

55

Sensory Systems

Concept Outline

55.1 Animals employ a wide variety of sensory receptors.

Categories of Sensory Receptors and Their Actions.

Sensory receptors can be classified according to the type of stimuli to which they can respond.

55.2 Mechanical and chemical receptors sense the body's condition.

Detecting Temperature and Pressure. Receptors within the skin respond to touch, pressure, pain, heat and cold.

Sensing Muscle Contraction and Blood Pressure. A muscle spindle responds to stretching of the muscle; receptors in arteries monitor changes in blood pressure.

Sensing Taste, Smell, and Body Position. Receptors that respond to chemicals produce sensations of taste and smell. Hair cells send nerve impulses when they are bent.

55.3 Auditory receptors detect pressure waves in the air.

The Ears and Hearing. Sound causes vibrations in the ear that bend hair cell processes, initiating a nerve impulse.

Sonar. Bats orient themselves in space by emitting sounds and detecting the time required for the sounds to bounce off objects and return to their ears.

55.4 Optic receptors detect light over a broad range of wavelengths.

Evolution of the Eye. True image-forming eyes evolved independently in several phyla.

Vertebrate Photoreceptors. Light causes a pigment molecule in a rod or cone cell to dissociate; this “bleaching” reaction activates the photoreceptor.

Visual Processing in the Vertebrate Retina. Action potentials travel from the retina of the eyes to the brain for visual perception.

55.5 Some vertebrates use heat, electricity, or magnetism for orientation.

Diversity of Sensory Experiences. Special receptors can detect heat, electrical currents, and magnetic fields.



FIGURE 55.1

Photoreceptors in the vertebrate eye. Rods, the broad, tubular cells, allow black-and-white vision, while cones, the short, tapered cells, are responsible for color vision. Not all vertebrates have both types of receptors.

All input from sensory neurons to the central nervous system arrives in the same form, as action potentials propagated by afferent (inward-conducting) sensory neurons. Different sensory neurons project to different brain regions, and so are associated with different sensory modalities (figure 55.1). The intensity of the sensation depends on the frequency of action potentials conducted by the sensory neuron. A sunset, a symphony, and a searing pain are distinguished by the brain only in terms of the identity of the sensory neuron carrying the action potentials and the frequency of these impulses. Thus, if the auditory nerve is artificially stimulated, the brain perceives the stimulation as sound. But if the optic nerve is artificially stimulated in exactly the same manner and degree, the brain perceives a flash of light.

55.1 Animals employ a wide variety of sensory receptors.

Categories of Sensory Receptors and Their Actions

Sensory information is conveyed to the CNS and perceived in a four-step process (figure 55.2): (1) *stimulation*—a physical stimulus impinges on a sensory neuron or an accessory structure; (2) *transduction*—the stimulus energy is used to produce electrochemical nerve impulses in the dendrites of the sensory neuron; (3) *transmission*—the axon of the sensory neuron conducts action potentials along an afferent pathway to the CNS; and (4) *interpretation*—the brain creates a sensory perception from the electrochemical events produced by afferent stimulation. We actually see (as well as hear, touch, taste, and smell) with our brains, not with our sense organs.

Sensory receptors differ with respect to the nature of the environmental stimulus that best activates their sensory dendrites. Broadly speaking, we can recognize three classes of environmental stimuli: (1) mechanical forces, which stimulate **mechanoreceptors**; (2) chemicals, which stimulate **chemoreceptors**; and (3) electromagnetic and thermal energy, which stimulate a variety of receptors, including the **photoreceptors** of the eyes (table 55.1).

The simplest sensory receptors are *free nerve endings* that respond to bending or stretching of the sensory neuron membrane, to changes in temperature, or to chemicals like oxygen in the extracellular fluid. Other sensory receptors are more complex, involving the association of the sensory neurons with specialized epithelial cells.

Sensing the External and Internal Environments

Exteroceptors are receptors that sense stimuli that arise in the external environment. Almost all of a vertebrate's exterior senses evolved in water before vertebrates invaded the land. Consequently, many senses of terrestrial vertebrates emphasize stimuli that travel well in water, using receptors that have been retained in the transition from the sea to the land. Mammalian hearing, for example, converts an airborne stimulus into a waterborne one, using receptors similar to those that originally evolved in the water. A few vertebrate sensory systems that function well in the water, such as the electrical organs of fish, cannot function in the air and are not found among terrestrial vertebrates. On the other hand, some land-dwellers have sensory systems, such as infrared receptors, that could not function in the sea.

Sensory systems can provide several levels of information about the external environment. Some sensory sys-

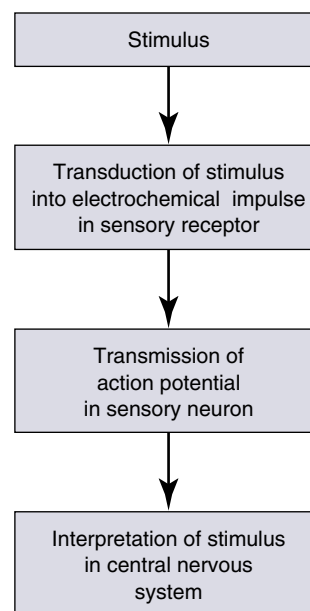


FIGURE 55.2
The path of sensory information. Sensory stimuli must be transduced into electrochemical nerve impulses that are conducted to the brain for interpretation.

Table 55.1 Classes of Environmental Stimuli

Mechanical Forces	Chemicals	Electromagnetic Energy
Pressure	Taste	Light
Gravity	Smell	Heat
Inertia	Humidity	Electricity
Sound		Magnetism
Touch		
Vibration		

tems provide only enough information to determine that an object is present; they call the animal's attention to the object but give little or no indication of where it is located. Other sensory systems provide information about the location of an object, permitting the animal to move toward it. Still other sensory systems enable the brain to construct a three-dimensional image of an object and its surroundings.

Interoceptors sense stimuli that arise from within the body. These internal receptors detect stimuli related to

Table 55.2 Sensory Transduction Among the Vertebrates

Stimulus	Receptor	Location	Structure	Transduction Process
INTEROCEPTION				
Temperature	Heat receptors and cold receptors	Skin, hypothalamus	Free nerve ending	Temperature change opens/closes ion channels in membrane
Touch	Meissner's corpuscles, Merkel cells	Surface of skin	Nerve ending within elastic capsule	Rapid or extended change in pressure deforms membrane
Vibration	Pacinian corpuscles	Deep within skin	Nerve ending within elastic capsule	Severe change in pressure deforms membrane
Pain	Nociceptors	Throughout body	Free nerve ending	Chemicals or changes in pressure or temperature open/close ion channels in membrane
Muscle stretch	Stretch receptors	Within muscles	Spiral nerve endings wrapped around muscle spindle	Stretch of spindle deforms membrane
Blood pressure	Baroreceptors	Arterial branches	Nerve endings over thin part of arterial wall	Stretch of arterial wall deforms membrane
EXTEROCEPTION				
Gravity	Statocysts	Outer chambers of inner ear	Otoliths and hair cells	Otoliths deform hair cells
Motion	Cupula	Semicircular canals of inner ear	Collection of hair cells	Fluid movement deforms hair cells
	Lateral line organ	Within grooves on body surface of fish	Collection of hair cells	Fluid movement deforms hair cells
Taste	Taste bud cells	Mouth; skin of fish	Chemoreceptors: epithelial cells with microvilli	Chemicals bind to membrane receptors
Smell	Olfactory neurons	Nasal passages	Chemoreceptors: ciliated neurons	Chemicals bind to membrane receptors
Hearing	Organ of Corti	Cochlea of inner ear	Hair cells between basilar and tectorial membranes	Sound waves in fluid deform membranes
Vision	Rod and cone cells	Retina of eye	Array of photosensitive pigments	Light initiates process that closes ion channels
Heat	Pit organ	Face of snake	Temperature receptors in two chambers	Receptors compare temperatures of surface and interior chambers
Electricity	Ampullae of Lorenzini	Within skin of fishes	Closed vesicles with asymmetrical ion channel distribution	Electrical field alters ion distribution on membranes
Magnetism	Unknown	Unknown	Unknown	Deflection at magnetic field initiates nerve impulses?

muscle length and tension, limb position, pain, blood chemistry, blood volume and pressure, and body temperature. Many of these receptors are simpler than those that monitor the external environment and are believed to bear

a closer resemblance to primitive sensory receptors. In the rest of this chapter, we will consider the different types of interoceptors and exteroceptors according to the kind of stimulus each is specialized to detect (table 55.2).

Sensory Transduction

Sensory cells respond to stimuli because they possess *stimulus-gated ion channels* in their membranes. The sensory stimulus causes these ion channels to open or close, depending on the sensory system involved. In doing so, a sensory stimulus produces a change in the membrane potential of the receptor cell. In most cases, the sensory stimulus produces a depolarization of the receptor cell, analogous to the excitatory postsynaptic potential (EPSP, described in chapter 54) produced in a postsynaptic cell in response to neurotransmitter. A depolarization that occurs in a sensory receptor upon stimulation is referred to as a **receptor potential** (figure 55.3*a*).

Like an EPSP, a receptor potential is graded: the larger the sensory stimulus, the greater the degree of depolarization. Receptor potentials also decrease in size (*decrement*) with distance from their source. This prevents small, irrelevant stimuli from reaching the cell body of the sensory

neuron. Once a threshold level of depolarization is reached, the receptor potential stimulates the production of action potentials that are conducted by a sensory axon into the CNS (figure 55.3*b*). The greater the sensory stimulus, the greater the depolarization of the receptor potential and the higher the frequency of action potentials. There is generally a logarithmic relationship between stimulus intensity and action potential frequency—a sensory stimulus that is ten times greater than another stimulus will produce action potentials at twice the frequency of the other stimulus. This allows the brain to interpret the incoming signals as indicating a sensory stimulus of a particular strength.

Sensory receptors transduce stimuli in the internal or external environment into graded depolarizations, which stimulates the production of action potentials. Sensory receptors may be classified on the basis of the type of stimulus energy to which they respond.

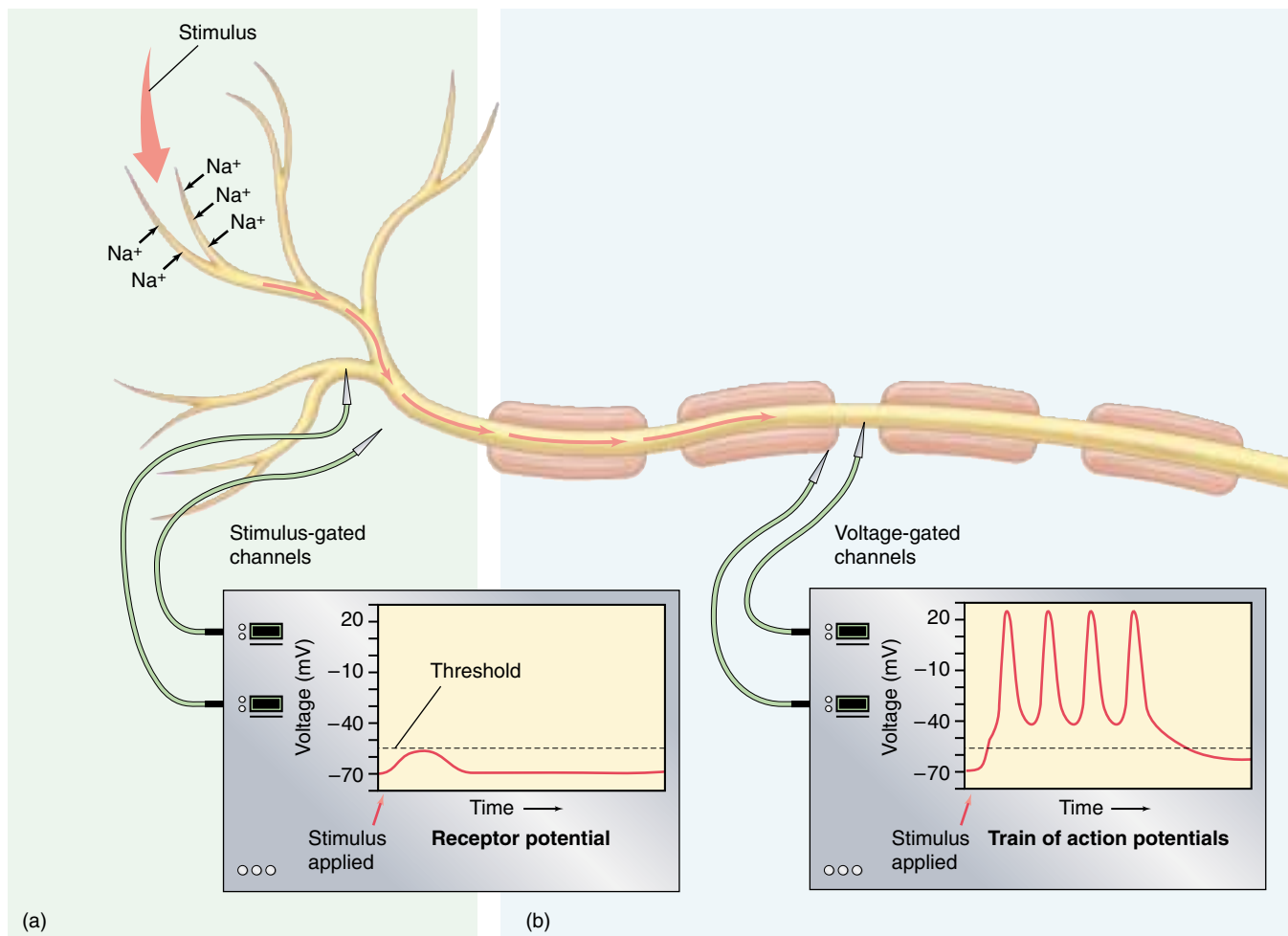


FIGURE 55.3

Events in sensory transduction. (a) Depolarization of a free nerve ending leads to a receptor potential that spreads by local current flow to the axon. (b) Action potentials are produced in the axon in response to a sufficiently large receptor potential.

55.2 Mechanical and chemical receptors sense the body's condition.

Detecting Temperature and Pressure

While the receptors of the skin, called the **cutaneous receptors**, are classified as interoceptors, they in fact respond to stimuli at the border between the external and internal environments. These receptors serve as good examples of the specialization of receptor structure and function, responding to heat, cold, pain, touch, and pressure.

The skin contains two populations of **thermoreceptors**, which are naked dendritic endings of sensory neurons that are sensitive to changes in temperature. *Cold receptors* are stimulated by a fall in temperature and inhibited by warming, while *warm receptors* are stimulated by a rise in temperature and inhibited by cooling. Cold receptors are located immediately below the epidermis, while warm receptors are located slightly deeper, in the dermis. Thermoreceptors are also found within the hypothalamus of the brain, where they monitor the temperature of the circulating blood and thus provide the CNS with information on the body's internal (core) temperature.

A stimulus that causes or is about to cause tissue damage is perceived as pain. The receptors that transmit impulses that are perceived by the brain as pain are called **nociceptors**. They consist of free nerve endings located throughout the body, especially near surfaces where damage is most likely to occur. Different nociceptors may respond to extremes in temperature, very intense mechanical stimulation, or specific chemicals in the extracellular fluid, including some that are released by injured cells. The thresholds of these sensory cells vary; some nociceptors are sensitive only to actual tissue damage, while others respond before damage has occurred.

Several types of mechanoreceptors are present in the skin, some in the dermis and others in the underlying subcutaneous tissue (figure 55.4). Morphologically specialized receptors that respond to fine touch are most concentrated on areas such as the fingertips and face. They are used to localize cutaneous stimuli very precisely and can be either phasic (intermittently activated) or tonic (continuously activated). The phasic receptors include *hair follicle receptors* and *Meissner's corpuscles*, which are present on body surfaces that do not contain hair, such as the fingers, palms, and nipples. The tonic receptors consist of *Ruffini endings* in the dermis and *touch dome endings (Merkel cells)* located near the surface of the skin. These receptors monitor the duration of a touch and the extent to which it is applied.

Deep below the skin in the subcutaneous tissue lie phasic, pressure-sensitive receptors called **Pacian corpuscles**. Each of these receptors consists of the end of an afferent axon, surrounded by a capsule of alternating layers of connective tissue cells and extracellular fluid. When sustained pressure is applied to the corpuscle, the elastic capsule absorbs much of the pressure and the axon ceases to produce impulses. Pacian corpuscles thus monitor only the onset and removal of pressure, as may occur repeatedly when something that vibrates is placed against the skin.

Different cutaneous receptors respond to touch, pressure, heat, cold, and pain. Some of these receptors are naked dendrites of sensory neurons, while others have supporting cells that modify the activities of their sensory dendrites.

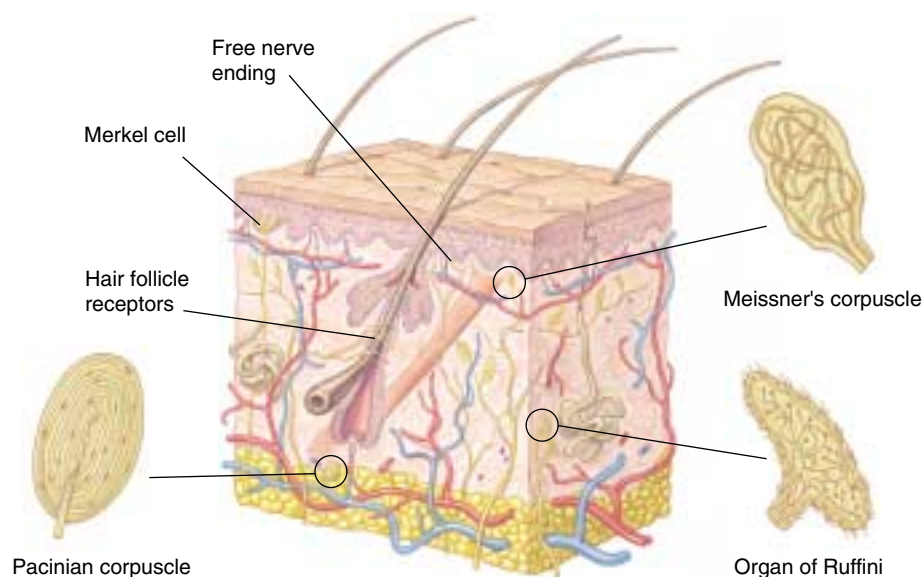


FIGURE 55.4

Sensory receptors in human skin.

Cutaneous receptors may be free nerve endings or sensory dendrites in association with other supporting structures.

Sensing Muscle Contraction and Blood Pressure

Mechanoreceptors contain sensory cells with ion channels that are sensitive to a mechanical force applied to the membrane. These channels open in response to mechanical distortion of the membrane, initiating a depolarization (receptor potential) that causes the sensory neuron to generate action potentials.

Muscle Length and Tension

Buried within the skeletal muscles of all vertebrates except the bony fishes are muscle spindles, sensory stretch receptors that lie in parallel with the rest of the fibers in the muscle (figure 55.5). Each spindle consists of several thin muscle fibers wrapped together and innervated by a sensory neuron, which becomes activated when the muscle, and therefore the spindle, is stretched. Muscle spindles, together with other receptors in tendons and joints, are known as **proprioceptors**, which are sensory receptors that provide information about the relative position or movement of the animal's body parts. The sensory neurons conduct action potentials into the spinal cord, where they synapse with somatic motor neurons that innervate the muscle. This pathway constitutes the muscle stretch reflex, including the knee-jerk reflex, previously discussed in chapter 54.

When a muscle contracts, it exerts tension on the tendons attached to it. The Golgi tendon organs, another type

of proprioceptor, monitor this tension; if it becomes too high, they elicit a reflex that inhibits the motor neurons innervating the muscle. This reflex helps to ensure that muscles do not contract so strongly that they damage the tendons to which they are attached.

Blood Pressure

Blood pressure is monitored at two main sites in the body. One is the *carotid sinus*, an enlargement of the left and right internal carotid arteries, which supply blood to the brain. The other is the *aortic arch*, the portion of the aorta very close to its emergence from the heart. The walls of the blood vessels at both sites contain a highly branched network of afferent neurons called **baroreceptors**, which detect tension in the walls. When the blood pressure decreases, the frequency of impulses produced by the baroreceptors decreases. The CNS responds to this reduced input by stimulating the sympathetic division of the autonomic nervous system, causing an increase in heart rate and vasoconstriction. Both effects help to raise the blood pressure, thus maintaining homeostasis. A rise in blood pressure, conversely, reduces sympathetic activity and stimulates the parasympathetic division, slowing the heart and lowering the blood pressure.

Mechanical distortion of the plasma membrane of mechanoreceptors produces nerve impulses that serve to monitor muscle length from skeletal muscle spindles and to monitor blood pressure from baroreceptors within arteries.

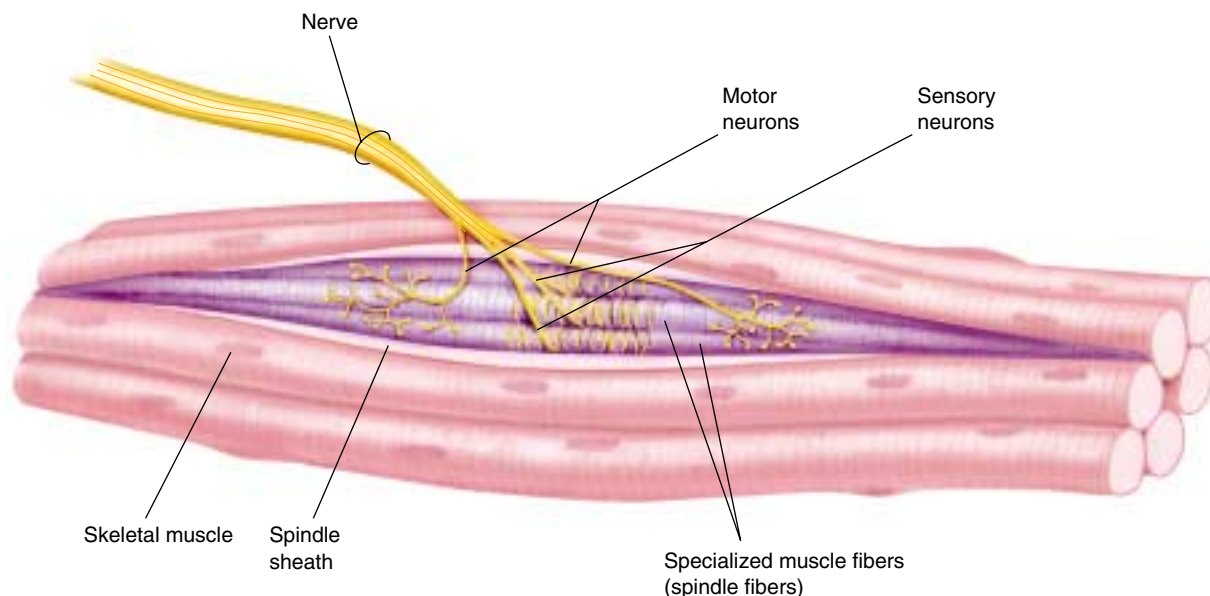


FIGURE 55.5

A muscle spindle is a stretch receptor embedded within skeletal muscle. Stretching of the muscle elongates the spindle fibers and stimulates the sensory dendritic endings wrapped around them. This causes the sensory neurons to send impulses to the CNS, where they synapse with motor neurons.

Sensing Taste, Smell, and Body Position

Some sensory cells, called **chemoreceptors**, contain membrane proteins that can bind to particular chemicals in the extracellular fluid. In response to this chemical interaction, the membrane of the sensory neuron becomes depolarized, leading to the production of action potentials. Chemoreceptors are used in the senses of taste and smell and are also important in monitoring the chemical composition of the blood and cerebrospinal fluid.

Taste

Taste buds—collections of chemosensitive epithelial cells associated with afferent neurons—mediate the sense of taste in vertebrates. In a fish, the taste buds are scattered over the surface of the body. These are the most sensitive vertebrate chemoreceptors known. They are particularly sensitive to amino acids; a catfish, for example, can distinguish between two different amino acids at a concentration of less than 100 parts per billion (1 g in 10,000 L of water)! The ability to taste the surrounding water is very important to bottom-feeding fish, enabling them to sense the presence of food in an often murky environment.

The taste buds of all terrestrial vertebrates are located in the epithelium of the tongue and oral cavity, within raised areas called *papillae* (figure 55.6). Humans have four kinds of taste buds—salty, sweet, sour, and bitter. The salty taste is produced by the effects of sodium (Na^+) and the sour taste by the effects of hydrogen (H^+). Organic molecules that produce the sweet and bitter tastes, such as sugars and quinine, respectively, are varied in structure. Taste buds that respond best to specific tastes are concentrated in specific regions of the tongue: sweet at the tip, sour at the sides, bitter at the back, and salty over most of the tongue's surface. Our complex perception of taste is the result of different combinations of impulses in the sensory neurons from these four kinds of taste buds, together with information related to smell. The effect of smell on the sense of taste can easily be demonstrated by eating an onion with the nose open and then eating it with the nose plugged.

Like vertebrates, many arthropods also have taste chemoreceptors. For example, flies, because of their mode of searching for food, have taste receptors in sensory hairs located on their feet. The sensory hairs contain different chemoreceptors that are able to detect sugars, salts, and

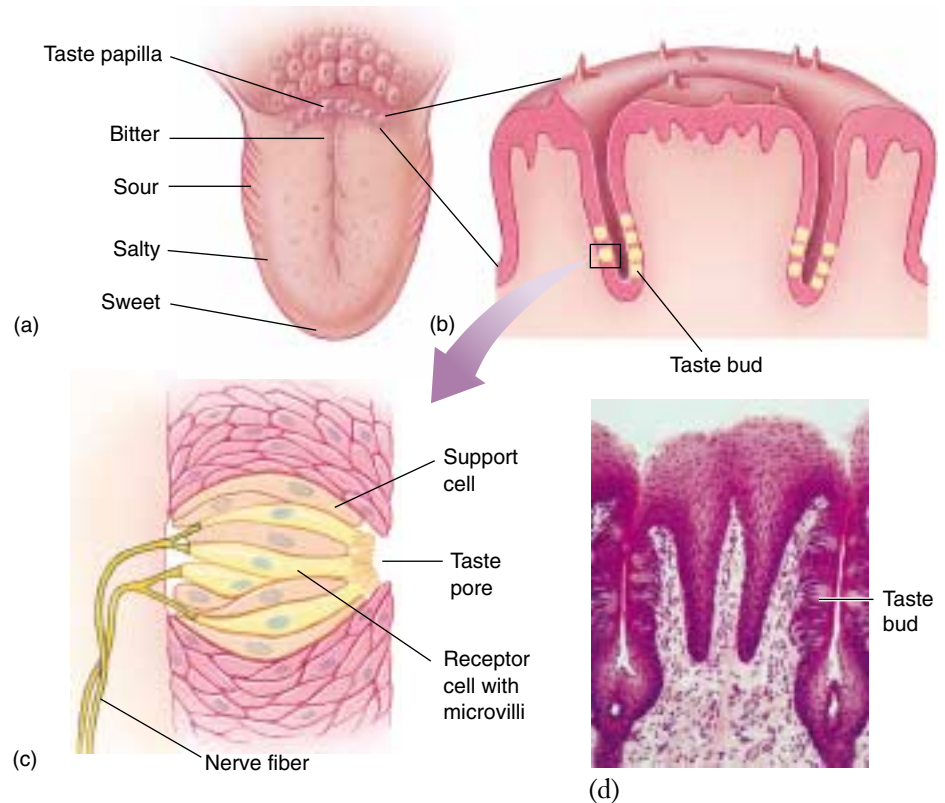


FIGURE 55.6

Taste. (a) Human beings have four kinds of taste buds (bitter, sour, salty, and sweet), located on different regions of the tongue. (b) Groups of taste buds are typically organized in sensory projections called papillae. (c) Individual taste buds are bulb-shaped collections of chemosensitive receptors that open out into the mouth through a pore. (d) Photomicrograph of taste buds in papillae.

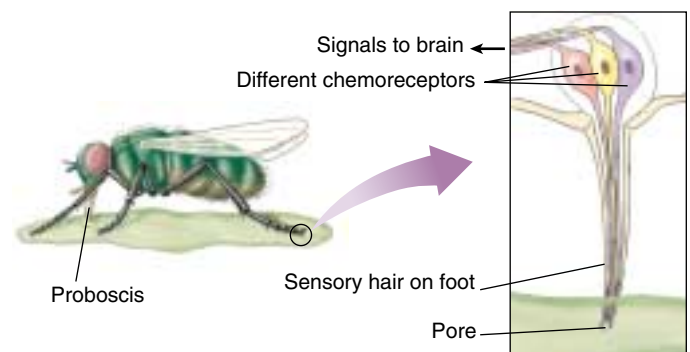


FIGURE 55.7

Many insects taste with their feet. In the blowfly shown here, chemoreceptors extend into the sensory hairs on the foot. Each different chemoreceptor detects a different type of food molecule. When the fly steps in a food substance, it can taste the different food molecules and extend its proboscis for feeding.

other molecules (figure 55.7). They can detect a wide variety of tastes by the integration of stimuli from these chemoreceptors. If they step on potential food, the proboscis (the tubular feeding apparatus) extends to feed.

Smell

In terrestrial vertebrates, the sense of smell, or olfaction, involves chemoreceptors located in the upper portion of the nasal passages (figure 55.8). These receptors are bipolar neurons whose dendrites end in tassels of cilia that project into the nasal mucosa, and whose axon projects directly into the cerebral cortex. A terrestrial vertebrate uses its sense of smell in much the same way that a fish uses its sense of taste—to sample the chemical environment around it. Because terrestrial vertebrates are surrounded by air rather than water, their sense of smell has become specialized to detect airborne particles (but these particles must first dissolve in extracellular fluid before they can activate the olfactory receptors). The sense of smell can be extremely acute in many mammals, so much so that a single odorant molecule may be all that is needed to excite a given receptor.

Although humans can detect only four modalities of taste, they can discern thousands of different smells. New research suggests that there may be as many as a thousand different genes coding for different receptor proteins for smell. The particular set of olfactory neurons that respond to a given odor might serve as a “fingerprint” the brain can use to identify the odor.

Internal Chemoreceptors

Sensory receptors within the body detect a variety of chemical characteristics of the blood or fluids derived from the blood, including cerebrospinal fluid. Included among these receptors are the *peripheral chemoreceptors* of the aortic and carotid bodies, which are sensitive primarily to plasma pH, and the *central chemoreceptors* in the medulla oblongata of the brain, which are sensitive to the pH of cerebrospinal fluid. These receptors were discussed together with the regulation of breathing in chapter 53. When the breathing rate is too low, the concentration of plasma CO_2 increases, producing more carbonic acid and causing a fall in the blood pH. The carbon dioxide can also enter the cerebrospinal fluid and cause a lowering of the pH, thereby stimulating the central chemoreceptors. This chemoreceptor stimulation indirectly affects the respiratory control center of the brain stem, which increases the breathing rate. The aortic bodies can also respond to a lowering of blood oxygen concentrations, but this effect is normally not significant unless a person goes to a high altitude.

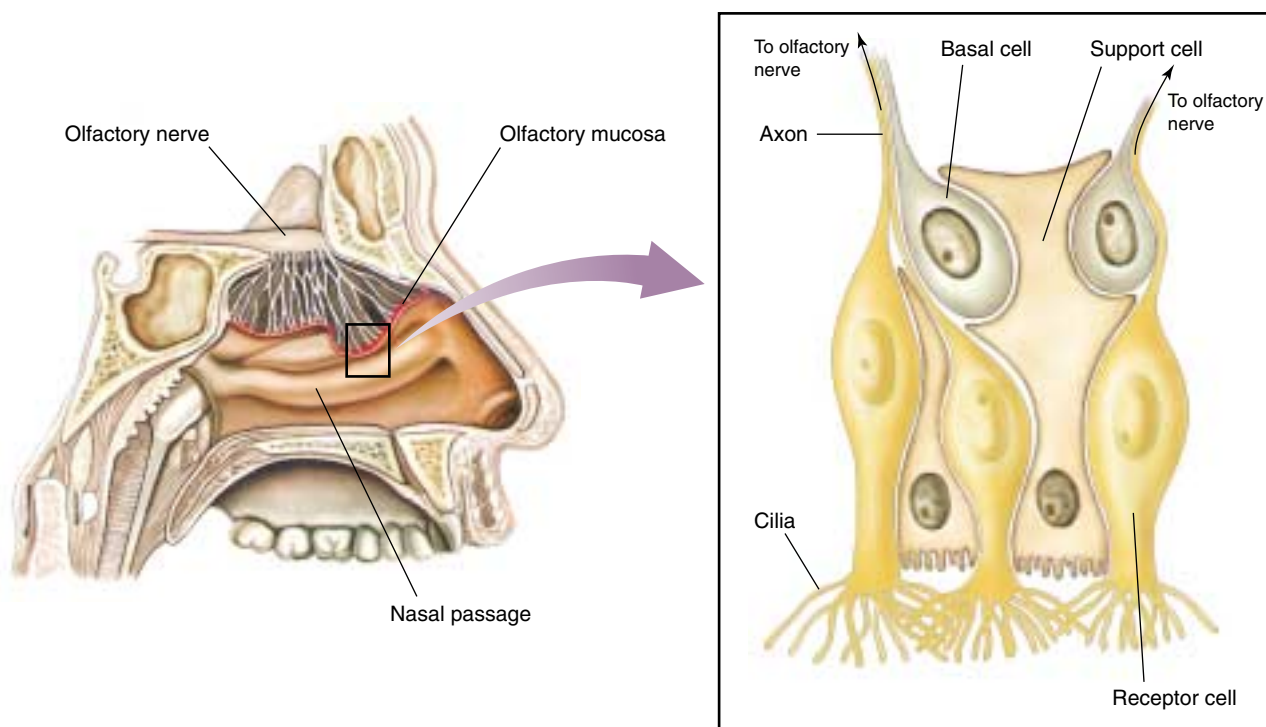


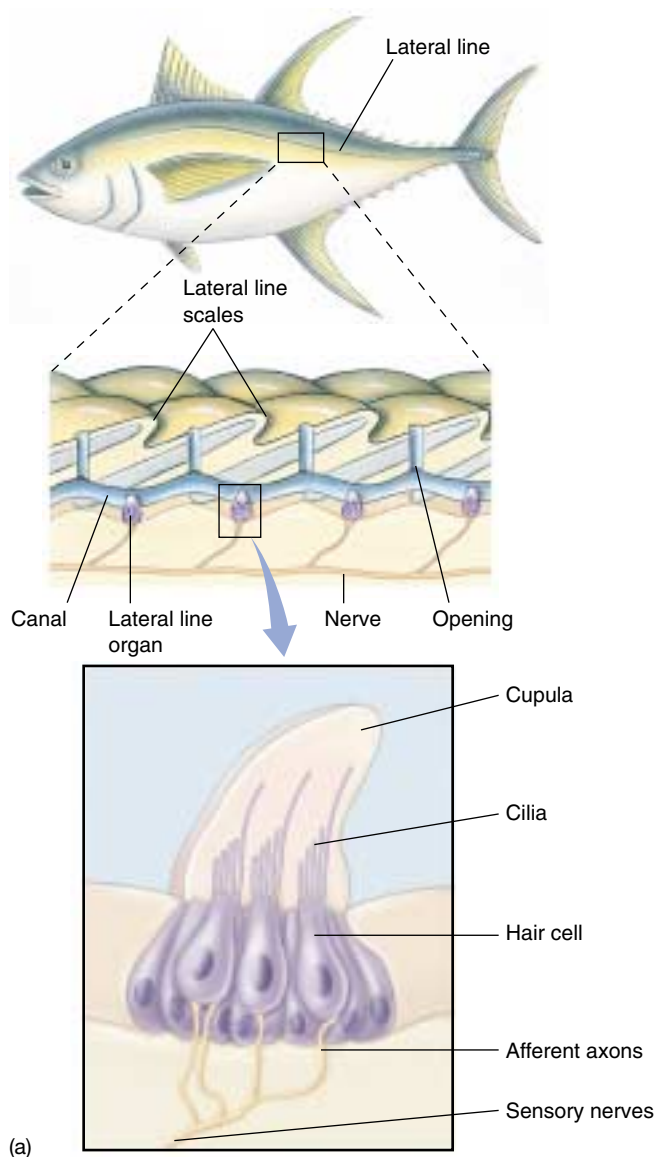
FIGURE 55.8

Smell. Humans detect smells by means of olfactory neurons located in the lining of the nasal passages. The axons of these neurons transmit impulses directly to the brain via the olfactory nerve. Basal cells regenerate new olfactory neurons to replace dead or damaged cells. Olfactory neurons typically live about one month.

The Lateral Line System

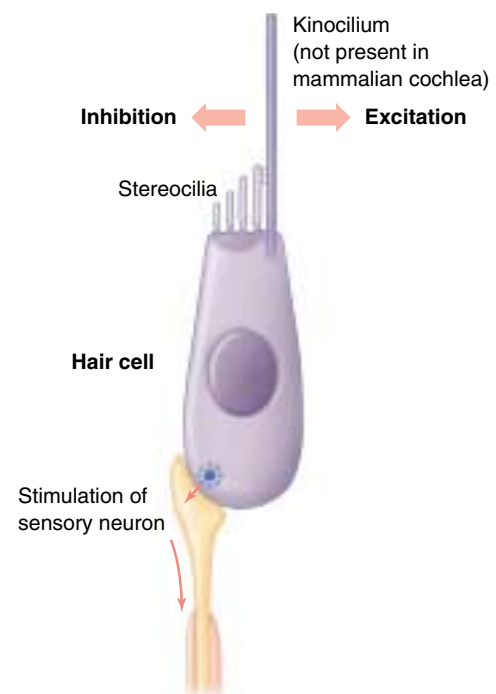
The lateral line system provides fish with a sense of “distant touch,” enabling them to sense objects that reflect pressure waves and low-frequency vibrations. This enables a fish to detect prey, for example, and to swim in synchrony with the rest of its school. It also enables a blind cave fish to sense its environment by monitoring changes in the patterns of water flow past the lateral line receptors. The lateral line system is found in amphibian larvae, but is lost at metamorphosis and is not present in any terrestrial vertebrate. The sense provided by the lateral line system supplements the fish’s sense of hearing, which is performed by a different sensory structure. The structures and mechanisms involved in hearing will be described in a later section.

The lateral line system consists of sensory structures within a longitudinal canal in the fish’s skin that extends



along each side of the body and within several canals in the head (figure 55.9a). The sensory structures are known as hair cells because they have hairlike processes at their surface that project into a gelatinous membrane called a *cupula* (Latin, “little cup”). The hair cells are innervated by sensory neurons that transmit impulses to the brain.

Hair cells have several hairlike processes of approximately the same length, called *stereocilia*, and one longer process called a *kinocilium* (figure 55.9b). Vibrations carried through the fish’s environment produce movements of the cupula, which cause the hairs to bend. When the stereocilia bend in the direction of the kinocilium, the associated sensory neurons are stimulated and generate a receptor potential. As a result, the frequency of action potentials produced by the sensory neuron is increased. If the stereocilia are bent in the opposite direction, on the other hand, the activity of the sensory neuron is inhibited.



(b)

FIGURE 55.9

The lateral line system. (a) This system consists of canals running the length of the fish’s body beneath the surface of the skin. Within these canals are sensory structures containing hair cells with cilia that project into a gelatinous cupula. Pressure waves traveling through the water in the canals deflect the cilia and depolarize the sensory neurons associated with the hair cells. (b) Hair cells are mechanoreceptors with hairlike cilia that project into a gelatinous membrane. The hair cells of the lateral line system (and the membranous labyrinth of the vertebrate inner ear) have a number of smaller cilia called stereocilia and one larger kinocilium. When the cilia bend in the direction of the kinocilium, the hair cell releases a chemical transmitter that depolarizes the associated sensory neuron. Bending of the cilia in the opposite direction has an inhibitory effect.

Gravity and Angular Acceleration

Most invertebrates can orient themselves with respect to gravity due to a sensory structure called a *statocyst*. Statocysts generally consist of ciliated hair cells with the cilia embedded in a gelatinous membrane containing crystals of calcium carbonate. These “stones,” or *statoliths*, increase the mass of the gelatinous membrane so that it can bend the cilia when the animal’s position changes. If the animal tilts to the right, for example, the statolith membrane will bend the cilia on the right side and activate associated sensory neurons.

A similar structure is found in the membranous labyrinth of the inner ear of vertebrates. The labyrinth is a system of fluid-filled membranous chambers and tubes that constitute the organs of equilibrium and hearing in vertebrates. This membranous labyrinth is surrounded by bone and perilymph, which is similar in ionic content to interstitial fluid. Inside, the chambers and tubes are filled with endolymph fluid, which is similar in ionic content to intracellular fluid. Though intricate, the entire structure is very small; in a human, it is about the size of a pea.

The receptors for gravity in vertebrates consist of two chambers of the membranous labyrinth called the utricle and saccule (figure 55.10). Within these structures are hair cells with stereocilia and a kinocilium, similar to those in the lateral line system of fish. The hairlike processes are embedded within a gelatinous membrane containing calcium carbonate crystals; this is known as an *otolith membrane*, because of its location in the inner ear (*oto* is derived from the Greek word for ear). Because the otolith organ is oriented differently in the utricle and saccule, the utricle is more sensi-

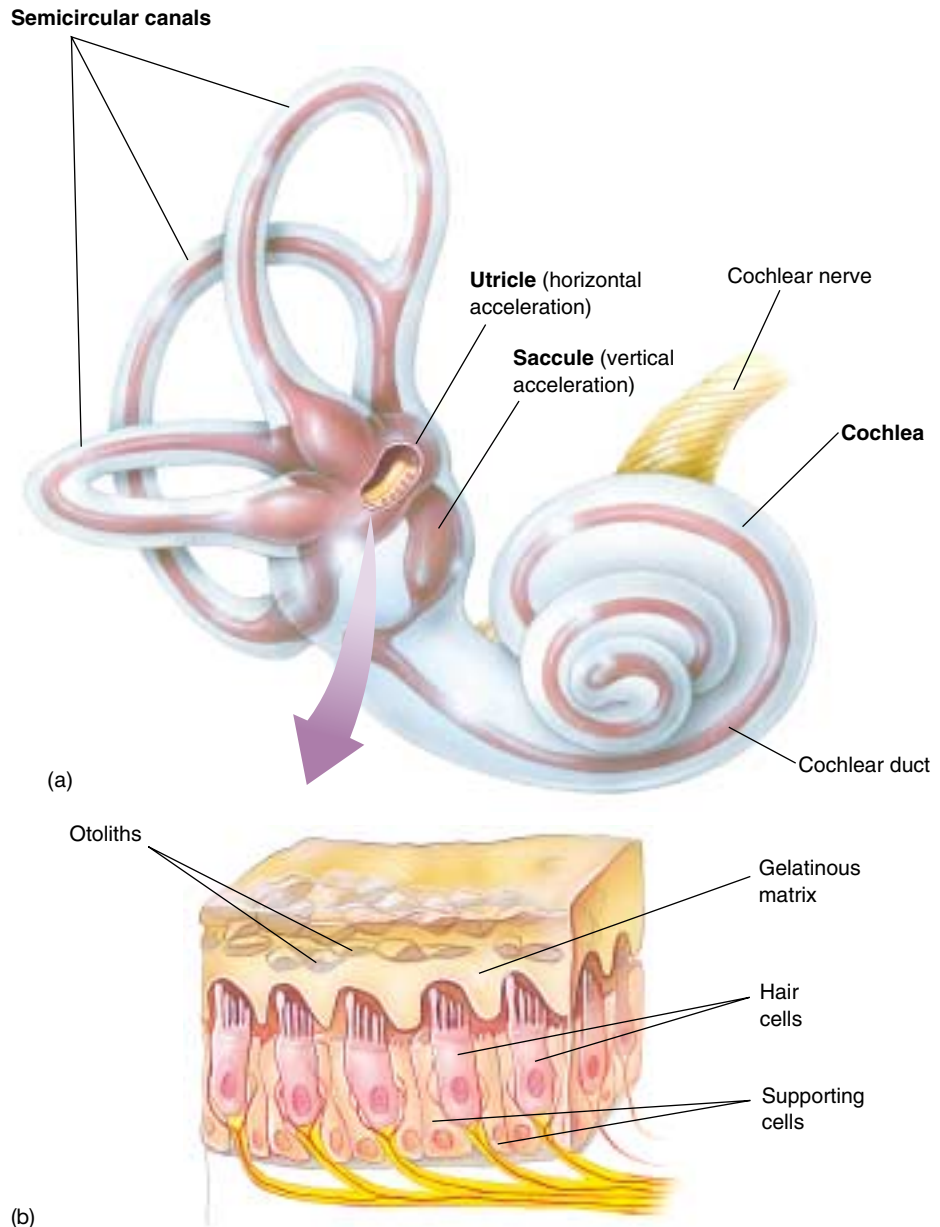


FIGURE 55.10

The structure of the utricle and saccule. (a) The relative positions of the utricle and saccule within the membranous labyrinth of the human inner ear. (b) Enlargement of a section of the utricle or saccule showing the otoliths embedded in the gelatinous matrix that covers the hair cells.

tive to horizontal acceleration (as in a moving car) and the saccule to vertical acceleration (as in an elevator). In both cases, the acceleration causes the stereocilia to bend and consequently produces action potentials in an associated sensory neuron.

The membranous labyrinth of the utricle and saccule is continuous with three semicircular canals, oriented in different planes so that angular acceleration in any direction can be detected (figure 55.11). At the ends of the canals are swollen chambers called *ampullae*, into which protrude the cilia of another group of hair cells. The tips of the cilia are embedded within a sail-like wedge of gelatinous material called a *cupula* (similar to the cupula of the fish lateral line system) that protrudes into the endolymph fluid of each semicircular canal.

When the head rotates, the fluid inside the semicircular canals pushes against the cupula and causes the cilia to bend. This bending either depolarizes or hyperpolarizes the hair cells, depending on the direction in which the cilia are bent. This is similar to the way the lateral line system

works in a fish: if the stereocilia are bent in the direction of the kinocilium, a depolarization (receptor potential) is produced, which stimulates the production of action potentials in associated sensory neurons.

The saccule, utricle, and semicircular canals are collectively referred to as the *vestibular apparatus*. While the saccule and utricle provide a sense of linear acceleration, the semicircular canals provide a sense of angular acceleration. The brain uses information that comes from the vestibular apparatus about the body's position in space to maintain balance and equilibrium.

Receptors that sense chemicals originating outside the body are responsible for the senses of odor, smell, and taste. Internal chemoreceptors help to monitor chemicals produced within the body and are needed for the regulation of breathing. Hair cells in the lateral line organ of fishes detect water movements, and hair cells in the vestibular apparatus of terrestrial vertebrates provide a sense of acceleration.

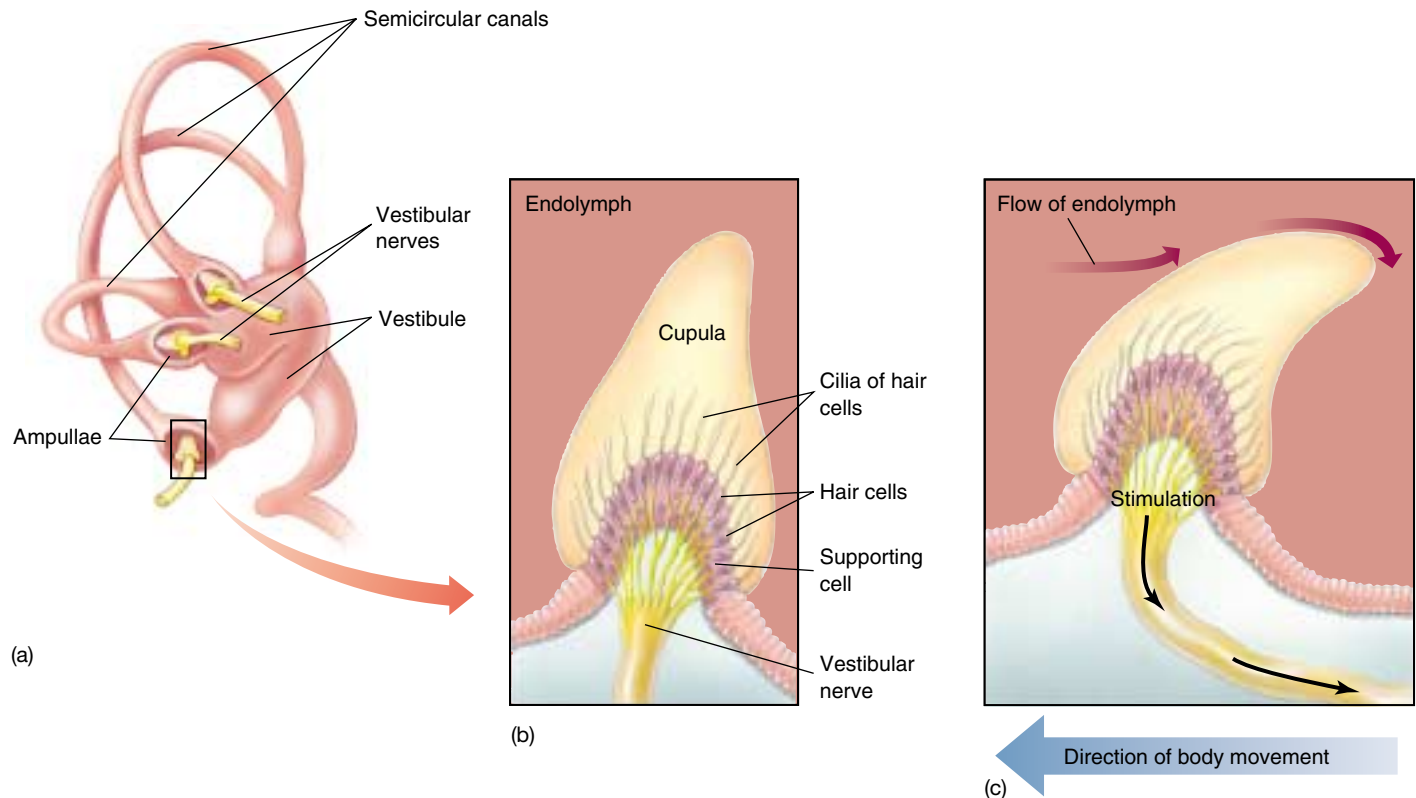


FIGURE 55.11

The structure of the semicircular canals. (a) The position of the semicircular canals in relation to the rest of the inner ear.

(b) Enlargement of a section of one ampulla, showing how hair cell cilia insert into the cupula. (c) Angular acceleration in the plane of the semicircular canal causes bending of the cupula, thereby stimulating the hair cells.

55.3 Auditory receptors detect pressure waves in the air.

The Ears and Hearing

Fish detect vibrational pressure waves in water by means of their lateral line system. Terrestrial vertebrates detect similar vibrational pressure waves in air by means of similar hair cell mechanoreceptors in the inner ear. Hearing actually works better in water than in air because water transmits pressure waves more efficiently. Despite this limitation, hearing is widely used by terrestrial vertebrates to monitor their environments, communicate with other members of the same species, and to detect possible sources of danger (figure 55.12). Auditory stimuli travel farther and more quickly than chemical ones, and auditory receptors provide better directional information than do chemoreceptors. Auditory stimuli alone, however, provide little information about distance.

Structure of the Ear

Fish use their lateral line system to detect water movements and vibrations emanating from relatively nearby objects, and their hearing system to detect vibrations that originate from a greater distance. The hearing system of fish consists of the otolith organs in the membranous labyrinth (utricle and saccule) previously described, together with a very small outpouching of the membranous labyrinth called the lagena. Sound waves travel through the body of the fish as easily as through the surrounding water, as the body is composed primarily of water. Therefore, an object of different density is needed in order for the sound to be detected. This function is served by the otolith (calcium carbonate crystals) in many fish. In catfish, minnows, and suckers, however, this function is served by an air-filled swim bladder that vibrates with the sound. A chain of small bones, Weberian ossicles, then transmits the vibrations to the saccule in some of these fish.

In the ears of terrestrial vertebrates, vibrations in air may be channeled through an ear canal to the eardrum, or tympanic membrane. These structures are part of the *outer ear*. Vibrations of the tympanic membrane cause movement of three small bones (ossicles)—the *malleus* (hammer), *incus* (anvil), and *stapes* (stirrup)—that are located in a bony cavity known as the *middle ear* (figure 55.13). These middle ear ossicles are analogous to the Weberian ossicles in fish. The



FIGURE 55.12

Kangaroo rats have specialized ears. Kangaroo rats (*Dipodomys*) are unique in having an enlarged tympanic membrane (eardrum), a lengthened and freely rotating malleus (ear bone), and an increased volume of air-filled chambers in the middle ear. These and other specializations result in increased sensitivity to sound, especially to low-frequency sounds. Experiments have shown that the kangaroo rat's ears are adapted to nocturnal life and allow them to hear the low-frequency sounds of their predators, such as an owl's wingbeats or a sidewinder rattlesnake's scales rubbing against the ground. Also, the ears seem to be adapted to the poor sound-carrying quality of dry, desert air.

middle ear is connected to the throat by the *Eustachian tube*, which equalizes the air pressure between the middle ear and the external environment. The “ear popping” you may have experienced when flying in an airplane or driving on a mountain is caused by pressure equalization between the two sides of the eardrum.

The stapes vibrates against a flexible membrane, the *oval window*, which leads into the *inner ear*. Because the oval window is smaller in diameter than the tympanic membrane, vibrations against it produce more force per unit area, transmitted into the inner ear. The inner ear consists of the cochlea (Latin for “snail”), a bony structure containing part of the membranous labyrinth called the cochlear duct. The cochlear duct is located in the center of the cochlea; the area above the cochlear duct is the *vestibular canal*, and the area below is the *tympanic canal*. All three chambers are filled with fluid, as previously described. The oval window opens to the upper vestibular canal, so that when the stapes causes it to vibrate, it produces pressure waves of fluid. These pressure waves travel down to the tympanic canal, pushing another flexible membrane, the *round window*, that transmits the pressure back into the middle ear cavity (see figure 55.13).

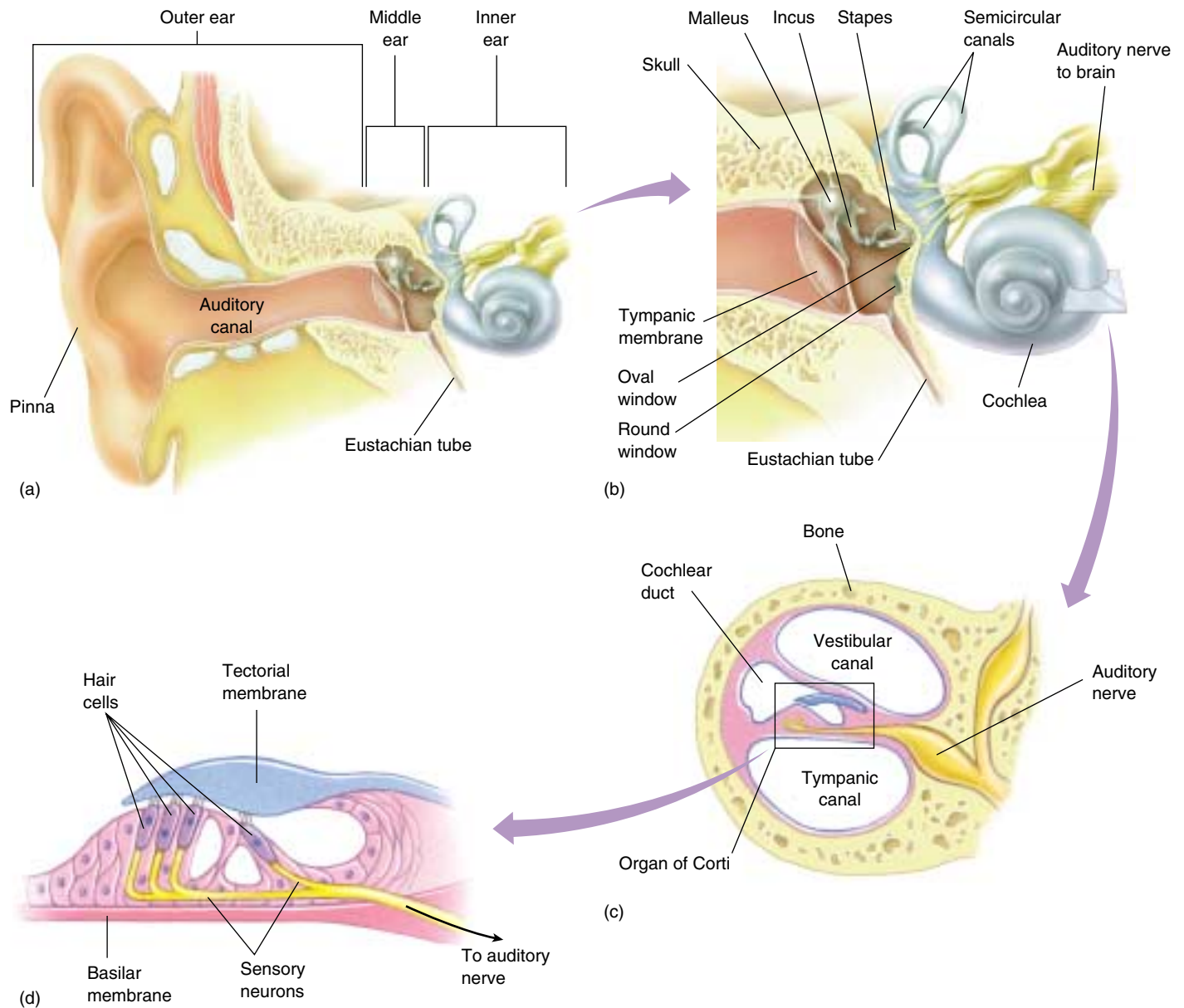


FIGURE 55.13

Structure of the human ear. (a) Sound waves passing through the ear canal produce vibrations of the tympanic membrane, which cause movement of the (b) middle ear ossicles (the malleus, incus, and stapes) against an inner membrane called the oval window. Vibration of the oval window sets up pressure waves that (c and d) travel through the fluid in the vestibular and tympanic canals of the cochlea.

Transduction in the Cochlea

As the pressure waves produced by vibrations of the oval window are transmitted through the cochlea to the round window, they cause the cochlear duct to vibrate. The bottom of the cochlear duct, called the *basilar membrane*, is quite flexible and vibrates in response to these pressure waves. The surface of the basilar membrane contains sensory hair cells, similar to those of the vestibular apparatus and lateral line system but lacking a kinocilium. The cilia from the hair cells project into an overhanging gelatinous membrane, the *tectorial membrane*. This sensory apparatus,

consisting of the basilar membrane, hair cells with associated sensory neurons, and tectorial membrane, is known as the **organ of Corti**.

As the basilar membrane vibrates, the cilia of the hair cells bend in response to the movement of the basilar membrane relative to the tectorial membrane. As in the lateral line organs and the vestibular apparatus, the bending of these cilia depolarizes the hair cells. The hair cells, in turn, stimulate the production of action potentials in sensory neurons that project to the brain, where they are interpreted as sound.

Frequency Localization in the Cochlea

The basilar membrane of the cochlea consists of elastic fibers of varying length and stiffness, like the strings of a musical instrument, embedded in a gelatinous material. At the base of the cochlea (near the oval window), the fibers of the basilar membrane are short and stiff. At the far end of the cochlea (the apex), the fibers are 5 times longer and 100 times more flexible. Therefore, the resonant frequency of the basilar membrane is higher at the base than at the apex; the base responds to higher pitches, the apex to lower.

When a wave of sound energy enters the cochlea from the oval window, it initiates a traveling up-and-down motion of the basilar membrane. However, this wave imparts most of its energy to that part of the basilar membrane with a resonant frequency near the frequency of the sound wave, resulting in a maximum deflection of the basilar membrane at that point (figure 55.14). As a result, the hair cell depolarization is greatest in that region, and the afferent axons from that region are stimulated to produce action potentials more than those from other regions. When these action potentials arrive in the brain, they are interpreted as representing a sound of that particular frequency, or pitch.

The flexibility of the basilar membrane limits the frequency range of human hearing to between approximately 20 and 20,000 cycles per second (hertz) in children. Our ability to hear high-pitched sounds decays progressively throughout middle age. Other vertebrates can detect sounds at frequencies lower than 20 hertz and much higher than 20,000 hertz. Dogs, for example, can detect sounds at 40,000 hertz, enabling them to hear high-pitched dog whistles that seem silent to a human listener.

Hair cells are also innervated by efferent axons from the brain, and impulses in those axons can make hair cells less sensitive. This central control of receptor sensitivity can increase an individual's ability to concentrate on a particular auditory signal (for example, a single voice) in the midst of background noise, which is effectively "tuned out" by the efferent axons.

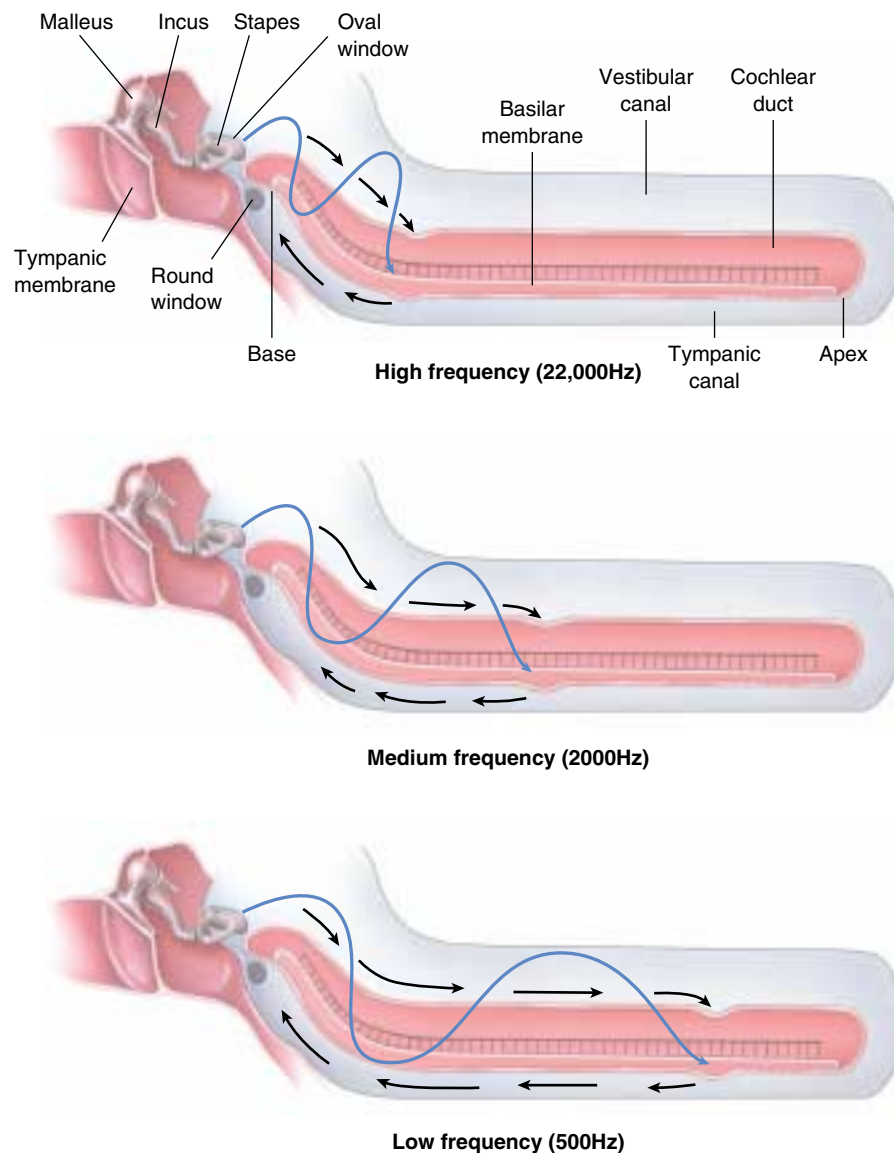


FIGURE 55.14 Frequency localization in the cochlea. The cochlea is shown unwound, so that the length of the basilar membrane can be seen. The fibers within the basilar membrane vibrate in response to different frequencies of sound, related to the pitch of the sound. Thus, regions of the basilar membrane show maximum vibrations in response to different sound frequencies. Notice that low-frequency (pitch) sounds vibrate the basilar membrane more toward the apex, while high frequencies cause vibrations more toward the base.

The middle ear ossicles vibrate in response to sound waves, creating fluid vibrations within the inner ear. This causes the hair cells to bend, transducing the sound into action potentials. The pitch of a sound is determined by which hair cells (and thus which sensory neurons) are activated by the vibration of the basilar membrane.

Sonar

Because terrestrial vertebrates have two ears located on opposite sides of the head, the information provided by hearing can be used by the CNS to determine *direction* of a sound source with some precision. Sound sources vary in strength, however, and sounds are attenuated (weakened) to varying degrees by the presence of objects in the environment. For these reasons, auditory sensors do not provide a reliable measure of *distance*.

A few groups of mammals that live and obtain their food in dark environments have circumvented the limitations of darkness. A bat flying in a completely dark room easily avoids objects that are placed in its path—even a wire less than a millimeter in diameter (figure 55.15). Shrews use a similar form of “lightless vision” beneath the ground, as do whales and dolphins beneath the sea. All of these mammals perceive distance by means of sonar. They emit sounds and then determine the time it takes these sounds to reach an

object and return to the animal. This process is called echolocation. A bat, for example, produces clicks that last 2 to 3 milliseconds and are repeated several hundred times per second. The three-dimensional imaging achieved with such an auditory sonar system is quite sophisticated.

Being able to “see in the dark” has opened a new ecological niche to bats, one largely closed to birds because birds must rely on vision. There are no truly nocturnal birds; even owls rely on vision to hunt, and do not fly on dark nights. Because bats are able to be active and efficient in total darkness, they are one of the most numerous and widespread of all orders of mammals.

Some mammals emit sounds and then determine the time it takes for the sound to return, using the method of sonar to locate themselves and other objects in a totally dark environment by the characteristics of the echo. Bats are the most adept at this echolocation.



FIGURE 55.15

Sonar. As it flies, a bat emits high-frequency “chirps” and listens for the return of the chirps after they are reflected by objects such as moths. By timing how long it takes for a chirp to return, the bat can locate its prey and catch it even in total darkness.

55.4 Optic receptors detect light over a broad range of wavelengths.

Evolution of the Eye

Vision begins with the capture of light energy by photoreceptors. Because light travels in a straight line and arrives virtually instantaneously, visual information can be used to determine both the direction and the distance of an object. No other stimulus provides as much detailed information.

Many invertebrates have simple visual systems with photoreceptors clustered in an eyespot. Simple eyespots can be made sensitive to the direction of a light source by the addition of a pigment layer which shades one side of the eye. Flatworms have a screening pigmented layer on the inner and back sides of both eyespots allowing stimulation of the photoreceptor cells only by light from the front of the animal (figure 55.16). The flatworm will turn and swim in the direction in which the photoreceptor cells are the least stimulated. Although an eyespot can perceive the direction of light, it cannot be used to construct a visual image. The members of four phyla—annelids, mollusks, arthropods, and chordates—have evolved well-developed, image-forming eyes. True image-forming eyes in these phyla, though strikingly similar in structure, are believed to have evolved independently (figure 55.17). Interestingly, the photoreceptors in all of them use the same light-capturing molecule, suggesting that not many alternative molecules are able to play this role.

Structure of the Vertebrate Eye

The eye of a human is typical of the vertebrate eye (figure 55.18). The “white of the eye” is the sclera, formed of tough connective tissue. Light enters the eye through a transparent cornea, which begins to focus the light. This

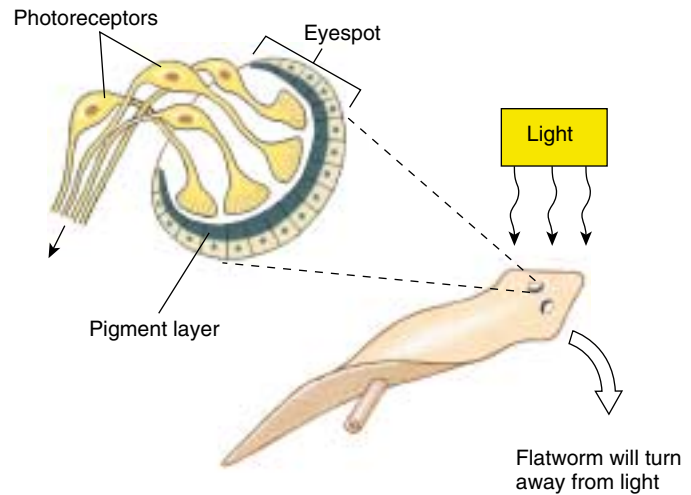


FIGURE 55.16
Simple eyespots in the flatworm. Eyespots will detect the direction of light because a pigmented layer on one side of the eyespot screens out light coming from the back of the animal. Light is thus the strongest coming from the front of the animal; flatworms will respond by turning away from the light.

occurs because light is refracted (bent) when it travels into a medium of different density. The colored portion of the eye is the iris; contraction of the iris muscles in bright light decreases the size of its opening, the pupil. Light passes through the pupil to the lens, a transparent structure that completes the focusing of the light onto the retina at the back of the eye. The lens is attached by the *suspensory ligament* to the ciliary muscles.

The shape of the lens is influenced by the amount of tension in the suspensory ligament, which surrounds the

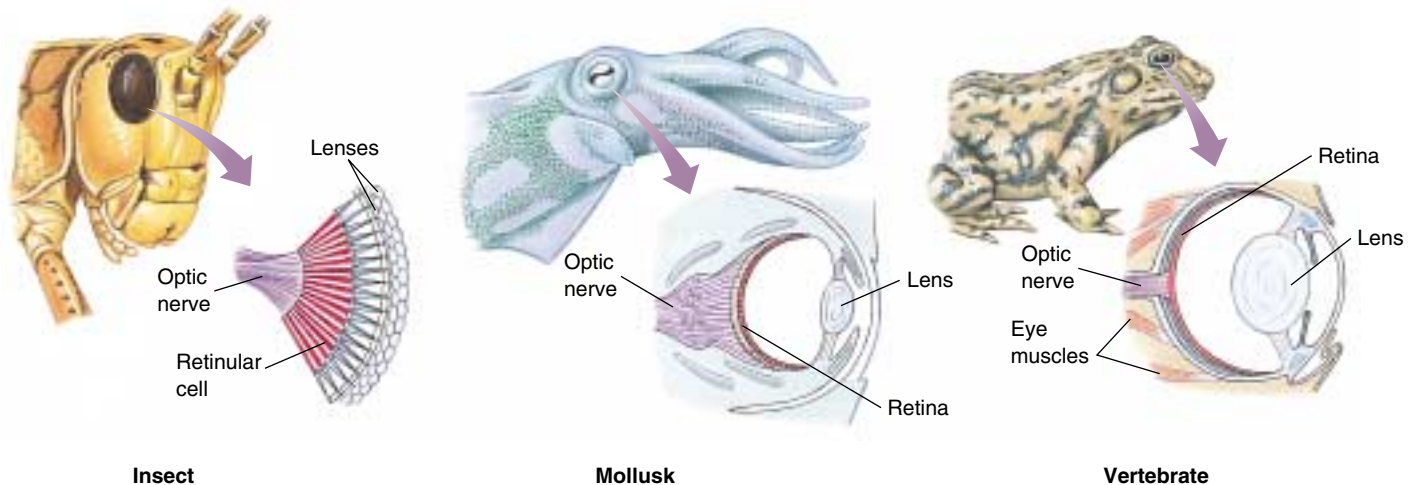


FIGURE 55.17
Eyes in three phyla of animals. Although they are superficially similar, these eyes differ greatly in structure and are not homologous. Each has evolved separately and, despite the apparent structural complexity, has done so from simpler structures.

lens and attaches it to the circular ciliary muscle. When the ciliary muscle contracts, it puts slack in the suspensory ligament and the lens becomes more rounded and powerful. This is required for close vision; in far vision, the ciliary muscles relax, moving away from the lens and tightening the suspensory ligament. The lens thus becomes more flattened and less powerful, keeping the image focused on the retina. People who are nearsighted or farsighted do not properly focus the image on the retina (figure 55.19). Interestingly, the lens of an amphibian or a fish does not change shape; these animals instead focus images by moving their lens in and out, just as you would do to focus a camera.

Annelids, mollusks, arthropods, and vertebrates have independently evolved image-forming eyes. The vertebrate eye admits light through a pupil and then focuses this light by means of an adjustable lens onto the retina at the back of the eye.

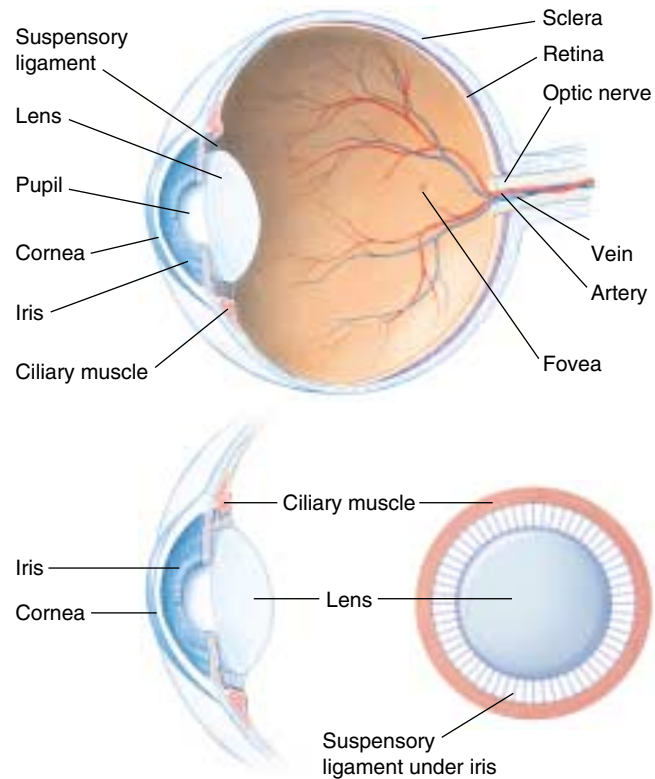


FIGURE 55.18
Structure of the human eye. The transparent cornea and lens focus light onto the retina at the back of the eye, which contains the rods and cones. The center of each eye's visual field is focused on the fovea. Focusing is accomplished by contraction and relaxation of the ciliary muscle, which adjusts the curvature of the lens.

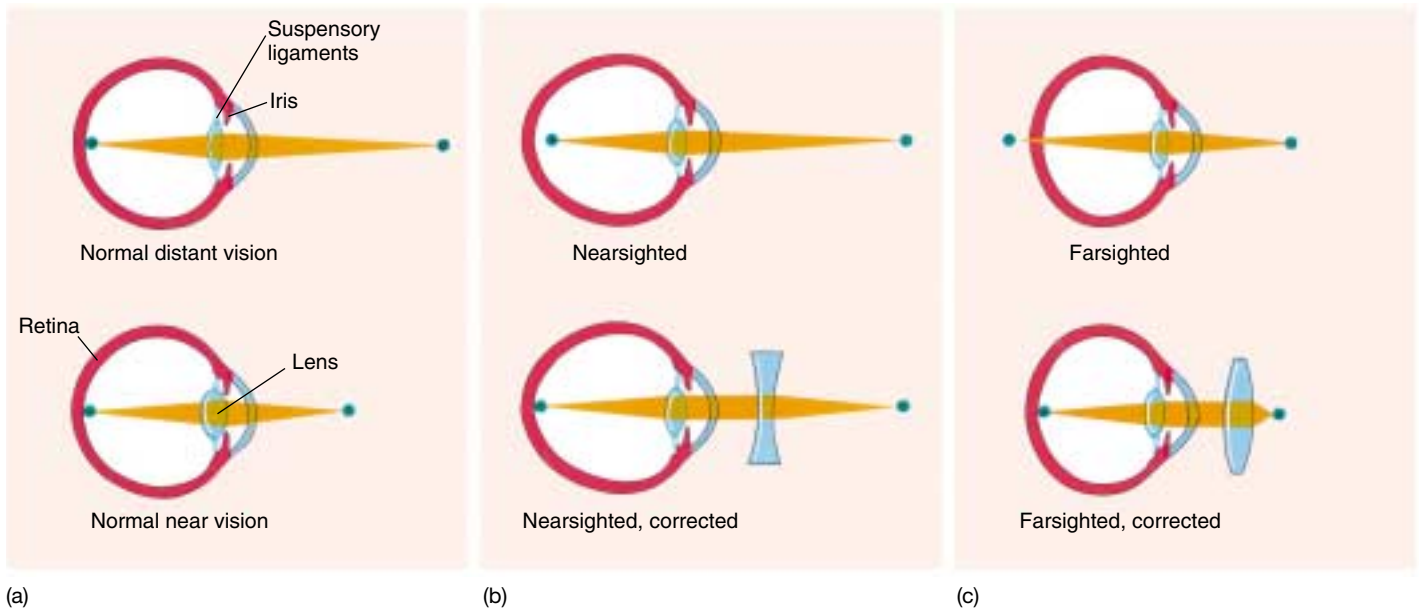


FIGURE 55.19
Focusing the human eye. (a) In people with normal vision, the image remains focused on the retina in both near and far vision because of changes produced in the curvature of the lens. When a person with normal vision stands 20 feet or more from an object, the lens is in its least convex form and the image is focused on the retina. (b) In nearsighted people, the image comes to a focus in front of the retina and the image thus appears blurred. (c) In farsighted people, the focus of the image would be behind the retina because the distance from the lens to the retina is too short.

Vertebrate Photoreceptors

The vertebrate retina contains two kinds of photoreceptors, called rods and cones (figure 55.20). Rods are responsible for black-and-white vision when the illumination is dim, while cones are responsible for high visual acuity (sharpness) and color vision. Humans have about 100 million rods and 3 million cones in each retina. Most of the cones are located in the central region of the retina known as the fovea, where the eye forms its sharpest image. Rods are almost completely absent from the fovea.

Rods and cones have the same basic cellular structure. An inner segment rich in mitochondria contains numerous vesicles filled with neurotransmitter molecules. It is connected by a narrow stalk to the outer segment, which is packed with hundreds of flattened discs stacked on top of one another. The light-capturing molecules, or photopigments, are located on the membranes of these discs.

In rods, the photopigment is called rhodopsin. It consists of the protein opsin bound to a molecule of *cis*-retinal (figure 55.21), which is derived from carotene, a photosynthetic pigment in plants. The photopigments of cones, called photopsins, are structurally very similar to rhodopsin. Humans have three kinds of cones, each of which possesses a photopsin consisting of *cis*-retinal bound to a protein with a slightly different amino acid sequence. These differences shift the *absorption maximum*—the region of the electromagnetic spectrum that is best absorbed by the pigment—(figure 55.22). The absorption maximum of the *cis*-retinal in rhodopsin is 500 nanometers (nm); the absorption maxima of the three kinds of cone photopsins, in contrast, are 455 nm (blue-absorbing), 530 nm (green-absorbing), and 625 nm (red-absorbing). These differences in the light-absorbing properties of the photopsins are responsible for the different color sensitivities of the three kinds of cones, which are often referred to as simply blue, green, and red cones.

Most vertebrates, particularly those that are diurnal (active during the day), have color vision, as do many insects. Indeed, honeybees can see light in the near-ultraviolet range, which is invisible to the human eye. Color vision requires the presence of more than one photopigment in different receptor cells, but not all animals with color vision have the three-cone system characteristic of humans and other primates. Fish, turtles, and birds, for example, have four or five kinds of cones; the “extra” cones enable these animals to see near-ultraviolet light. Many mammals (such as squirrels), on the other hand, have only two types of cones.

The retina is made up of three layers of cells (figure 55.23): the layer closest to the external surface of the eyeball consists of the rods and cones, the next layer contains bipolar cells, and the layer closest to the cavity of the eye is composed of ganglion cells. Thus, light must first pass through the ganglion cells and bipolar cells in order to reach the photoreceptors! The rods and cones synapse

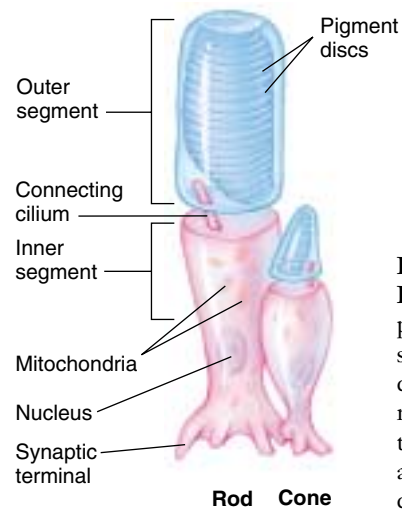


FIGURE 55.20
Rods and cones. The pigment-containing outer segment in each of these cells is separated from the rest of the cell by a partition through which there is only a narrow passage, the connective cilium.

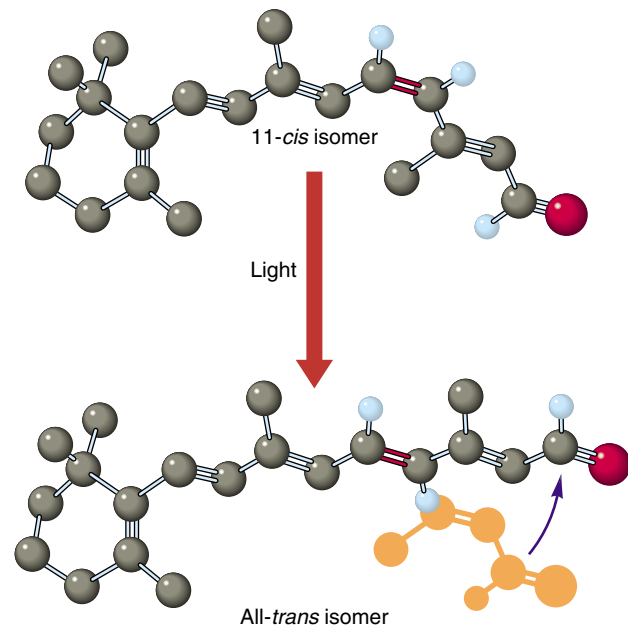


FIGURE 55.21
Absorption of light. When light is absorbed by a photopigment, the 11-*cis* isomer of retinal, the light-capturing portion of the pigment undergoes a change in shape: the linear end of the molecule (at the right in this diagram) rotates about a double bond (indicated here in red). The resulting isomer is referred to as all-*trans* retinal. This change in retinal’s shape initiates a chain of events that leads to hyperpolarization of the photoreceptor.

with the bipolar cells, and the bipolar cells synapse with the ganglion cells, which transmit impulses to the brain via the optic nerve. The flow of sensory information in the retina is therefore opposite to the path of light through the retina. It should also be noted that the retina contains two additional types of neurons, horizontal cells and amacrine cells. Stimulation of horizontal cells by photoreceptors at

the center of a spot of light on the retina can inhibit the response of photoreceptors peripheral to the center. This lateral inhibition enhances contrast and sharpens the image.

Sensory Transduction in Photoreceptors

The transduction of light energy into nerve impulses follows a sequence that is the inverse of the usual way that sensory stimuli are detected. This is because, in the dark, the photoreceptors release an inhibitory neurotransmitter that hyperpolarizes the bipolar neurons. Thus inhibited, the bipolar neurons do not release excitatory neurotransmitter to the ganglion cells. Light *inhibits* the photoreceptors from releasing their inhibitory neurotransmitter, and by this means, *stimulates* the bipolar cells and thus the ganglion cells, which transmit action potentials to the brain.

A rod or cone contains many Na^+ channels in the plasma membrane of its outer segment, and in the dark, many of these channels are open. As a consequence, Na^+ continuously diffuses into the outer segment and across the narrow stalk to the inner segment. This flow of Na^+ that occurs in the absence of light is called the dark current, and it causes the membrane of a photoreceptor to be somewhat depolarized in the dark. In the light, the Na^+ channels in the outer segment rapidly close, reducing the dark current and causing the photoreceptor to hyperpolarize.

Researchers have discovered that cyclic guanosine monophosphate (cGMP) is required to keep the Na^+ channels open, and that the channels will close if the cGMP is converted into GMP. How does light cause this conversion and consequent closing of the Na^+ channels? When a photopigment absorbs light, *cis*-retinal isomerizes and dissociates from opsin in what is known as the bleaching reaction. As a result of this dissociation, the opsin protein changes shape. Each opsin is associated with over a hundred regulatory *G proteins* (see chapters 7 and 54). When the opsin changes shape, the G proteins dissociate, releasing subunits that activate hundreds of molecules of the enzyme *phosphodiesterase*. This enzyme converts cGMP to GMP, thus closing the Na^+ channels at a rate of about 1000 per second and inhibiting the dark current. The absorption of a single photon of light can block the entry of more than a million sodium ions, thereby causing the photoreceptor to hyperpolarize and release less inhibitory neurotransmitters. Freed from inhibition, the bipo-

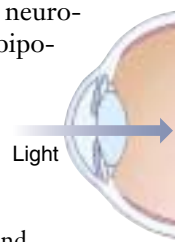


FIGURE 55.23

Structure of the retina. Note that the rods and cones are at the rear of the retina, not the front. Light passes through four other types of cells in the retina before it reaches the rods and cones. Once the photoreceptors are activated, they stimulate bipolar cells, which in turn stimulate ganglion cells. The direction of nerve impulses in the retina is thus opposite to the direction of light.

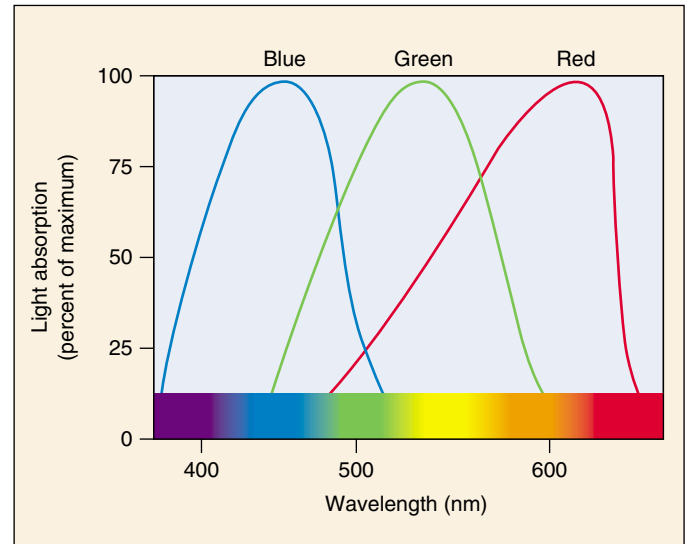
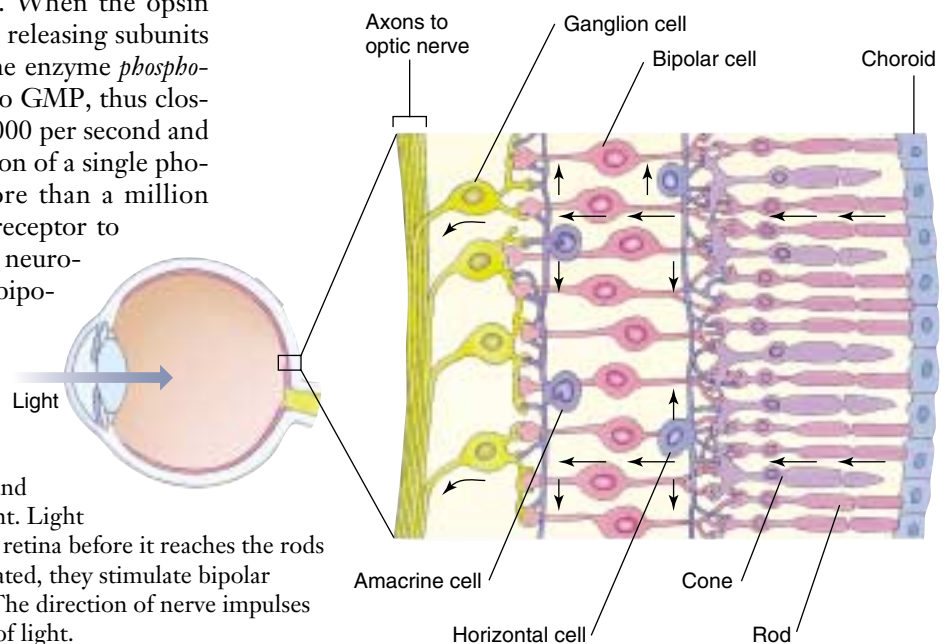


FIGURE 55.22

Color vision. The absorption maximum of *cis*-retinal in the rhodopsin of rods is 500 nanometers (nm). However, the “blue cones” have their maximum light absorption at 455 nm; the “green cones” at 530 nm, and the red cones at 625 nm. The brain perceives all other colors from the combined activities of these three cones’ systems.

lar cells activate ganglion cells, which transmit action potentials to the brain.

Photoreceptor rods and cones contain the photopigment *cis*-retinal, which dissociates in response to light and indirectly activates bipolar neurons and then ganglion cells.



Visual Processing in the Vertebrate Retina

Action potentials propagated along the axons of ganglion cells are relayed through structures called the lateral geniculate nuclei of the thalamus and projected to the occipital lobe of the cerebral cortex (figure 55.24). There the brain interprets this information as light in a specific region of the eye's receptive field. The pattern of activity among the ganglion cells across the retina encodes a point-to-point map of the receptive field, allowing the retina and brain to image objects in visual space. In addition, the frequency of impulses in each ganglion cell provides information about the light intensity at each point, while the relative activity of ganglion cells connected (through bipolar cells) with the three types of cones provides color information.

The relationship between receptors, bipolar cells, and ganglion cells varies in different parts of the retina. In the fovea, each cone makes a one-to-one connection with a bipolar cell, and each bipolar cell synapses, in turn, with one ganglion cell. This point-to-point relationship is responsible for the high acuity of foveal vision. Outside the fovea, many rods can converge on a single bipolar cell, and many bipolar cells can converge on a single ganglion cell. This convergence permits the summation of neural activity, making the area of the retina outside of the fovea more sensitive to dim light than the fovea, but at the expense of acuity and color vision. This is why dim objects, such as faint stars at night, are best seen when you don't look directly at them. It has been said that we use the periphery of the eye as a detector and the fovea as an inspector.

Color blindness is due to an inherited lack of one or more types of cones. People with normal color vision are *trichromats*; those with only two types of cones are *dichromats*. People with this condition may lack red cones (have *protanopia*), for example, and have difficulty distinguishing red from green. Men are far more likely to be color blind than women, because the trait for color blindness is carried on the X chromosome; men have only one X chromosome per cell, whereas women have two X chromosomes and so can carry the trait in a recessive state.

Binocular Vision

Primates (including humans) and most predators have two eyes, one located on each side of the face. When both eyes are trained on the same object, the image that each sees is slightly different because each eye views the object from a different angle. This slight displacement of the images (an effect called parallax) permits **binocular vision**, the ability to perceive three-dimensional images and to sense depth. Having their eyes facing forward maximizes the field of overlap in which this stereoscopic vision occurs.

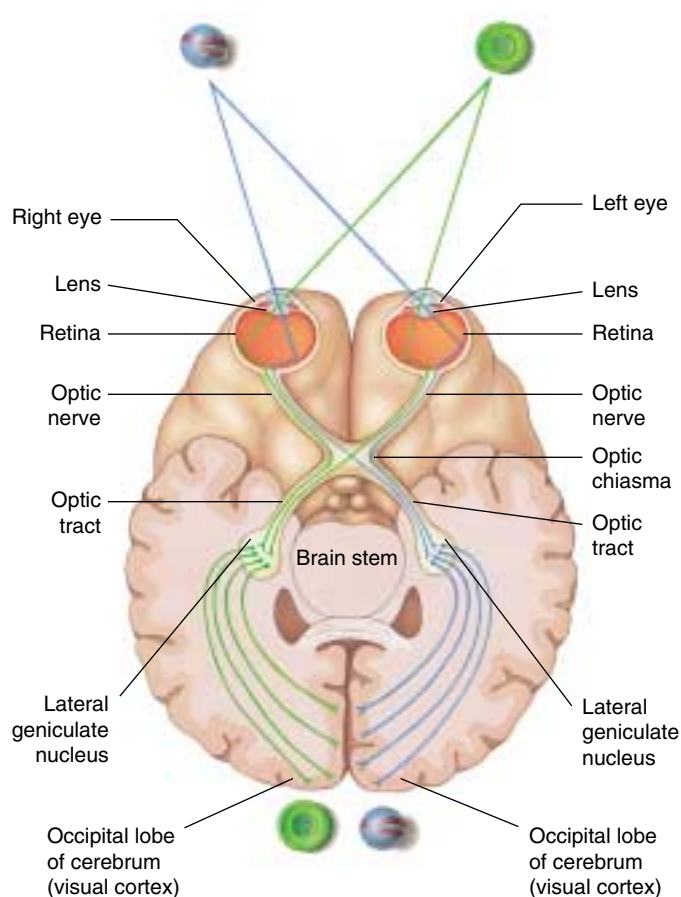


FIGURE 55.24

The pathway of visual information. Action potentials in the optic nerves are relayed from the retina to the lateral geniculate nuclei, and from there to the visual cortex of the occipital lobes. Notice that the medial fibers of the optic nerves cross to the other side at the optic chiasm, so that each hemisphere of the cerebrum receives input from both eyes.

In contrast, prey animals generally have eyes located to the sides of the head, preventing binocular vision but enlarging the overall receptive field. Depth perception is less important to prey than detection of potential enemies from any quarter. The eyes of the American Woodcock, for example, are located at exactly opposite sides of its skull so that it has a 360-degree field of view without turning its head! Most birds have laterally placed eyes and, as an adaptation, have two foveas in each retina. One fovea provides sharp frontal vision, like the single fovea in the retina of mammals, and the other fovea provides sharper lateral vision.

The axons of ganglion cells transmit action potentials to the thalamus, which in turn relays visual information to the occipital lobe of the brain. The fovea provides high visual acuity, whereas the retina outside the fovea provides high sensitivity to dim light. Binocular vision with overlapping visual fields provides depth perception.

55.5 Some vertebrates use heat, electricity, or magnetism for orientation.

Diversity of Sensory Experiences

Vision is the primary sense used by all vertebrates that live in a light-filled environment, but visible light is by no means the only part of the electromagnetic spectrum that vertebrates use to sense their environment.

Heat

Electromagnetic radiation with wavelengths longer than those of visible light is too low in energy to be detected by photoreceptors. Radiation from this *infrared* (“below red”) portion of the spectrum is what we normally think of as radiant heat. Heat is an extremely poor environmental stimulus in water because water has a high thermal capacity and readily absorbs heat. Air, in contrast, has a low thermal capacity, so heat in air is a potentially useful stimulus. However, the only vertebrates known to have the ability to sense infrared radiation are the snakes known as pit vipers.

The pit vipers possess a pair of heat-detecting pit organs located on either side of the head between the eye and the nostril (figure 55.25). The pit organs permit a blindfolded rattlesnake to accurately strike at a warm, dead rat. Each pit organ is composed of two chambers separated by a membrane. The infrared radiation falls on the membrane and warms it. Thermal receptors on the membrane are stimulated. The nature of the pit organ’s thermal receptor is not known; it probably consists of temperature-sensitive neurons innervating the two chambers. The two pit organs appear to provide stereoscopic information, in much the same way that two eyes do. Indeed, the information transmitted from the pit organs is processed by the visual center of the snake brain.

Electricity

While air does not readily conduct an electrical current, water is a good conductor. All aquatic animals generate electrical currents from contractions of their muscles. A number of different groups of fishes can detect these electrical currents. The *electrical fish* even have the ability to produce electrical discharges from specialized electrical organs. Electrical fish use these weak discharges to locate their prey and mates and to construct a three-dimensional image of their environment even in murky water.

The elasmobranchs (sharks, rays, and skates) have electroreceptors called the ampullae of Lorenzini. The receptor cells are located in sacs that open through jelly-filled canals to pores on the body surface. The jelly is a very good conductor, so a negative charge in the opening of the canal can depolarize the receptor at the base, causing the release of neurotransmitter and increased activity of sensory neurons. This allows sharks, for example, to detect the electrical fields generated by the muscle contrac-

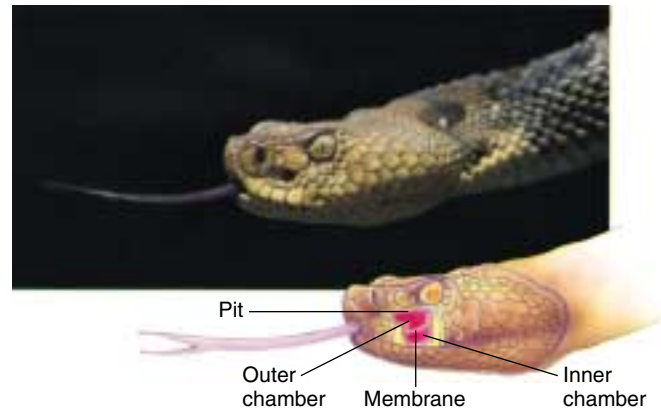


FIGURE 55.25

“Seeing” heat. The depression between the nostril and the eye of this rattlesnake opens into the pit organ. In the cutaway portion of the diagram, you can see that the organ is composed of two chambers separated by a membrane. Snakes known as pit vipers have this unique ability to sense infrared radiation (heat).

tions of their prey. Although the ampullae of Lorenzini were lost in the evolution of teleost fish (most of the bony fish), electroreception reappeared in some groups of teleost fish that use sensory structures analogous to the ampullae of Lorenzini. Electroreceptors evolved yet another time, independently, in the duck-billed platypus, an egg-laying mammal. The receptors in its bill can detect the electrical currents created by the contracting muscles of shrimp and fish, enabling the mammal to detect its prey at night and in muddy water.

Magnetism

Eels, sharks, bees, and many birds appear to navigate along the magnetic field lines of the earth. Even some bacteria use such forces to orient themselves. Birds kept in blind cages, with no visual cues to guide them, will peck and attempt to move in the direction in which they would normally migrate at the appropriate time of the year. They will not do so, however, if the cage is shielded from magnetic fields by steel. Indeed, if the magnetic field of a blind cage is deflected 120° clockwise by an artificial magnet, a bird that normally orients to the north will orient toward the east-southeast. There has been much speculation about the nature of the magnetic receptors in these vertebrates, but the mechanism is still very poorly understood.

Pit vipers can locate warm prey by infrared radiation (heat), and many aquatic vertebrates can locate prey and ascertain the contours of their environment by means of electroreceptors.

**Summary****Questions****Media Resources****55.1 Animals employ a wide variety of sensory receptors.**

- Mechanoreceptors, chemoreceptors, and photoreceptors are responsive to different categories of sensory stimuli; interoceptors and exteroceptors respond to stimuli that originate in the internal and external environments, respectively.

1. Can you name a sensory receptor that does not produce a membrane depolarization?



- Introduction to sense organs
- Receptors and sensations
- Somatic senses

55.2 Mechanical and chemical receptors sense the body's condition.

- Muscle spindles respond to stretching of the skeletal muscle.
- The sensory organs of taste are taste buds, scattered over the surface of a fish's body but located on the papillae of the tongue in terrestrial vertebrates.
- Chemoreceptors in the aortic and carotid bodies sense the blood pH and oxygen levels, helping to regulate breathing.
- Hair cells in the membranous labyrinth of the inner ear provide a sense of acceleration.

2. What mechanoreceptors detect muscle stretch and the tension on a tendon?



- Smell
- Taste
- Sense of balance
- Sense of rotational acceleration

3. What structures in the vertebrate ear detect changes in the body's position with respect to gravity? What structures detect angular motion?



- Sense of taste
- Sense of smell
- Equilibrium

55.3 Auditory receptors detect pressure waves in the air.

- In terrestrial vertebrates, sound waves cause vibrations of ear membranes.
- Different pitches of sounds vibrate different regions of the basilar membrane, and therefore stimulate different hair cells.
- Bats and some other vertebrates use sonar to provide a sense of "lightless vision."

4. How are sound waves transmitted and amplified through the middle ear? How is the pitch of the sound determined?



- Art Activity
Human ear anatomy



- Hearing

55.4 Optic receptors detect light over a broad range of wavelengths.

- A flexible lens focuses light onto the retina, which contains the photoreceptors.
- Light causes the photodissociation of the visual pigment, thereby blocking the dark current and hyperpolarizing the photoreceptor; this inverse effect stops the inhibitory effect of the photoreceptor and thereby activates the bipolar cells.

5. How does focusing in fishes and amphibians differ from that in other vertebrates?



- Art Activity
Human eye anatomy

6. When a photoreceptor absorbs light, what happens to the Na⁺ channels in its outer segment?



- Vision

55.5 Some vertebrates use heat, electricity, or magnetism for orientation.

- The pit organs of snakes allows them to detect the position and movements of prey. Many aquatic vertebrates can detect electrical currents produced by muscular contraction. Some vertebrates can orient themselves using the earth's magnetic field.

7. Why do rattlesnakes strike a moving lightbulb?



- Chemoreceptors

8. How do sharks detect their prey? Why don't terrestrial vertebrates have this sense?