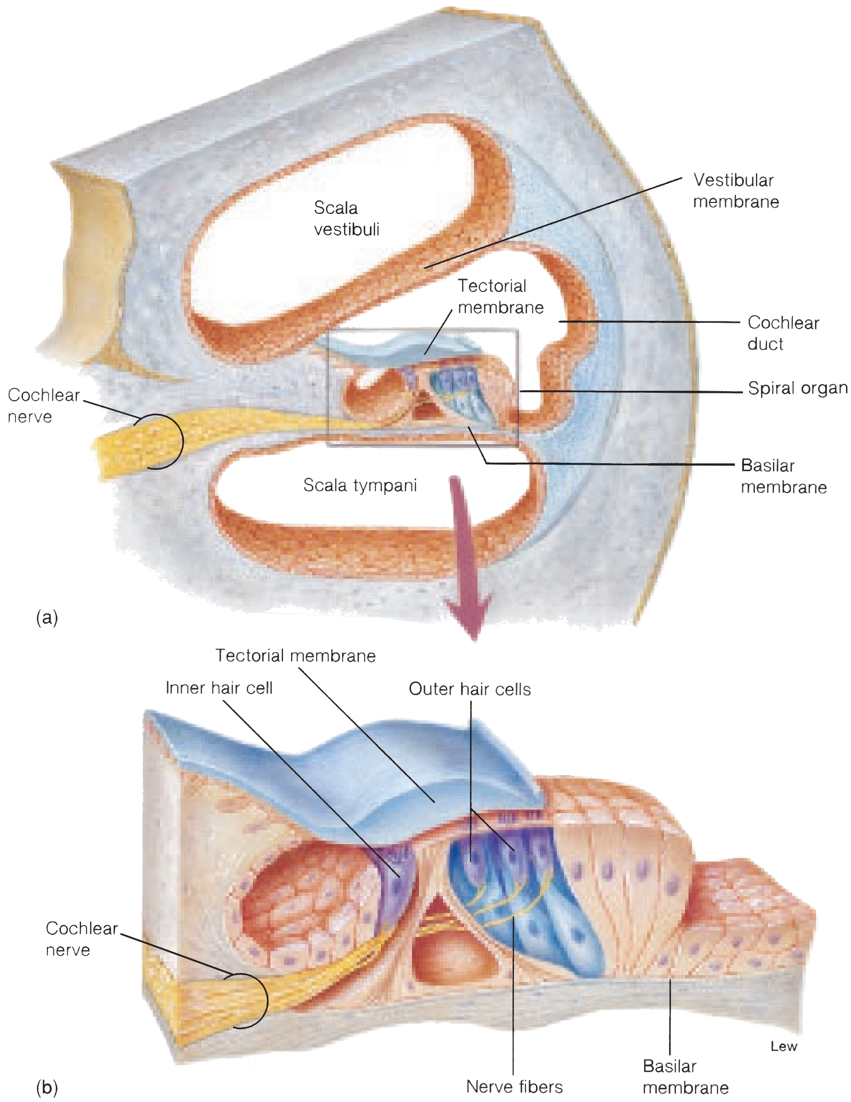

FIGURE 15.34 A section of the cochlea showing (*a*) the spiral organ within the cochlear duct and (*b*) the spiral organ in greater detail.

Within the cochlear duct is a specialized structure called the **spiral organ** (organ of Corti). The sound receptors that transform mechanical vibrations into nerve impulses are located along the basilar membrane of this structure, making it the functional unit of hearing. The epithelium of the spiral organ consists of supporting cells and hair cells (figs. 15.34 and 15.35). The bases of the hair cells are anchored in the basilar membrane, and their tips are embedded in the **tectorial membrane,** which forms a gelatinous canopy over them.

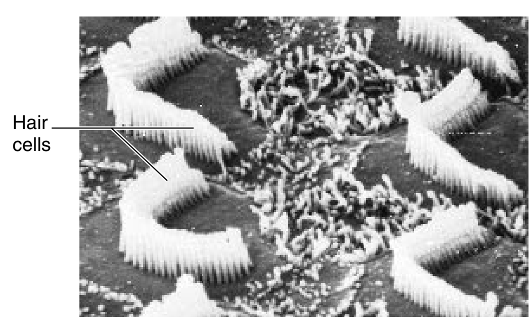

FIGURE 15.35 A scanning electron micrograph of the hair cells of the spiral organ.

organ of Corti; from Alfonso Corti, Italian anatomist. 1822–88.

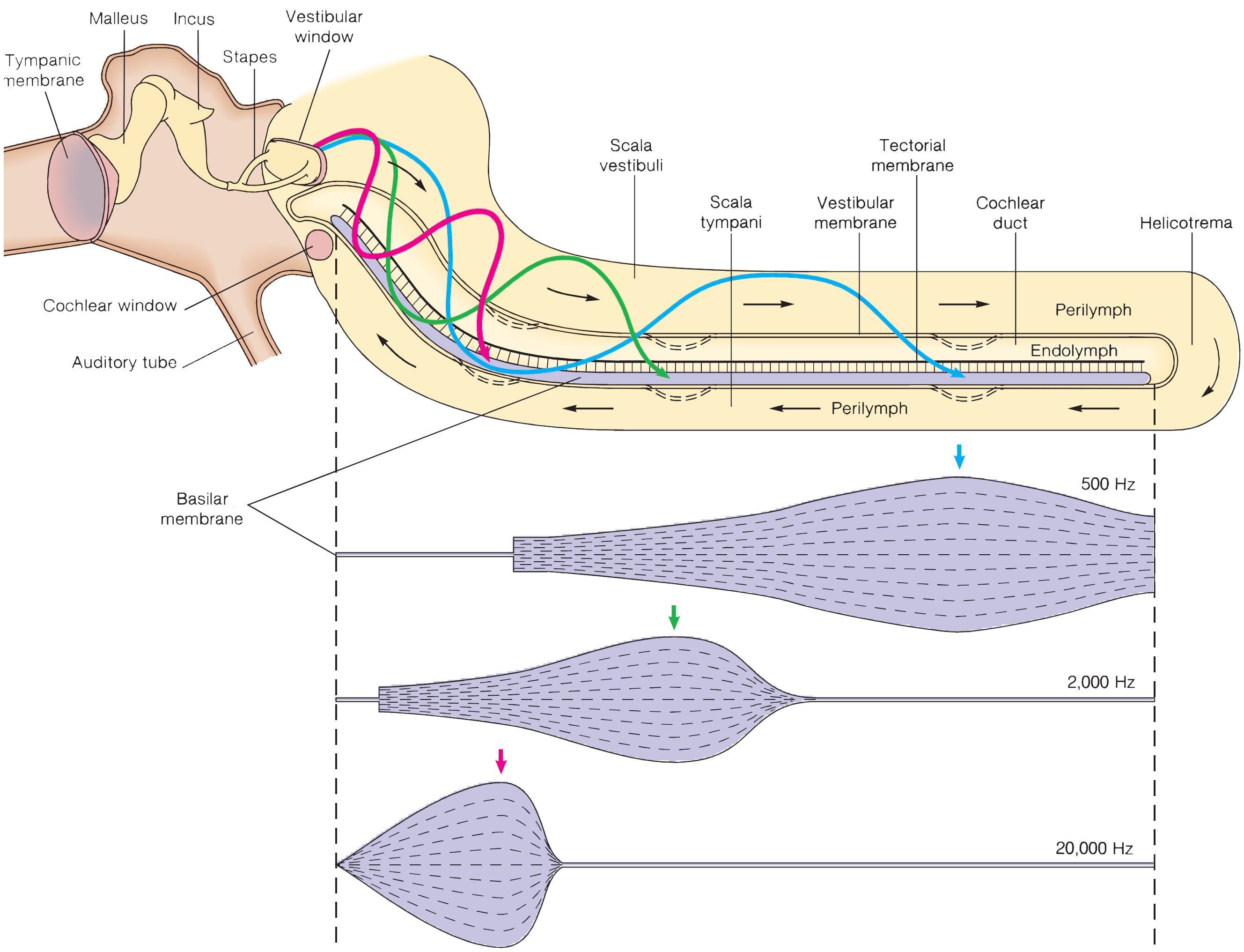

FIGURE 15.36 An illustration of the cochlea, straightened to show the mechanism of sound-wave generation at specific sites along the basilar membrane. The scala vestibuli and the scala tympani, which contain perilymph, are continuous at the helicotrema. The cochlear duct, which contains endolymph, separates the scala vestibuli and the scala tympani. Sounds of low frequency (blue arrow) cause pressure waves of perilymph to pass through the helicotrema and displace the basilar membrane near its apex. Sounds of medium frequency (green arrow) cause pressure waves to displace the basilar membrane near its center. Sounds of high frequency (red arrow) cause pressure waves to displace the basilar membrane near its base. (The frequency of sound waves is measured in hertz [H_z].)

Sound Waves and Neural Pathways for Hearing

Sound Waves

Sound waves travel in all directions from their source, like ripples in a pond after a stone is dropped. These waves of energy are characterized by their frequency and their intensity. The *frequency*, or number of waves that pass a given point in a given time, is measured in *hertz (Hz)*. The *pitch* of a sound is directly related to its frequency—the higher the frequency of a sound, the higher its pitch. For example, striking the high C on a piano produces a high frequency of sound that has a high pitch.

The *intensity*, or loudness of a sound, is directly related to the amplitude of the sound waves. Sound intensity is measured in units known as *decibels (dB)*. A sound that is barely audible—at the threshold of hearing—has an intensity of zero decibels. Every 10 decibels indicates a tenfold increase in sound intensity: a sound is 10 times higher than threshold at 10 dB, 100 times higher at 20 dB, a million times higher at 60 dB, and 10 billion times higher at 100 dB. The healthy human ear can detect very small differences in sound intensity—from 0.1 to 0.5 dB.

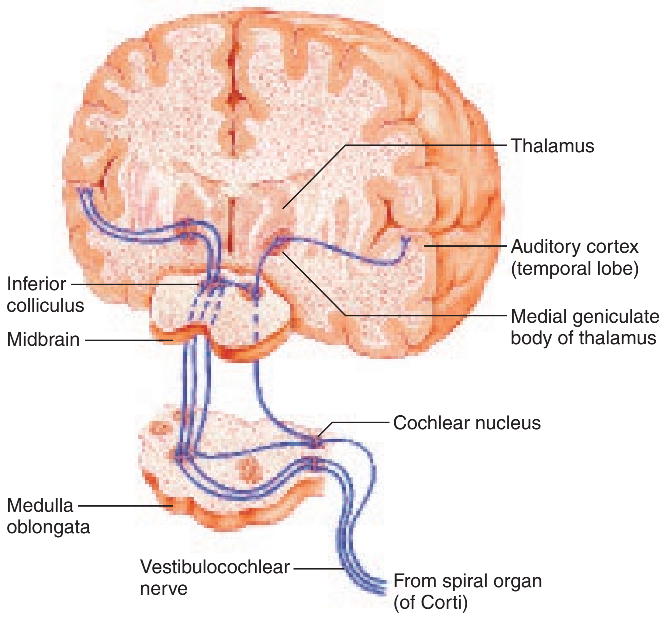

FIGURE 15.37 Neural pathways for the sense of hearing.

A snore can be as loud as 70 dB, as compared with 105 dB for a power mower. Frequent or prolonged exposure to sounds with intensities over 90 dB (including amplified rock music) can result in hearing loss.

Sound waves funneled through the external acoustic canal produce extremely small vibrations of the tympanic membrane. Movements of the tympanum during ordinary speech (with an average intensity of 60 dB) are estimated to be equal to the diameter of a molecule of hydrogen.

Sound waves passing through the solid medium of the auditory ossicles are amplified about 20 times as they reach the footplate of the stapes, which is seated within the vestibular window. As the vestibular window is displaced, pressure waves pass through the fluid medium of the scala vestibuli (fig. 15.36) and pass around the helicotrema to the scala tympani. Movements of perilymph within the scala tympani, in turn, displace the cochlear window into the tympanic cavity.

When the sound frequency (pitch) is sufficiently low, there is adequate time for the pressure waves of perilymph within the scala vestibuli to travel around the helicotrema to the scala tympani. As the sound frequency increases, however, these pressure waves do not have time to travel all the way to the apex of the cochlea. Instead, they are transmitted through the vestibular membrane, which separates the scala vestibuli from the cochlear duct, and through the basilar membrane, which separates the cochlear duct from the scala tympani, to the perilymph of the scala tympani. The distance that these pressure waves travel, therefore, decreases as the sound frequency increases.

Sounds of low pitch (with frequencies below about 50 Hz) cause movements of the entire length of the basilar membrane—from the base to the apex. Higher sound frequencies result in maximum displacement of the basilar membrane closer to its base, as illustrated in figure 15.36.

Displacement of the basilar membrane and hair cells by movements of perilymph causes the hair cell microvilli that are embedded in the tectorial membrane to bend. This stimulation excites the sensory cells, which causes the release of an unknown neurotransmitter that excites sensory endings of the cochlear nerve.

Neural Pathways for Hearing

Cochlear sensory neurons in the *vestibulocochlear nerve* (VIII) synapse with neurons in the medulla oblongata, which project to the inferior colliculi of the midbrain (fig. 15.37). Neurons in this area in turn project to the thalamus, which sends axons to the auditory cortex of the temporal lobe, where the auditory sensations (nerve impulses) are perceived as sound.

Mechanics of Equilibrium

Maintaining equilibrium is a complex process that depends on continuous input from sensory neurons in the vestibular organs of both inner ears. Although the vestibular organs are the principal source of sensory information for equilibrium, the photoreceptors of the eyes, tactile receptors within the skin, and

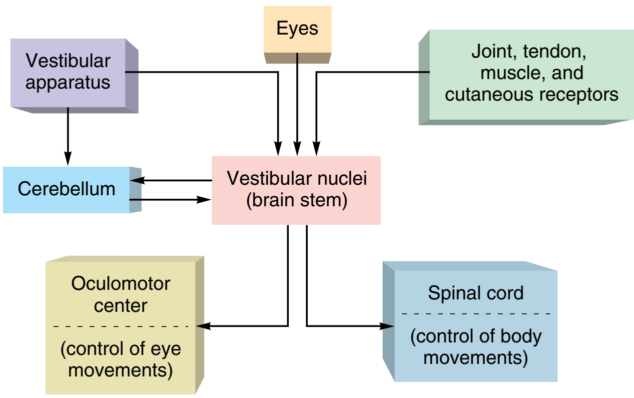

FIGURE 15.38 The neural processing involved in maintaining equilibrium and balance.

proprioceptors of tendons, muscles, and joints also provide sensory input that is needed to maintain equilibrium (fig. 15.38).

The vestibular organs provide the CNS with two kinds of receptor information. One kind is provided by receptors within the *saccule* and *utricle*, which are sensitive to gravity and to linear acceleration and deceleration of the head, as occur when riding in a car. The other is provided by receptors within the *semicircular ducts*, which are sensitive to rotational movements, as occur when turning the head, spinning, or tumbling.

The receptor hair cells of the vestibular organs contain 20 to 50 microvilli and one cilium, called a **kinocilium** (*ki''no-sil'e-um*) (fig. 15.39). When the hair cells are displaced in the direction of the kinocilium, the cell membrane is depressed and becomes depolarized. When the hair cells are displaced in the opposite direction, the membrane becomes hyperpolarized.

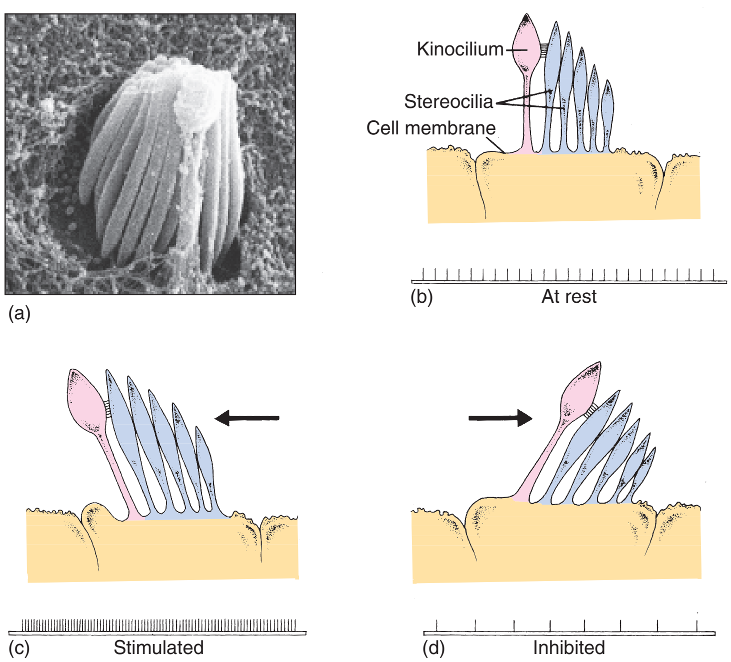

FIGURE 15.39 Sensory hair cells of a vestibular organ. (*a*) A scanning electron photomicrograph of a kinocilium. (*b*) Sensory hairs (microvilli) and one kinocilium. (*c*) When hair cells are bent in the direction of the kinocilium, the cell membrane is depressed (see arrow) and the sensory neuron innervating the hair cell is stimulated. (*d*) When the hairs are bent in the opposite direction, the sensory neuron is inhibited.

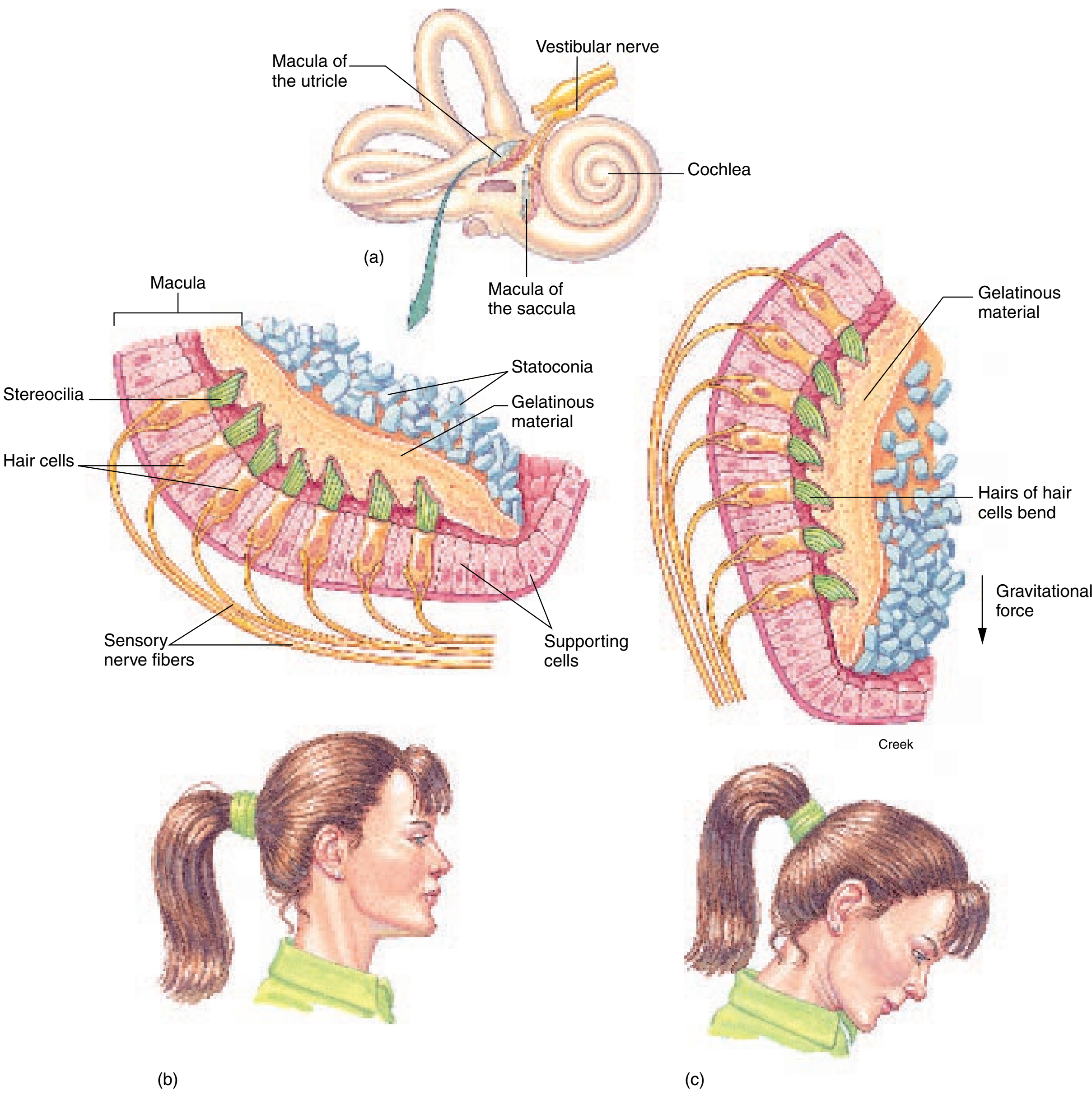

FIGURE 15.40 (*a*) Maculae of the inner ear. (*b*) When the head is upright, the weight of the statoconia applies direct pressure to the sensitive cytoplasmic extensions of the hair cells. (*c*) As the head is tilted forward, the extensions of the hair cells bend in response to gravitational force and cause the hair cells to be stimulated.

Saccule and Utricle

Receptor hair cells of the saccule and utricle are located in a small, thickened area of the walls of these organs called the **macula** (*mak'yoo-lă*) (fig. 15.40). Cytoplasmic extensions of the hair cells project into a gelatinous mass, called the **statoconial** (otolithic) **membrane,** that supports microscopic crystals of calcium carbonate called **statoconia** (otoliths). The statoconia increase the weight of the statoconial membrane, which results in a higher *inertia* (resistance to change in movement).

When a person is upright, the hairs of the utricle project vertically into the statoconial membrane, whereas those of the saccule project horizontally. During forward acceleration, the statoconial membrane lags behind the hair cells, so the hair cells of the utricle are bent backward. This is similar to the backward

macula: L. *macula*, spot

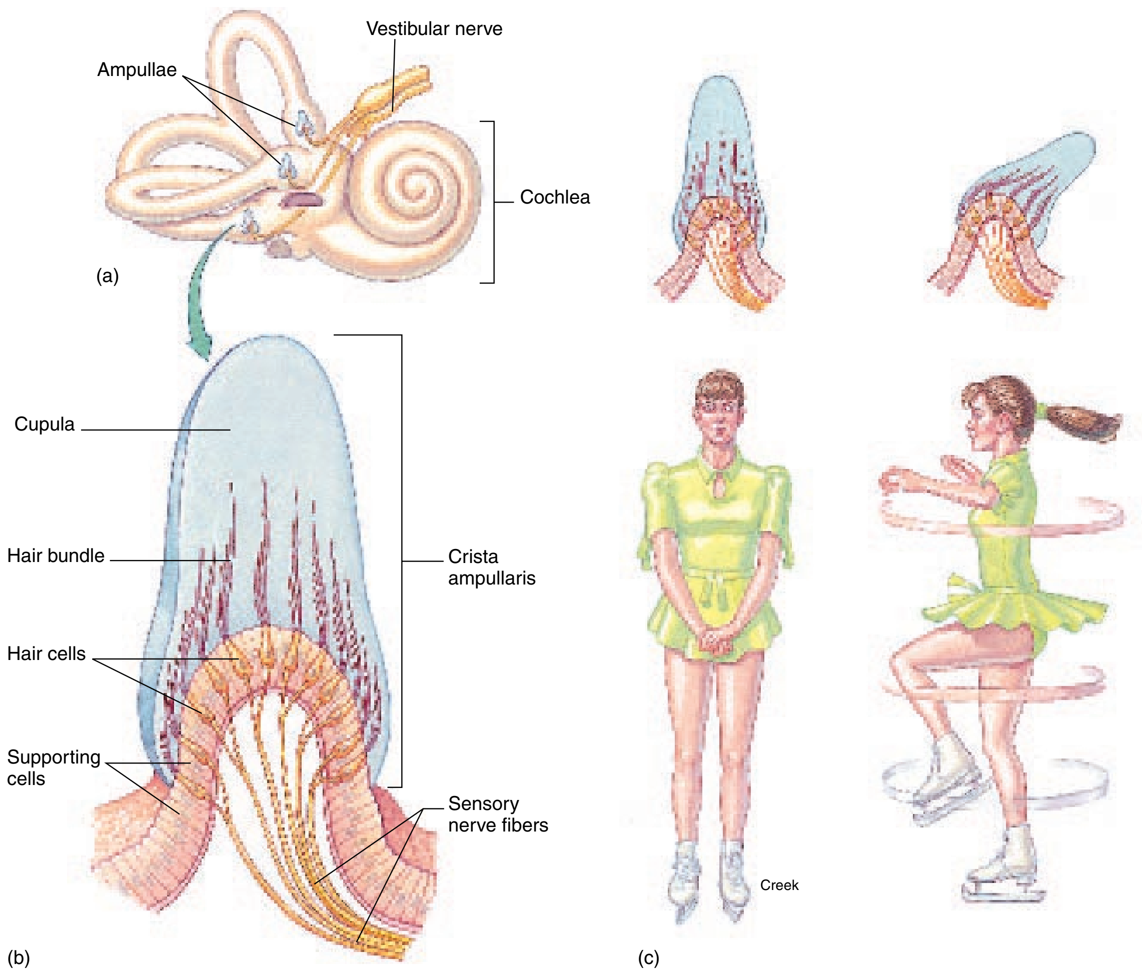

FIGURE 15.41 (*a*) Ampullae within the inner ear. (*b*) A crista ampullaris within an ampulla. (*c*) Movement of the endolymph during rotation causes the cupula to displace, thus stimulating the hair cells.

thrust of the body when a car accelerates rapidly forward. The inertia of the statoconial membrane similarly causes the hair cells of the saccule to be pushed upward when a person jumps from a raised platform. Thus, because of the orientation of their hair cell processes, the utricle is more sensitive to horizontal acceleration, and the saccule is more sensitive to vertical acceleration. The changed pattern of action potentials in sensory nerve fibers that results from stimulation of the hair cells allows us to maintain our equilibrium with respect to gravity during linear acceleration.

Sensory impulses from the vestibular organs are conveyed to the brain by way of the vestibular nerve, a component of the vestibulocochlear nerve.

Semicircular Canals

Receptors of the semicircular canals are contained within the ampulla at the base of each semicircular duct. An elevated area of the ampulla called the **crista ampullaris** (*am''poo-lar'is*) contains numerous hair cells and supporting cells (fig. 15.41). Like the saccule and utricle, the hair cells have cytoplasmic extensions that project into a dome-shaped gelatinous mass called the **cupula** (*ky-oop'loo-lă*). When the hair cells within the cupula are bent by rapid displacement of the fluid within the semicircular ducts, as in spinning around, sensory impulses travel to the brain by way of the vestibular nerve.

Neural Pathways

Stimulation of the hair cells in the vestibular apparatus activates the sensory neurons of the vestibular nerve. These fibers transmit impulses through the vestibulocochlear nerve to the cerebellum and to the vestibular nuclei of the medulla oblongata. The vestibular nuclei, in turn, send fibers to the oculomotor center of

cupula: L. *cupula*, cup-shaped

the brain stem and to the spinal cord. Neurons in the oculomotor center control eye movements, and neurons in the spinal cord stimulate movements of the head, neck, and limbs. Movements of the eyes and body produced by these pathways serve to maintain balance and track the visual field during rotation.

The dizziness and nausea that some people experience when they spin rapidly is explained by the activity occurring within the vestibular organs. When a person first begins to spin, the inertia of the endolymph within the semicircular ducts causes the cupula to bend in the opposite direction. As the spin continues, however, the endolymph and the cupula will eventually be moving in the same direction and at the same speed. If movement is suddenly stopped, the greater inertia of the endolymph causes it to continue moving in the direction of spin and to bend the cupula in that direction.

Bending of the cupula after movement has stopped affects muscular control of the eyes and body. The eyes slowly drift in the direction of the previous spin, and then are rapidly jerked back to the midline position, producing involuntary movements called *postrotatory vestibular nystagmus (ni-stag'mus).* People experiencing this effect may feel that they are spinning, or that the room is. The loss of equilibrium that results is called *vertigo.* If the vertigo is sufficiently severe, or if the person is particularly susceptible, the autonomic nervous system may become involved. This can produce dizziness, pallor, sweating, and nausea.

Knowledge Check

19. List the structures of the outer ear, middle ear, and inner ear and explain the function of each as related to hearing.
20. Use a flow chart to describe how sound waves in air within the external acoustic canal are transduced into movements of the basilar membrane.
21. Explain how movements of the basilar membrane can code for different sound frequencies (pitches).
22. Explain how the vestibular organs maintain a sense of balance and equilibrium.

CLINICAL CONSIDERATIONS

Numerous disorders and diseases afflict the sensory organs. Some of these occur during the sensitive period of prenatal development; others, some of which are avoidable, can occur at any time of life. Still other sensory impairments are the result of changes associated with the natural aging process. The loss of a sense frequently involves a traumatic adjustment. Fortunately, however, when a sensory function is impaired or lost, the other senses seem to become keener to lessen the extent of the handicap. A blind person, for example, compensates somewhat for the loss of sight by developing a remarkable hearing ability.

Entire specialties of medicine are devoted to specific sensory organs. It is beyond the scope of this text to attempt a comprehensive discussion of the numerous diseases and dysfunctions of these organs. Some general comments will be made, however, on the diagnosis of sensory disorders and on developmental problems that can affect the eyes and ears. In addition, the more common diseases and dysfunctions of the eyes and ears are noted.

Diagnosis of Eye and Ear Disorders

Eye

There are two distinct professional specialties concerned with the structure and function of the eye. *Optometry* is the paramedical profession concerned with assessing vision and treating visual problems. An *optometrist* prescribes corrective lenses or visual training but is not a medical doctor and does not treat eye diseases. *Ophthalmology (of''thal-mol'ŏ-je)* is the specialty of medicine concerned with diagnosing and treating eye diseases.

Although the eyeball is an extremely complex organ, it is quite accessible to examination. The following devices are frequently employed: (1) a *cycloplegic drug,* which is instilled into the eyes to dilate the pupils and temporarily inactivate the ciliary muscles; (2) a *Snellen's chart,* which is used to determine the visual acuity of a person standing 20 feet from the chart (a reading of 20/20 is considered normal for the test); (3) an *ophthalmoscope,* which contains a light, mirrors, and lenses to illuminate and magnify the interior of the eyeball so that the structures within may be examined; and (4) a *tonometer,* which is used to measure ocular tension, important in detecting glaucoma.

Ear

Otorhinolaryngology (o''to-ri''no-lar''in-gol'ŏ-je) is the specialty of medicine dealing with the diagnosis and treatment of diseases or conditions of the ear, nose, and throat. *Audiology* is the study of hearing, particularly assessment of the ear and its functioning.

There are three common instruments or techniques used to examine the ears to determine auditory function: (1) an *otoscope* is an instrument used to examine the tympanic membrane of the ear (abnormalities of this membrane are informative when diagnosing specific auditory problems, including middle-ear infections); (2) *tuning fork tests* are useful in determining hearing acuity and especially for discriminating the various kinds of hearing loss; and (3) *audiometry* is a functional examination for hearing sensitivity and speech discrimination.

Developmental Problems of the Eyes and Ears

Although there are many congenital abnormalities of the eyes and ears, most of them are rare. For these organs, the sensitive period of development is between 24 and 45 days after conception. Indeed, 85% of newborns suffer anomalies if infected during this interval. Most congenital disorders of the eyes and ears are caused by genetic factors or intrauterine infections such as *rubella virus.*

Snellen's chart: from Herman Snellen, Dutch ophthalmologist, 1834–1908

Developmental Exposition

The Ear

EXPLANATION

The ear begins to develop at the same time as the eye, early during the fourth week. All three embryonic germ layers—ectoderm, mesoderm, and endoderm—are involved in the formation of the ear. Both types of ectoderm (neuroectoderm and surface ectoderm) play a role.

The ear of an adult is structurally and functionally divided into an **outer ear,** a **middle ear,** and an **inner ear,** each of which has a separate embryonic origin. The inner ear does not develop from deep embryonic tissue as one might expect, but rather be-

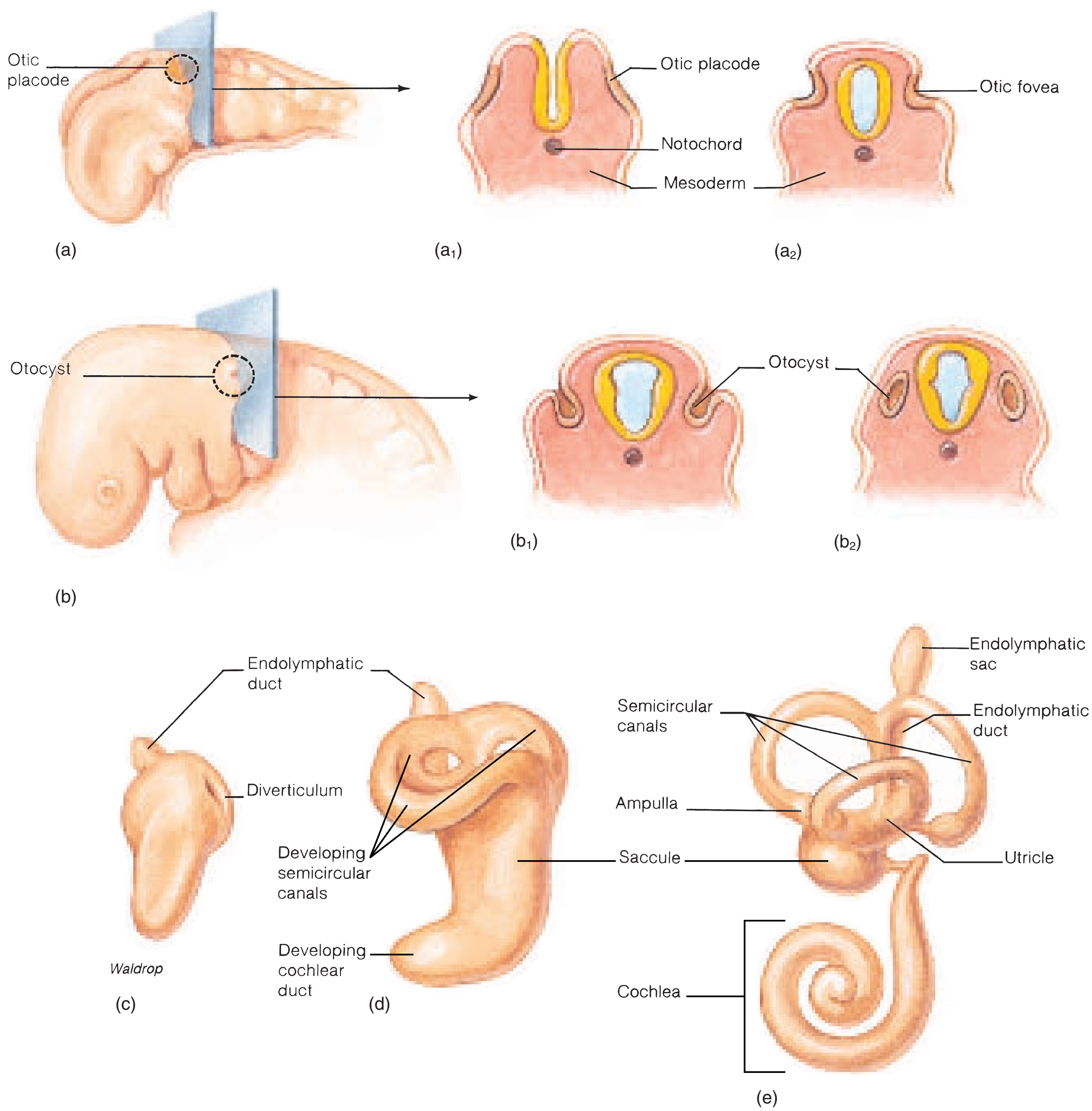

EXHIBIT II The development of the inner ear. (*a*) A lateral view of a 22-day-old embryo showing the position of a transverse cut through the otic placode. (a_1) The olic placode of surface ectoderm begins to invaginate at 22 days. (a_2) By 24 days, a distinct otic fovea has formed and the neural ectoderm is positioned to give rise to the brain, (*b*) A lateral view of a 28-day-old embryo showing the position of a transverse cut through the otocyst. (b_1) By 28 days, the otic fovea has become a distinct otocyst, (b_2) The otocyst is in position in the 30-day-old embryo, where it gives rise to the structures of the inner ear. (*c–e*) Lateral views of the differentiating otocyst into the cochlea and semicircular canals from the fifth to the eight week.

gins to form early in the fourth week when a plate of surface ectoderm called the **otic** (*o'tik*) **placode** appears lateral to the developing hindbrain (Ex. 15.2). The otic placode soon invaginates and forms an **otic fovea.** Toward the end of the fourth week, the outer edges of the invaginated otic fovea come together and fuse to form an **otocyst.** The otocyst soon pinches off and separates from the surface ectoderm. The otocyst further differentiates to form a dorsal **utricular portion** and a ventral **saccular portion.** Three separate diverticula extend outward from the utricular portion and develop into the **semicircular canals,** which later function in balance and equilibrium. A tubular diverticulum called the **cochlear duct** extends in a coiled fashion from the saccular portion and forms the membranous portion of the **cochlea** of the ear (exhibit II). The **spiral organ,** which is the functional portion of the cochlea, differentiates from cells along the wall of the cochlear duct (Ex. 15.3). The sensory nerves that innervate the inner ear are derived from neuroectoderm from the developing brain.

The differentiating otocyst is surrounded by mesodermal tissue that soon forms a cartilaginous **otic capsule** (exhibit III). As the otocyst and surrounding otic capsule grow, vacuoles containing the fluid **perilymph** form within the otic capsule. The vacuoles soon enlarge and coalesce to form the **perilymphatic space,** which divides into the **scala tympani** and the **scala vestibuli.** Eventually, the cartilaginous otic capsule ossifies to form the **bony** (osseous) **labyrinth** of the inner ear. The middle-ear chamber is referred to as the **tympanic cavity** and derives from the first pharyngeal pouch (exhibit IV). The **auditory ossicles,** which amplify incoming sound waves, derive from the first and second pharyngeal arch cartilages. As the tympanic cavity enlarges, it surrounds and encloses the developing ossicles (exhibit IV). The connection of the tympanic cavity to the pharynx gradually elongates to develop into the **auditory** (eustachian) **tube,** which remains patent throughout life and is important in maintaining an equilibrium of air pressure between the pharyngeal and tympanic cavities.

The outer ear includes the fleshy **auricle** attached to the side of the head and the tubular **external acoustic canal** that extends into the external acoustic meatus of the temporal bone of the skull. The external acoustic canal forms from the surface ectoderm that covers the dorsal end of the first branchial groove (Ex. 15.4). A solid epithelial plate called the **meatal plug** soon develops at the bottom of the funnel-shaped branchial groove. The meatal plug is involved in the formation of the inner wall of the external acoustic canal and contributes to the **tympanic membrane** (eardrum). The tympanic membrane has a dual origin from surface ectoderm and the endoderm lining the first pharyngeal pouch (exhibit IV).

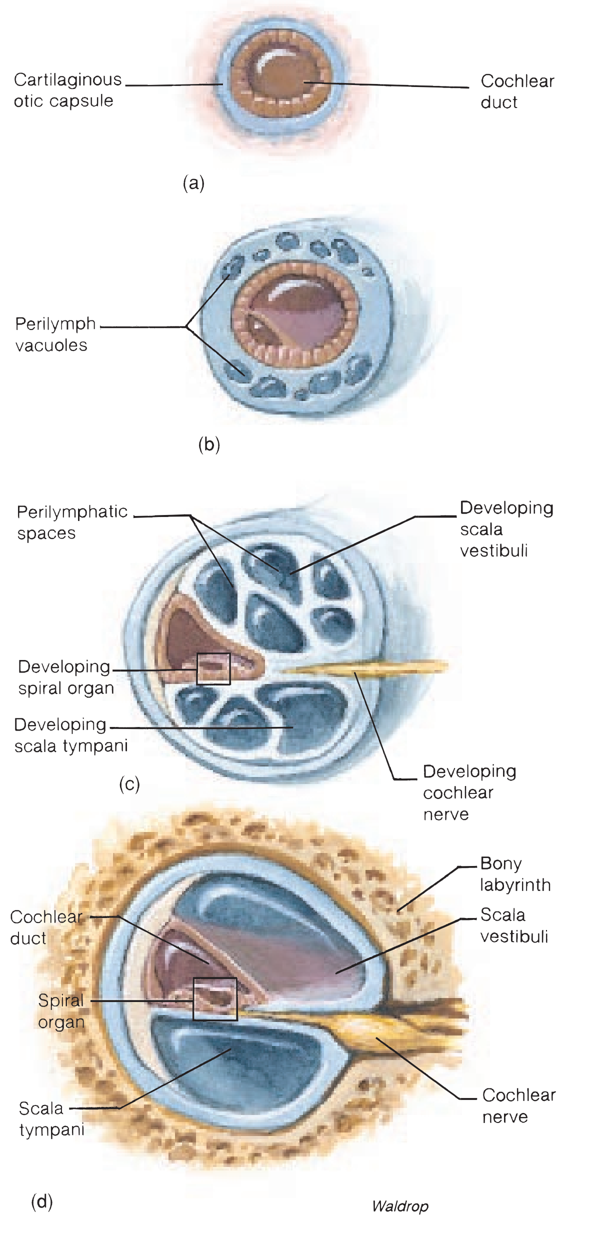

EXHIBIT III The formation of the cochlea and the spiral organ from the otic capsule. (*a–d*). Successive stages of development of the perilymphatic space and the spiral organ from the eighth to the twentieth week.

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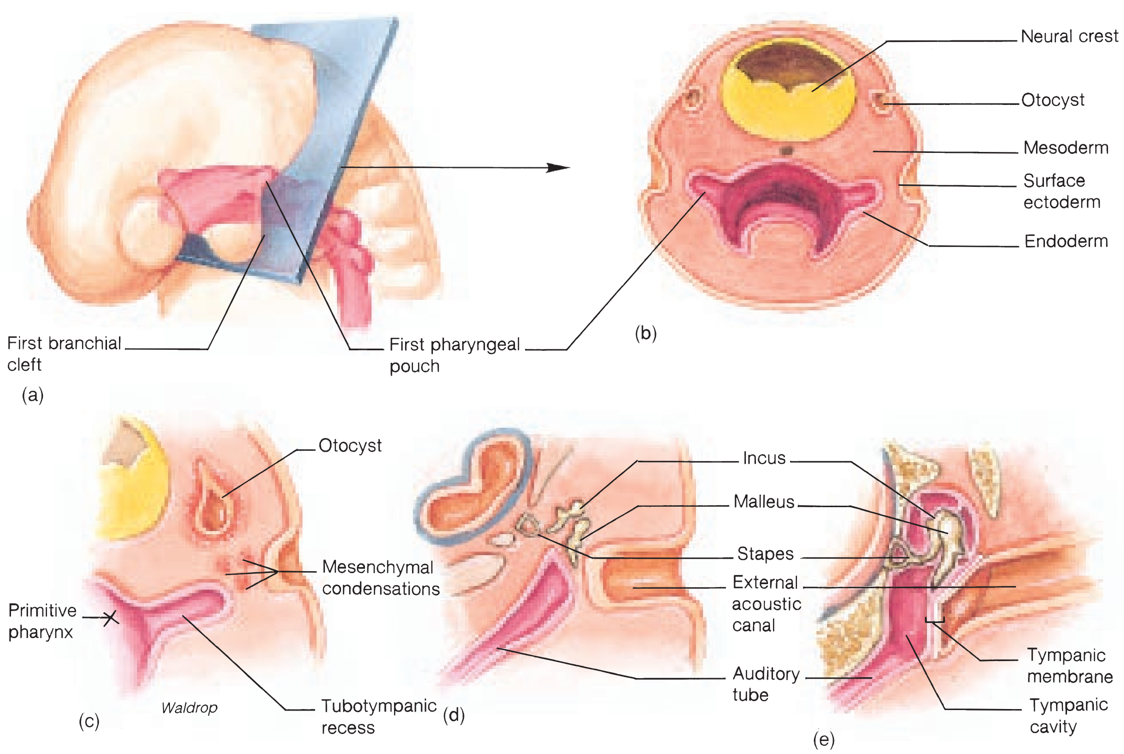


EXHIBIT IV The development of the outer- and middle-ear regions and the auditory ossicles (malleus, incus, and stapes). (*a*) A lateral view of a 4-week-old embryo showing the position of the cut depicted in the sequential development (*b–e*) (*b*) The embryo at 4 weeks illustrating the invagination of the surface ectoderm and the evagination of the endoderm at the level of the first pharyngeal pouch. (*c*) During the fifth week, mesenchymal condensations are apparent, from which the auditory ossicles will be derived. (*d*) Further invagination and evagination at 6 weeks correctly position the structures of the outer- and middle-ear regions. (*e*) By the end of the eighth week, the auditory ossicles, tympanic membrane, auditory tube, and external acoustic canal have formed.

If a pregnant woman contracts rubella (German measles), there is a 90% probability that the embryo or fetus will contract it also. An embryo afflicted with rubella is 30% more likely to be aborted, stillborn, or congenitally deformed than one that is not afflicted. Rubella interferes with the mitotic process, and thus causes underdeveloped organs. An embryo with rubella may suffer from a number of physical deformities, including *cataracts* and *glaucoma,* which are common deformities of the eye.

Eye

Most **congenital cataracts** are hereditary, but they may also be caused by maternal rubella infection during the critical fourth to sixth week of eye development. In this condition, the lens is opaque and frequently appears grayish white.

Cyclopia (*si-klo'pe-ă*) is a rare condition in which the eyes are partially fused into a median eye enclosed by a single orbit. Other severe malformations, which are incompatible with life, are generally expressed with this condition.

Ear

Congenital deafness is generally caused by an autosomal recessive gene but may also be caused by a maternal rubella infection. The actual functional impairment is generally either a defective set of auditory ossicles or improper development of the neurosensory structures of the inner ear.

Although the shape of the auricle varies widely, **auricular abnormalities** are not uncommon, especially in infants with chromosomal syndromes causing mental deficiencies. In addition, the external acoustic canal frequently does not develop in these children, producing a condition called **atresia** (*ă-tre′se-ă*) of the external acoustic canal.

Functional Impairments of the Eye

Few people have perfect vision. Slight variations in the shape of the eyeball or curvature of the cornea or lens cause an imperfect focal point of light rays onto the retina. Most variations are slight, however, and the error of refraction goes unnoticed. Severe deviations that are not corrected may cause blurred vision, fatigue, chronic headaches, and depression.

The primary clinical considerations associated with defects in the refractory structures or general shape of the eyeball are myopia, hyperopia, presbyopia, and astigmatism. **Myopia** (nearsightedness) is an elongation of the eyeball. As a result, light rays focus at a point in the vitreous humor in front of the retina (fig. 15.42). Only light rays from close objects can be focused clearly on the retina; distant objects appear blurred, hence the common term nearsightedness. **Hyperopia** (farsightedness) is a condition in which the eyeball is too short, which causes light rays to be brought to a focal point behind the retina. Although visual accommodation aids a hyperopic person, it generally does not help enough for the person to clearly see very close or distant objects. **Presbyopia** (*prez-be-o′pe-ă*) is a condition in which the lens tends to lose its elasticity and ability to accommodate. It is relatively common in people over 50 years of age. In order to read print on a page, a person with presbyopia must hold the page farther from the eyes than the normal reading distance. **Astigmatism** is a condition in which an irregular curvature of the cornea or lens of the eye distorts the refraction of light rays. If a person with astigmatism views a circle, the image will not appear clear in all 360 degrees; the part of the circle that appears blurred can be used to map the astigmatism.

Various glass or plastic lenses are generally prescribed for people with the visual impairments just described. Myopia may be corrected with a biconcave lens; hyperopia with a biconvex lens; and presbyopia with bifocals, or a combination of two lenses adjusted for near and distant vision. Correction for astigmatism requires a careful assessment of the irregularities and a prescription of a specially ground corrective lens.

As an alternative to a concave lens, a surgical procedure called **radial keratotomy** (*ker-ă-tot′ŏ-me*) is sometimes used to treat moderate myopia. In this technique, 8 to 16 microscopic slashes, like the spokes of a wheel, are made in the cornea from the center to the edge. The ocular pressure inside the eyeball bulges the weakened cornea and flattens its center, changing the focal length of the eyeball. In a relatively new laser surgery called **photorefractive keratectomy** (*ker-ă-tek′tŏ-me*) the cornea is flattened by vaporizing microscopic slivers from its surface.

myopia: Gk. *myein*, to shut; *ops*, eye
hyperopia: Gk. *hyper*, over; *ops*, eye
presbyopia: Gk. *presbys*, old man; *ops*, eye
astigmatism: Gk. *a*, without; *stigma*, point

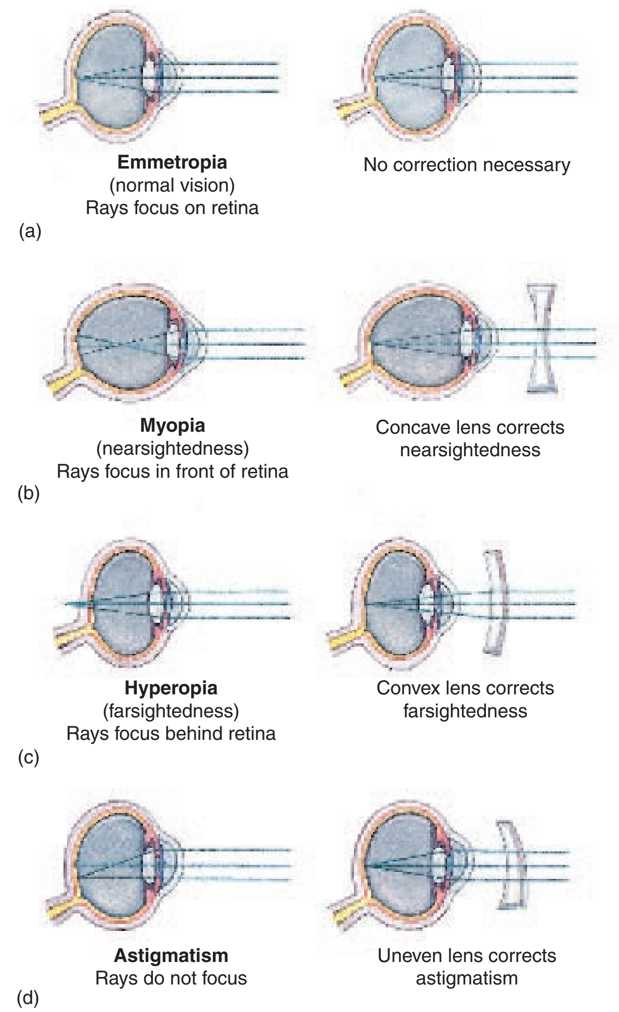


FIGURE 15.42 In a normal eye (*a*), parallel rays of light are brought to a focus on the retina by refraction in the cornea and lens. If the eye is too long, as in myopia (*b*), the focus is in front of the retina. This can be corrected by a concave lens. If the eye is too short, as in hyperopia (*c*), the focus is behind the retina. This is corrected by a convex lens. In astigmatism (*d*), light refraction is uneven because of an abnormal shape of the cornea or lens.

Cataracts

A cataract is a clouding of the lens that leads to a gradual blurring of vision and the eventual loss of sight. A cataract is not a growth within or upon the eye, but rather a chemical change in the protein of the lens. It is caused by injury, poisons, infections, or age degeneration. Recent evidence indicates that even excessive UV light may cause cataracts.

Cataracts are the leading cause of blindness. A cataract can be removed surgically, however, and vision restored by implanting

cataract: Gk. *katarrhegnynai*, to break down a tiny intraocular lens that either clips to the iris or is secured into the vacant lens capsule. Special contact lenses or thick lenses for glasses are other options.

Retinal Damage

Retinal detachment is a separation of the nervous or visual layer of the retina from the underlying pigment epithelium. It generally begins as a minute tear in the retina that gradually extends as vitreous fluid accumulates between the layers. Retinal detachment may result from hemorrhage, a tumor, degeneration, or trauma from a violent blow to the eye. A detached retina may be repaired by using laser beams, cryoprobes, or intense heat to destroy the tissue beneath the tear and rejoin the layers.

Bright sunlight or reflection from snow may be damaging to the retinae. Protective features include the eyelashes that disperse sunlight and the pigmented irises that absorb sunlight and reflexively constrict in bright light to narrow the diameter of the pupils. In addition, squinting in bright sunlight limits the amount of light entering the eyes.

Historically, certain groups of people dealt with bright sunlight problems in a number of ways. For example, Eskimos carved wooden eye masks with narrow slits to look through, and Tibetans wove sun visors from fine horsehair. Tinted lenses were available in the United States in the early 19th century, but it was not until the end of the First World War that sunglasses were developed by the U.S. Army Air Corps as a way to help pilots deal with high-altitude glare. The raybands and multicolored polarized lenses of today provide eye protection while displaying a style.

Macular Degeneration

Another retinal disorder, macular degeneration, is common after age 70, but its cause is not fully known. It occurs when the blood supply to the macular area of the retina is reduced, often eventually resulting in hemorrhages, or when other fluid collects in this area, reducing central vision sharpness. People with macular degeneration retain peripheral vision, but have difficulty focusing on an object directly in front of them. A simple home test called the *Amsler grid* can be used to detect this disorder in its early stages.

Strabismus

Strabismus is a condition in which both eyes do not focus on the same axis of vision. This prevents stereoscopic vision, and results in varied visual impairments. Strabismus is usually caused by a weakened extrinsic eye muscle.

Strabismus is assessed while the patient attempts to look straight ahead. If the afflicted eye is turned toward the nose, the condition is called convergent strabismus (**esotropia**). If the eye is turned outward, it is called divergent strabismus (**exotropia**). Disuse of the afflicted eye causes a visual impairment called **amblyopia.** Visual input from the normal eye and the eye with strabismus results in **diplopia** (*dip-lo′pe-ă*), or double vision. A normal, healthy person who has overindulged in alcoholic beverages may experience diplopia.

Infections and Diseases of the Eye

Infections

Infections and inflammation can occur in any of the accessory structures of the eye or in structures within or on the eyeball itself. The causes of infections are usually microorganisms, mechanical irritation, or sensitivity to particular substances.

Conjunctivitis (inflammation of the conjunctiva) may result from sensitivity to light, allergens, or an infection caused by viruses or bacteria. Bacterial conjunctivitis is commonly called "pinkeye."

Keratitis (inflammation of the cornea) may develop secondarily from conjunctivitis or be caused by such diseases as tuberculosis, syphilis, mumps, or measles. Keratitis is painful and may cause blindness if untreated.

A **chalazion** (*kă-la′ze-on*) is a tumor or cyst on the eyelid that results from infection of the tarsal glands and a subsequent blockage of the ducts of these glands.

A **sty (hordeola)** is a relatively common mild infection of the follicle of an eyelash or the sebaceous gland of the follicle. A sty may easily spread from one eyelash to another if untreated. Poor hygiene and the excessive use of cosmetics may contribute to its development.

Diseases

Trachoma (*tră-ko′mă*) is a highly contagious bacterial disease of the conjunctiva and cornea. Although rare in the United States, it is estimated that over 500 million people are afflicted with this disease. Trachoma responds well to treatment with sulfonamides and some antibiotics, but if untreated it will spread progressively until it covers the cornea. At this stage, vision is lost and the eye undergoes degenerative changes.

Glaucoma (*glau-ko′mă*) is the second leading cause of blindness and is particularly common in underdeveloped countries. Although it can afflict individuals of any age, 95% of the cases involve people over the age of 40. Glaucoma is characterized by an abnormal increase in the intraocular pressure of the eyeball. Aqueous humor does not drain through the scleral venous sinuses as quickly as it is produced. Accumulation of fluid causes compression of the blood vessels in the eyeball and compression of the optic nerve. Retinal cells die and the optic nerve may atrophy, producing blindness.

Infections, Diseases, and Functional Impairments of the Ear

Disorders of the ear are common and may affect both hearing and the vestibular functions. The ear is subject to numerous infections and diseases—some of which can be prevented.

Amsler grid: from Marc Amsler, Swiss opthalmologist, 1891–1968
amblyopia: Gk. *amblys,* dull; *ops,* vision
glaucoma: Gk. *glaukos,* gray

FIGURE 15.43 An implanted ventilation tube in the tympanic membrane following a myringotomy.

Infections and Diseases

External otitis (*o-ti′tis*) is a general term for infections of the outer ear. The causes of external otitis range from dermatitis to fungal and bacterial infections.

Acute purulent otitis media is a middle-ear infection. Pathogens that cause this disease usually enter through the auditory tube, often following a cold or tonsillitis. Children frequently have middle-ear infections because of their susceptibility to infections and their short and straight auditory tubes. As a middle-ear infection progresses to the inflammatory stage, the auditory tube closes and drainage is blocked. An intense earache is a common symptom of a middle-ear infection. The pressure from the inflammation may eventually rupture the tympanic membrane to permit drainage.

Repeated middle-ear infections, particularly in children, usually call for an incision of the tympanic membrane known as a **myringotomy** (*mir′′in-got′ŏ-me*) and the implantation of a tiny tube within the tympanic membrane (fig. 15.43). The tube, which is eventually sloughed out of the ear, permits the infection to heal and helps prohibit further infections by keeping the auditory tube open.

Perforation of the tympanic membrane may occur as the result of infections or trauma. The membrane might be ruptured, for example, by a sudden, intense noise. Spontaneous perforation of the membrane usually heals rapidly, but scar tissue may form and lessen sensitivity to sound vibrations.

Otosclerosis (*o′′to-sklĕ-ro′sis*) is a progressive deterioration of the normal bone in the bony labyrinth and its replacement with vascular spongy bone. This frequently causes hearing loss as the auditory ossicles are immobilized. Surgical scraping of the bone growth and replacing the stapes with a prosthesis usually restores hearing.

Ménière's (*mān-e-ārz′*) **disease** afflicts the inner ear and may cause hearing loss as well as equilibrium disturbance. The causes of Ménière's disease are not completely understood, but they are thought to be related to a dysfunction of the autonomic nervous system that causes a vasoconstriction within the inner ear. The disease is characterized by recurrent periods of **vertigo** (dizziness and a sensation of rotation), **tinnitus** (*tĭ-ni′tus*) (ringing in the ear), and progressive deafness in the affected ear. Ménière's disease is chronic and affects both sexes equally. It is more common in elderly people.

Auditory Impairment

Loss of hearing results from disease, trauma, or developmental problems involving any portion of the auditory apparatus, cochlear nerve and auditory pathway, or areas of auditory perception within the brain. Hearing impairment varies from slight disablement, which may or may not worsen, to total deafness. Some types of hearing impairment, including deafness, can be mitigated through hearing aids or surgery.

Two types of deafness are based on the structures involved. **Conduction deafness** is caused by an interference with the sound waves through the outer or middle ear. Conduction problems include impacted cerumen (wax), a ruptured tympanic membrane, a severe middle-ear infection, or adhesions (tissue growths) of one or more auditory ossicles *(otosclerosis)*. Medical treatment usually improves the hearing loss from conductive deafness.

Perceptive (sensorineural) deafness results from disorders that affect the inner ear, the cochlear nerve or nerve pathway, or auditory centers within the brain. Perceptive impairment ranges in severity from the inability to hear certain frequencies to total deafness. Perceptive deafness may be caused by diseases, trauma, or genetic or developmental problems. Elderly people frequently experience some perceptive deafness. The ability to perceive high-frequency sounds is generally lost first. Hearing aids may help some patients with perceptive deafness. This type of deafness is permanent, however, because it involves destruction of sensory structures that cannot regenerate.

Clinical Case Study Answer

When the handle of the vibrating tuning fork was placed on the mastoid process, the temporal bone transmitted sound waves directly to the inner ear. This bypassed the conductive components of the middle ear, which are (beginning with the first to receive sound waves) the tympanic membrane, malleus, incus, and stapes. Because the patient could hear well when the sound waves were transmitted through the temporal bone, it could be assumed that the inner-ear organs, as well as the neural pathways, were functioning. It was therefore concluded that the problem was in the conductive components. This is often the result of otosclerosis (a spongy proliferation of bone) or other conditions affecting the auditory ossicles and/or tympanic membrane, many of which are treatable surgically.

Ménière's disease: from Prosper Ménière, French physician, 1799–1862
vertigo: L. *vertigo*, dizziness
tinnitus: L. *tinnitus*, ting or tingle

CLINICAL PRACTICUM 15.1

A 40-year-old male presents at the Urgent Care Clinic after being hit in the face with a baseball. The patient complains of double vision and pain in his face. Upon physical exam, you observe that the right eye is fixed in a downward gaze, but the left eye moves normally. The patient's right cheek is also very tender. You order a CT scan to determine the extent of his facial injuries. A coronal image through the orbits and sinuses is displayed.

QUESTIONS

1. What bone is fractured?
2. What sinus is involved in this injury?
3. How could this fracture affect movement of the eye?

Chapter Summary

Overview of Sensory Perception (p. 488)

1. Sensory organs are specialized extensions of the nervous system that respond to specific stimuli and conduct nerve impulses.
2. A stimulus to a receptor that conducts an impulse to the brain is necessary for perception.
3. Sensory organs act as energy filters that permit perception of only a narrow range of energy.

Classification of the Senses (pp. 488–490)

1. The senses are classified according to structure or location of the receptors, or on the basis of the stimuli to which the receptors respond.
2. The receptor cells for the general senses are widespread throughout the body and are simple in structure. The receptor cells for the special sensory organs are localized in complex receptor organs and have extensive neural pathways.
3. The somatic senses arise in cutaneous receptors and proprioceptors; visceral senses arise in receptors located within the visceral organs.
4. Phasic receptors respond quickly to a stimulus but then adapt and decrease their firing rate. Tonic receptors produce a constant rate of firing.

Somatic Senses (pp. 490–494)

1. Corpuscles of touch, free nerve endings, and root hair plexuses are tactile receptors, responding to light touch.
2. Lamellated corpuscles are pressure receptors located in the deep dermis or hypodermis. They are also associated with synovial joints.
3. The organs of Ruffini and bulbs of Krause are both mechanoreceptors; they respond to deep and light pressure, respectively.
4. Free nerve endings respond to light touch and are the principal pain receptors. They also serve as thermoreceptors, responding to changes in temperature.
5. Joint kinesthetic receptors, neuromuscular spindles, and neurotendinous receptors are proprioceptors that are sensitive to changes in stretch and tension.

Olfactory Sense (pp. 495–496)

1. Olfactory receptors of the olfactory nerve respond to chemical stimuli and transmit the sensation of olfaction (smell) to the cerebral cortex.
2. Olfaction functions closely with gustation (taste) in that the receptors of both are chemoreceptors, requiring dissolved substances for stimuli.

Gustatory Sense (pp. 496–499)

1. Taste receptors in taste buds are chemoreceptors and transmit the sensation of gustation to the cerebral cortex.
2. Taste buds are found in the vallate and fungiform papillae of the tongue. Filiform papillae are not involved in taste perception; they give the tongue an abrasive feel.
3. The kinds of taste sensation are sweet, salty, sour, and bitter.

Visual Sense (pp. 499–514)

1. Protective structures of the eye include the eyebrow, eyelids, eyelashes, conjunctiva, and lacrimal gland.
2. Six extrinsic ocular muscles control the movement of the eyeball.
3. The eyeball consists of the fibrous tunic, which is divided into the sclera and cornea; the vascular tunic, which consists of the choroid, the ciliary body, and the iris; and the internal tunic, or retina. The retina has an outer pigmented layer and an inner nervous layer. The transparent lens is not part of any tunic.
4. Rod and cone cells, which are the photoreceptors in the nervous layer of the retina, respond to dim and colored light, respectively. Cone cells are concentrated in the fovea centralis, the area of keenest vision.
5. Rod and cone cells contain specific pigments that provide sensitivity to different light rays.
6. The visual process includes the transmission and refraction of light rays, accommodation of the lens, constriction of the pupil, and convergence of the eyes.

(a) Refraction is achieved as incoming light rays pass through the cornea, aqueous humor, lens, and vitreous humor.
(b) A sharp focus is accomplished as the curvature of the lens is changed by autonomic contraction of smooth muscles within the ciliary body.

7. Neural pathways from the retina to the superior colliculus help regulate eye and body movements. Most fibers from the retina project to the lateral geniculate body, and from there to the striate cortex.
8. The sensory components of the eye have been formed by 20 weeks; the accessory structures have been formed by 32 weeks.

Senses of Hearing and Balance (pp. 516–527)

1. The outer ear consists of the auricle and the external acoustic canal.
2. The middle ear (tympanic cavity), bounded by the tympanic membrane and the vestibular and cochlear windows, contains the auditory ossicles (malleus, incus, and stapes) and the auditory muscles (tensor tympani and stapedius).
3. The middle-ear cavity connects to the pharynx through the auditory tube.
4. The inner ear contains the spiral organ for hearing. It also contains the semicircular canals, saccule, and utricle (located in the vestibule) for maintaining balance and equilibrium.
5. The development of the ear begins during the fourth week and is complete by the thirty-second week.

Review Activities

Objective Questions

1. Which of the following conditions is (are) necessary for the perception of a sensation to take place?
   (a) presence of a stimulus
   (b) nerve impulse conduction
   (c) activation of a receptor
   (d) all of the above
2. The cutaneous receptor sensitized to detect deep pressure is
   (a) a root hair plexus.
   (b) a lamellated corpuscle.
   (c) a bulb of Krause.
   (d) a free nerve ending.
3. Proprioceptors that are located within the connective tissue capsule in synovial joints are called
   (a) neuromuscular spindles.
   (b) Golgi tendon organs.
   (c) neurotendinous receptors.
   (d) joint kinesthetic receptors.
4. The sensation of visceral pain perceived as arising from another somatic location is known as
   (a) related pain. (c) referred pain.
   (b) phantom pain. (d) parietal pain.
5. When a person with normal vision views an object from a distance of at least 20 feet,
   (a) the ciliary muscles are relaxed.
   (b) the suspensory ligament is taut.
   (c) the lens is flat, having the least convex shape.
   (d) all of the above apply.
6. Which of the following is an avascular ocular tissue?
   (a) the sclera (c) the ciliary body
   (b) the choroid (d) the iris
7. Additional light may enter the eyeball in response to contraction of
   (a) ciliary muscles.
   (b) pupillary dilator muscles.
   (c) pupillary constrictor muscles.
   (d) orbicularis oculi muscles.
8. The stimulation of hair cells in the semicircular ducts results from the movement of
   (a) endolymph.
   (b) perilymph.
   (c) the statoconial membrane.
9. The middle ear is separated from the inner ear by
   (a) the cochlear window.
   (b) the tympanic membrane.
   (c) the vestibular window.
   (d) both a and c.
10. Glasses with concave lenses help correct
   (a) presbyopia. (c) hyperopia.
   (b) myopia. (d) astigmatism.

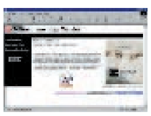
Essay Questions

1. What four events are necessary for perception of a sensation? Explain the statement that perception is the step beyond sensation in the taking in of environmental information.
2. List the senses of the body and differentiate between the special and somatic senses. How are these two classes of senses similar?
3. List the functions of proprioceptors and differentiate between the various types. What role do proprioceptors play in the kinesthetic sense?
4. Compare and contrast olfaction and gustation. Identify the cranial nerves that serve both of these senses and trace the sensory pathways of each.
5. Describe the accessory structures of the eye and list their functions.
6. Diagram the structure of the eyeball and label the sclera, cornea, choroid, macula lutea, ciliary body, suspensory ligament, lens, iris, pupil, retina, optic disc, and fovea centralis.
7. Outline and explain the process of focusing light rays onto the fovea centralis.
8. Diagram the ear and label the structures of the outer, middle, and inner ear.
9. Trace a sound wave through the structures of the ear and explain the mechanism of hearing.
10. Explain the mechanism by which equilibrium is maintained and the role played by the two kinds of receptor information.
11. Outline the major events in the development of the eye and ear. When are congenital deformities most likely to occur?

12. List some techniques used to examine the eye and the ear. Give examples of congenital abnormalities of the eye and ear.

Critical-Thinking Questions

1. Explain the phenomenon called sensory adaptation. What advantages does it confer? Can you think of any disadvantages?
2. You know your contact lens is somewhere in your eye, but you can't seem to find it. It's causing you great discomfort, and you're desperate to get it out. You're also worried that it might be displaced into the orbit. Considering the anatomy of the eye, do you have cause for concern? Why or why not?
3. How would you account for the high success rate of corneal transplants as compared to other types of tissue transplantations from one person to another?
4. Nearsighted adults may find that as they grow older they can read without glasses. Explain.
5. People with conduction deafness often speak quietly. By contrast, people with perceptive deafness tend to speak in tones that are louder than normal. Explain the difference in anatomical terms.
6. Describe the procedure called myringotomy. Why is it usually successful in treating children who suffer recurring middle-ear infections? Following this procedure, would a child still experience the discomfort of changing air pressure in the ear brought on by a rapid drop in elevation? (To help you answer these questions, consider the pouring advantage of punching two holes in an oil can—one across from the other—as opposed to punching a single hole.)



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