SENSORY RECEPTION

About two thousand years ago, Aristotle identified five human senses—sight, hearing, smell, taste, and touch—commonly referred to as the "five senses." Today, zoologists know that animals also have other senses. For example, invertebrates possess an impressive array of sensory receptors through which they receive information about their environment. Common examples include tactile receptors that sense touch; georeceptors that sense the pull of gravity; hygroreceptors that detect the water content of air; proprioceptors that respond to mechanically induced changes caused by stretching, compression, bending, and tension; phonoreceptors that are sensitive to sound; baroreceptors that respond to pressure changes; chemoreceptors that respond to air- and waterborne molecules; photoreceptors that sense light; and thermoreceptors that are influenced by temperature changes.

Most vertebrates have a sense of equilibrium (balance) and a sense of body movement, and they are also sensitive to fine touch, touch-pressure, heat, taste, vision, olfaction, audition, cold, pain, and various other tactile stimuli. In addition, receptors in the circulatory system register changes in blood pressure and blood levels of carbon dioxide and hydrogen ions, and receptors in the digestive system are involved in the perception of hunger and thirst.

Overall, an animal's senses limit and define its impression of the environment. In fact, all awareness depends on the reception and decoding of stimuli from the external environment and from within an animal's body. The rest of this chapter examines how animals use sensory information to help maintain homeostasis.

Sensory receptors consist of cells that can convert environmental information (stimuli) into nerve impulses. A **stimulus** (pl., stimuli) is any form of energy an animal can detect with its receptors. All receptors are **transducers** ("to change over"); that is, they convert one form of energy into another. Because all nerve impulses are the same, different types of receptors convert different kinds of stimuli, such as light or heat, into a local electrical potential called the **generator potential.** If the generator potential reaches the sensory neuron's threshold potential, it causes channels in the plasma membrane to open and creates an action potential. The impulse then travels along the cell's axon toward a synaptic junction and becomes information going to the central nervous system or brain.

As presented in the beginning of this chapter, all action potentials are alike. Furthermore, an action potential is an all-or-none phenomenon; it either occurs or it doesn't. How, then, does a common action potential give rise to different sensations, such as taste, color, or sound, or different degrees of sensation? In those animals that have brains, some nerve signals from specific receptors always end up in a specific part of the brain for interpretation; therefore, a stimulus that goes to the optic center is interpreted as a visual stimulus. Another factor that characterizes a particular stimulus is its intensity. When the stimulus strength increases, the number of action potentials per unit of time also increases. Thus, the brain can perceive the intensity and type of stimulus from the timing of the impulses and the "wiring" of neurons.

Sensory receptors have the following basic features:

1. They contain sensitive receptor cells or finely branched peripheral endings of sensory neurons that respond to a stimulus by creating a generator potential.
2. Their structure is designed to receive a specific stimulus.
3. Their receptor cells synapse with afferent nerve fibers that travel to the central nervous system along specific neural pathways.
4. In the central nervous system, the nerve impulse is translated into a recognizable sensation, such as sound.

INVERTEBRATE SENSORY RECEPTORS

An animal's behavior is largely a function of its responses to environmental information. Invertebrates possess an impressive array of receptor structures through which they receive information about their environment. Some common examples are now discussed from a structural and functional perspective.

BARORECEPTORS

Baroreceptors (Gr. *baros*, weight + receptor) sense changes in pressure. However, zoologists have not identified any specific structures for baroreception in invertebrates. Nevertheless, responses to pressure changes have been identified in ocean-dwelling copepod crustaceans, ctenophores, jellyfish medusae, and squids. Some intertidal crustaceans coordinate migratory activity with daily tidal movements, possibly in response to pressure changes accompanying water depth changes.

CHEMORECEPTORS

Chemoreceptors (Gr. *chemeia*, pertaining to chemistry) respond to chemicals. Chemoreception is a direct sense in that molecules act specifically to stimulate a response. Chemoreception is the oldest and most universal sense in the animal kingdom. For example, protozoa have a chemical sense; they respond with avoidance behavior to acid, alkali, and salt stimuli. Specific chemicals attract predatory ciliates to their prey. The chemoreceptors of many aquatic invertebrates are located in pits or depressions, through which water carrying the specific chemicals may be circulated. In arthropods, the chemoreceptors are usually on the antennae, mouthparts, and legs in the form of hollow hairs (**sensilla;** sing., sensillum) containing chemosensory neurons (figure 24.13).

The types of chemicals to which invertebrates respond are closely associated with their lifestyles. Examples include chemoreceptors that provide information that the animal uses to perform tasks, such as humidity detection, pH assessment, prey tracking, food recognition, and mate location. With respect to mate location, the antennae of male silkworm moths *(Bombyx mori)* can detect one bombykol molecule in over a trillion molecules of air. Female silk moths secrete bombykol as a sex attractant, which

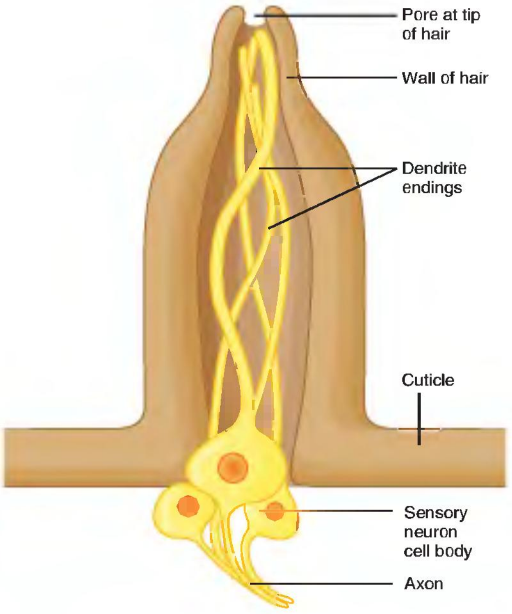

FIGURE 24.13

Invertebrate Chemoreceptor. Cross section through an insect sensillum. The receptor is a projection of the cuticle with a pore at the tip. Each chemoreceptor generally contains four to five dendrites, which lead to sensory neuron cell bodies underneath the cuticle. Each sensory cell has its own spectrum of chemical responses. Thus, a single sensillum with four or five dendrites and cell bodies may be capable of discriminating many different chemicals.

enables a male to find a female at night from several miles downwind, an ability that confers obvious reproductive advantage in a widely dispersed species.

GEORECEPTORS

Georeceptors (Gr. *ge*, earth + receptor) respond to the force of gravity. This gives an animal information about its orientation relative to "up" and "down." Most georeceptors are **statocysts** (Gr. *statos*, standing + *kystis*, bladder) (figure 24.14). Statocysts consist of a fluid-filled chamber lined with cilia-bearing sensory epithelium; within the chamber is a solid granule called a **statolith** (Gr. *lithos*, stone). Any movement of the animal changes the position of the statolith and moves the fluid, thus altering the intensity and pattern of information arising from the sensory epithelium. For example, when an animal moves, both the movement of the statolith and the flow of fluid over the sensory epithelium provide information about the animal's linear and rotational acceleration relative to the environment.

Statocysts are found in various gastropods, cephalopods, crustaceans, nemertines, polychaetes, and scyphozoans. These animals use information from statocysts in different ways. For example, burrowing invertebrates cannot rely on photoreceptors for orientation; instead, they rely on georeceptors for orientation within the substratum. Planktonic animals orient in their three-dimensional aquatic environment using statocysts. This is especially important at night and in deep water where there is little light.

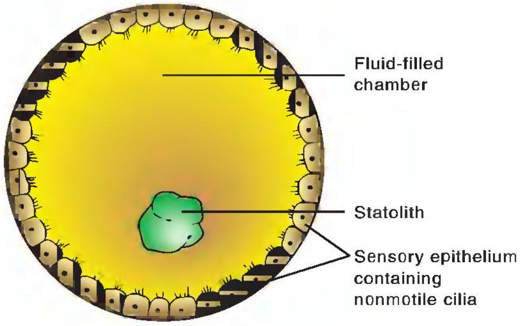

FIGURE 24.14

Invertebrate Georeceptor. A statocyst (cross section) consists of a fluid-filled chamber containing a solid granule called the statolith. The inner lining of the chamber contains tactile epithelium from which cilia associated with underlying neurons project.

In addition to having statocysts, a number of aquatic insects detect gravity from air bubbles trapped in certain passageways (e.g., tracheal tubes). Analogous to the air bubble in a carpenter's level, these air bubbles move according to their orientation to gravity. The air bubbles stimulate sensory bristles that line the tubes.

HYGRORECEPTORS

Hygroreceptors (Gr. *hygros*, moist) detect the water content of air. For example, some insects have hygroreceptors that can detect small changes in the ambient relative humidity. This sense enables them to seek environments with a specific humidity or to modify their physiology or behavior with respect to the ambient humidity (e.g., to control the opening or closing of spiracles). Zoologists have identified a variety of hygrosensory structures on the antennae, palps, underside of the body, and near the spiracles of insects. However, how a hygroreceptor transduces humidity into an action potential is not known.

PHONORECEPTORS

True **phonoreceptors** (Gr. *phone*, voice + receptor) that respond to sound have been demonstrated only in insects, arachnids, and centipedes, although other invertebrates seem to respond to sound-induced vibrations of the substratum. For example, crickets, grasshoppers, and cicadas possess phonoreceptors called **tympanic** or **tympanal organs** (figure 24.15). This organ consists of a tough, flexible tympanum that covers an internal sac that allows the tympanum to vibrate when sound waves strike it. Sensory neurons attached to the tympanum are stimulated and produce a generator potential.

Most arachnids possess phonoreceptors in their cuticle called slit sense organs that can sense sound-induced vibrations.

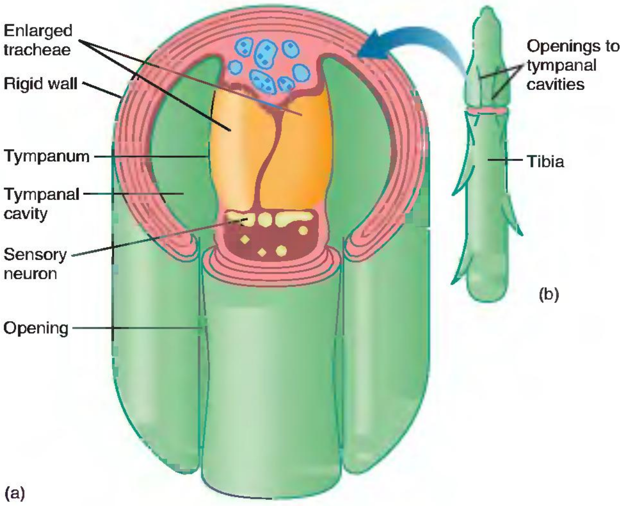

FIGURE 24.15

Invertebrate Phonoreceptor (Tympanal Organ). *(a)* This organ functions on the drumhead principle. The flattened outer wall (tympanum) of each trachea functions as a "drumhead." As the tympanum vibrates in response to sound waves, pressure changes within the tracheae affect the sensory neuron, causing a generator potential. *(b)* The slit openings on the leg (tibia) of a cricket lead to the tympanal cavities.

Centipedes have organs of Tomosvary, which some zoologists believe may be sensitive to sound. However, the physiology of both slit sense organs and organs of Tomosvary is poorly understood.

PHOTORECEPTORS

Photoreceptors (Gr. *photos,* light + receptor) are sensitive to light. All photoreceptors possess light-sensitive pigments (e.g., carotenoids, rhodopsin). These pigments absorb photons of light energy and then produce a generator potential. Beyond this basic commonality, the complexity and arrangement of photoreceptors within various animals vary incredibly.

Certain flagellated protozoa (*Euglena*) that contain chlorophyll possess a mass of bright red photoreceptor granules called the **stigma** (pl., stigmata) (figure 24.16*a*). The granules are carotenoid pigments. The actual photoreceptor is the swelling at the base of the flagellum. The stigma probably serves as a shield, which is essential if the photoreceptor is to detect light coming from certain directions but not from others. Thus, the photoreceptor plus the stigma enable *Euglena* to orient itself so that its photoreceptor is exposed to light. This helps the protozoan maintain itself in the region of the water column where sufficient light is available for photosynthesis.

Some animals, such as the earthworm *Lumbricus,* have simple unicellular photoreceptor cells scattered over the epidermis or concentrated in particular areas of the body. Others possess multicellular photoreceptors that can be classified into three basic types: ocelli, compound eyes, and complex eyes.

An **ocellus** (L. dim of *oculus,* eye) (pl., ocelli) is simply a small cup lined with light-sensitive receptors and backed by light-absorbing pigment (figure 24.16*b*). The light-sensitive cells are called retinular cells and contain a photosensitive pigment. Stimulation by light causes a chemical change in the pigment, leading to a generator potential, which causes an action potential that sensory neurons carry for interpretation elsewhere in the animal's body. This type of visual system gives an animal information about light direction and intensity, but not image formation. Ocelli are common in many phyla (e.g., Annelida, Mollusca, and Arthropoda).

Compound eyes consist of a few to many distinct units called **ommatidia** (Gr. *ommato,* eye + *ium,* little) (sing., ommatidium) (figure 24.16*c*). Although compound eyes occur in some annelids and bivalve molluscs, they are best developed and understood in arthropods. A compound eye may contain thousands of ommatidia, each oriented in a slightly different direction from the others as a result of the eye's overall convex shape. The visual field of a compound eye is very wide, as anyone who has tried to catch a fly knows. Each ommatidium has its own nerve tract leading to a large optic nerve. The visual fields of adjacent ommatidia overlap to some degree. Thus, if an object within the total visual field shifts position, the level of stimulation of several ommatidia changes. As a result of this physiology, as well as a sufficiently sophisticated central nervous system, compound eyes are very effective in detecting movements and are probably capable of forming an image. In addition, most compound eyes can adapt to changes in light intensities, and some provide for color vision. Color vision is particularly important in active, day-flying, nectar-drinking insects, such as honeybees. Honeybees learn to recognize particular flowers by color, scent, and shape.

The **complex camera eyes** of squids and octopuses are the best image-forming eyes among the invertebrates. In fact, the giant squid's eye is the largest of any animal's, exceeding 38 cm in diameter. Cephalopod eyes are often compared to those of vertebrates because they contain a thin, transparent cornea, and a lens that focuses light on the retina and is suspended by, and controlled by, ciliary muscles (figure 24.16*d*). However, the complex eyes of squids are different from the vertebrate eye in that the receptor sites on the retinal layer face in the direction of light entering the eye. In the vertebrate eye, the retinal layer is inverted, and the receptors are the deepest cells in the retina. Both eyes are focusing and image-forming, although the process differs in detail. In terrestrial vertebrates, muscles that alter the shape (thickness) of the lens focus light. In fishes and cephalopods, light is focused by muscles that move the lens toward or away from the retina (like moving a magnifying glass back and forth to achieve proper focus), and by altering the shape of the eyeball.

PROPRIOCEPTORS

Proprioceptors (L. *proprius,* one's self + receptor), commonly called "stretch receptors," are internal sense organs that respond to mechanically induced changes caused by stretching, compression, bending, or tension. These receptors give an animal information about the movement of its body parts and their positions

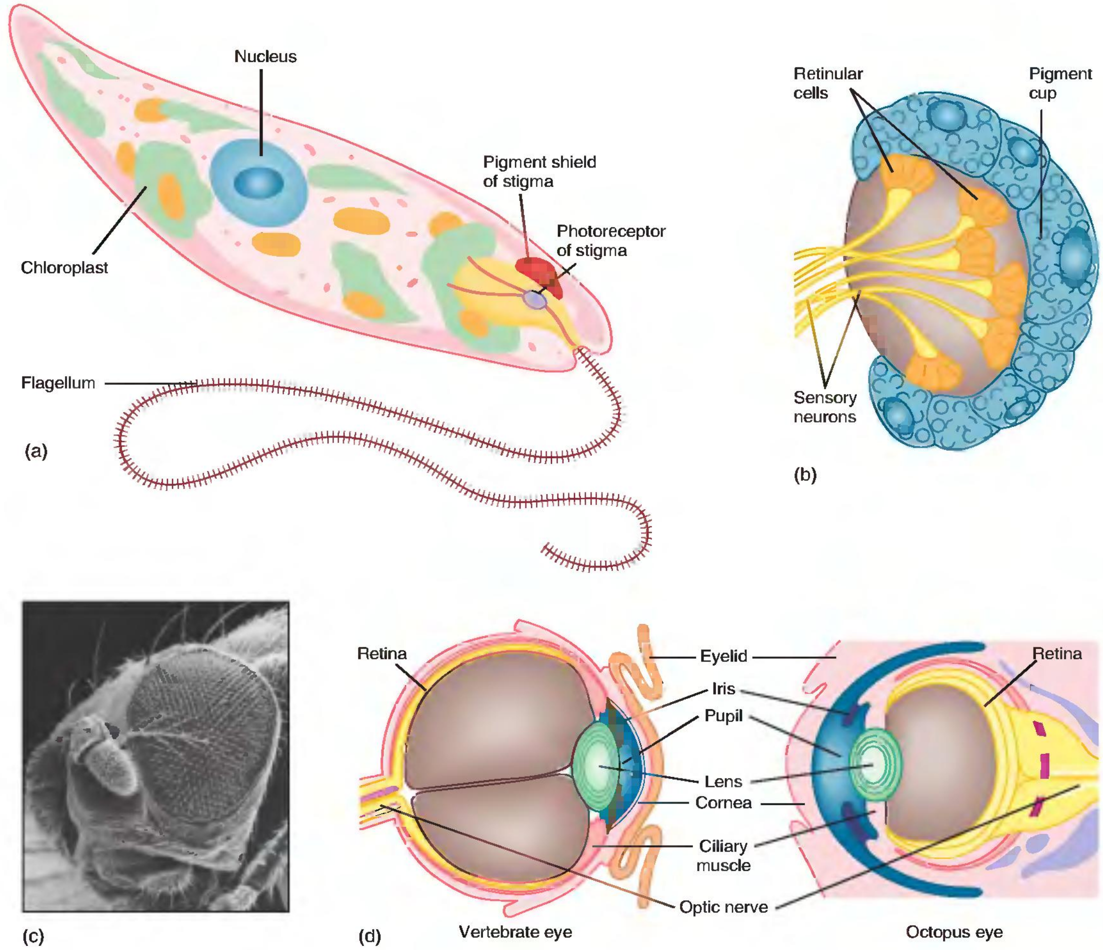

FIGURE 24.16

Invertebrate Photoreceptors. *(a)* Stigma. The protozoan, *Euglena,* contains a mass of bright red granules called the stigma. The actual photoreceptor is the swelling at the base of the flagellum. *(b)* Ocellus. The inverted pigment cup ocellus of a flatworm. *(c)* Compound eye. The compound eye of a fly contains hundreds of ommatidia. Note the eye's convex shape; no two ommatidia are oriented in precisely the same direction (SEM). *(d)* Complex camera eyes. Comparison of a vertebrate eye and an octopus eye (vertical sections).

relative to each other. Proprioceptors have been most thoroughly studied in arthropods, where they are associated with appendage joints and body extensor muscles (figure 24.17). In these animals, the sensory neurons involved in proprioception are associated with and attached to some part of the body that is stretched. These parts may be specialized muscle cells, elastic connective-tissue fibers, or various membranes that span joints. As these structures change shape, sensory nerve endings of the attached nerves distort accordingly and initiate a generator potential.

TACTILE RECEPTORS

Tactile (touch) receptors are generally derived from modifications of epithelial cells associated with sensory neurons. Most tactile receptors of animals involve projections from the body surface. Examples include various bristles, spines, setae, and tubercles. When an animal contacts an object in the environment, these receptors are mechanically deformed. These deformations activate the receptor, which, in turn, activates underlying sensory neurons, initiating a generator potential.

Most tactile receptors are also sensitive to mechanically induced vibrations propagated through water or a solid substrate. For example, tube-dwelling polychaetes bear receptors that allow them to retract quickly into their tubes in response to movements in their surroundings. Web-building spiders have tactile receptors that can sense struggling prey in webs through vibrations of the web threads.

THERMORECEPTORS

Thermoreceptors (Gr. *therme,* heat + receptors) respond to temperature changes. Some invertebrates can directly sense differences in environmental temperatures. For example, the protozoan

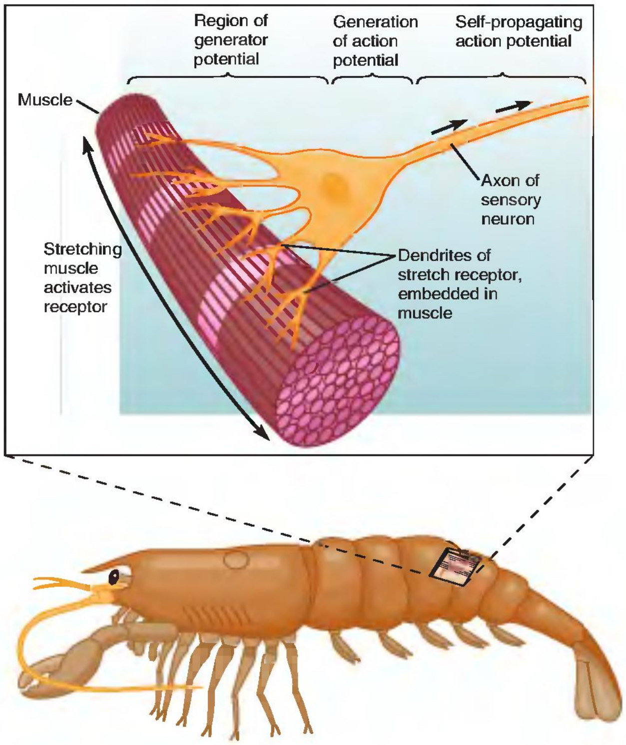

FIGURE 24.17

Invertebrate Proprioceptor. Crayfish stretch receptors are neurons attached to muscles. In this example, when the crayfish arches its abdomen while swimming, the stretch receptor detects the change in muscle length. When the muscle is stretched, so is the receptor. The stretch increases the sodium permeability of the receptor cell plasma membrane by mechanically opening sodium channels. The inflow of sodium ions produces depolarization and a generator potential that evokes an action potential. The axon of the sensory neuron then transmits the action potential to the central nervous system, where it is interpreted.

Paramecium collects in areas where water temperature is moderate, and it avoids temperature extremes. Somehow, a heat-sensing mechanism draws leeches and ticks to warm-blooded hosts. Certain insects, some crustaceans, and the horseshoe crab (*Limulus*) can also sense thermal variations. In all of these cases, however, specific receptor structures have not been identified.

VERTEBRATE SENSORY RECEPTORS

Vertebrate sensory receptors reflect adaptations to the nature of sensory stimuli in different external and internal environments. Each environment has chemical and physical characteristics that affect the kinds of energy and molecules that carry sensory information. For example, your external environment consists of the media thar surrounds you: the earth thar you stand on and the air that you breathe. Other animals may have different external environments: a trout may be immersed in the cool, clear water of a mountain stream; a turtle may be submerged in the turbid water of a swamp; and a salmon may be swimming in the salty water of the sea.

Each of the previous media contains only certain environmental stimuli. For example, air transmits light very well and conducts sound waves rather efficiently. But air can carry only a limited assortment of small molecules detectable using the sense of smell and can pass little or no electrical energy. In water, however, sound travels both faster and farther than in air, and water dissolves and carries a wide range of chemicals. Water, especially seawater, is also an excellent conductor of electricity, but it absorbs (and hence fails to transmit) many wavelengths of light. As these examples indicate, *vertebrate sensory receptors (organs), like invertebrate sensory receptors, have evolved in ways that relate to the environment in which they must function.*

Many underlying similarities unite all vertebrate senses. For each sense, there is a fascinating story of environmental information, the evolutionary adaptation of receptor cells to detect that information, and the processing in the central nervous system of the information so that the animal can use it. What follows is a discussion of particular vertebrate receptors (e.g., lateral-line systems, ears, eyes, skin sensors) that detect changes in the external environment, and of several receptors (e.g., pain, proprioception) that detect changes in the internal environment of some familiar vertebrate animals.

LATERAL-LINE SYSTEM AND ELECTRICAL SENSING

Specialized organs for equilibrium and gravity detection, audition, and magnetoreception have evolved from the lateral-line system of fishes. The **lateral-line system** for electrical sensing is in the head and body areas of most fishes, some amphibians, and the platypus (figure 24.18*a*). It consists of sensory pores in the epidermis of the skin that connect to canals leading into **electroreceptors** called **ampullary organs** (figure 24.18*b*). These organs can sense electrical currents in the surrounding water. Most living organisms generate weak electrical fields. The ability to detect these fields helps a fish to find mates, capture prey, or avoid predators. This is an especially valuable sense in deep, turbulent, or murky water, where vision is of little use. In fact, some fishes actually generate electrical fields and then use their electroreceptors (electrocommunication) to detect how surrounding objects distort the field. This allows these fishes to navigate in murky or turbulent waters.

LATERAL-LINE SYSTEM AND MECHANORECEPTION

A **mechanoreceptor** is excited by mechanical pressures or distortions (e.g., sound, touch, and muscular contractions). The lateral-line system of cyclostomes, sharks, some of the more advanced fishes, and aquatic amphibians includes several different kinds of hair-cell mechanoreceptors called **neuromasts.** Neuromasts are in

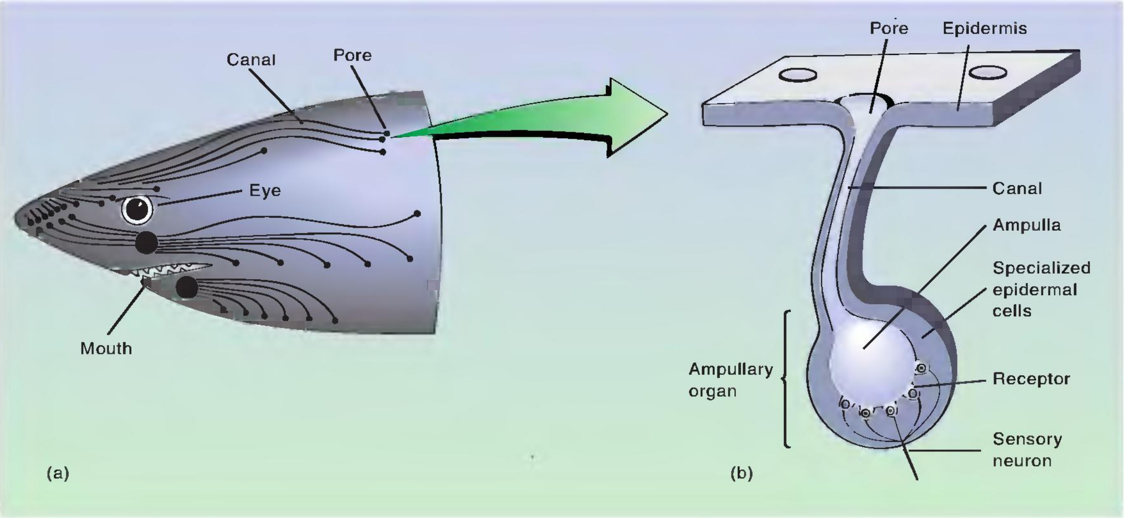

FIGURE 24.18

Lateral-Line System and Electrical Sensing. *(a)* In jawless fishes, jawed fishes, and amphibians, electroreceptors are in the epidermis along the sides of the head and body. *(b)* Pores of the lateral-line system lead into canals that connect to an ampullary organ that functions in electroreception and the production of a generator potential.

pits along the body, but not in the head region (figure 24.19*a*,*b*). All neuromasts are responsive to local water displacement or disturbance. When the water near the lateral line moves, it moves the water in the pits and distorts the hair cells, causing a generator potential in the associated sensory neurons (figure 24.19*c*). Thus, the animal can detect the direction and force of water currents and the movement of other animals or prey in the water. For example, this sense enables a trout to orient with its head upstream.

HEARING AND EQUILIBRIUM IN AIR

Hearing may initially have been important to vertebrates as a mechanism to alert them to either nearby or faraway potentially dangerous activity. It also became important in the search for food and mates, and in communication. Hearing (audition) and equilibrium (balance) are considered together because both sensations are received in the same vertebrate organ—the ear. The vertebrate ear has two functional units: (1) the auditory apparatus is concerned with hearing, and (2) the vestibular apparatus is concerned with posture and equilibrium.

Sound results when pressure waves transmit energy through some medium, such as air or water. Hearing in air poses serious problems for vertebrates, since middle-ear transformers are sound pressure sensors, but in air, sound produces less than 0.1% of the pressure it produces in water. *Adaptation to hearing in air resulted from the evolution of an acoustic transformer that incorporates a thin, stretched membrane, called either an eardrum, tympanic membrane, or tympanum, that is exposed to the air.*

The tympanum first evolved in the amphibians. The ears of anurans (frogs) consist of a tympanum, a middle ear, and an inner ear (figure 24.20). The tympanum is modified integument stretched over a cartilaginous ring. It vibrates in response to sounds and transmits these movements to the middle ear, a chamber behind the tympanum. Touching the tympanum is an ossicle (a small bone or bony structure) called the columella or stapes. The opposite end of the columella (stapes) touches the membrane of the oval window, which stretches between the middle and inner ears. High-frequency (1,000 to 5,000 Hz) sounds strike the tympanum and are transmitted through the middle ear via the columella and cause pressure waves in the fluid of the semicircular canals. These pressure waves in the inner ear fluid stimulate receptor cells. A second small ossicle, the operculum, also touches the oval window. Substrate-borne vibrations transmitted through the front appendages and the pectoral girdle cause this ossicle to vibrate. The resulting pressure waves in the inner ear stimulate a second patch of sensory receptor cells that is sensitive to low-frequency (100 to 1,000 Hz) sounds. Muscles attached to the operculum and columella can lock either or both of these ossicles, allowing a frog to screen out either high- or low-frequency sounds. *This mechanism is adaptive because frogs use low- and high-frequency sounds in different situations. For example, mating calls are high-frequency sounds that are of primary importance for only part of the year (breeding season). At other times, low-frequency sounds may warn of approaching predators.*

Salamanders lack a tympanum and middle ear. They live in streams, ponds, and caves, and beneath leaf litter. They have no mating calls, and the only sounds they hear are probably transmitted through the substratum and skull to the inner ear.

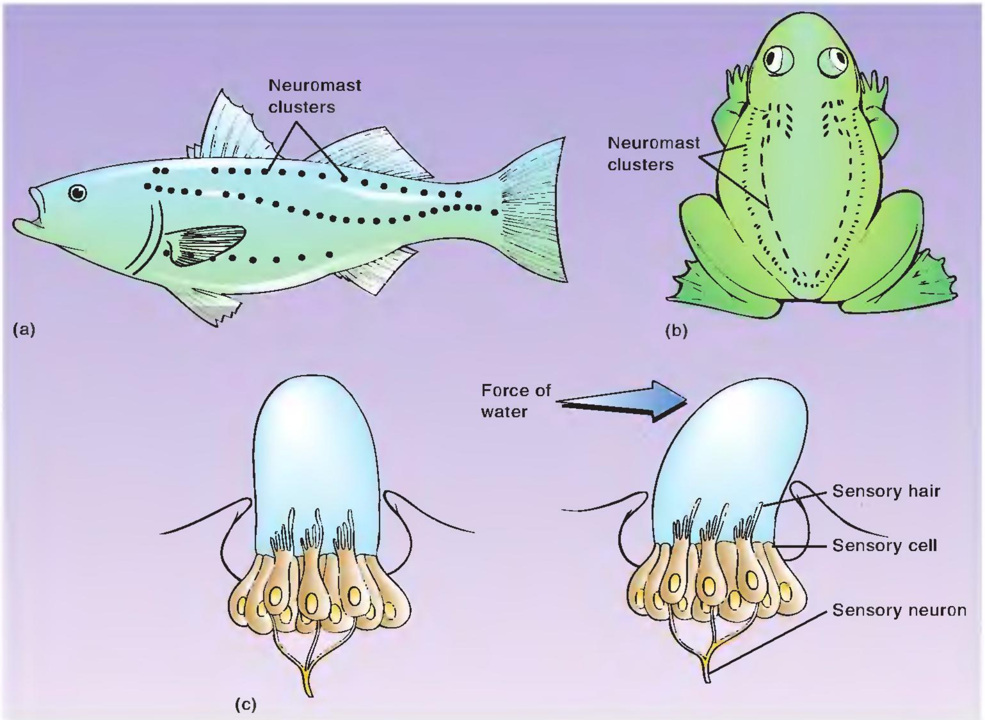

FIGURE 24.19

Lateral-Line System and Mechanoreception. The lateral-line system of *(a)* a bony fish and *(b)* a frog, showing the various neuromast clusters. *(c)* Action of neuromast stimulation. The water movement (blue arrow) forces the cap-like structure covering a group of neuromast cells to bend or distort, thereby distorting the small sensory hairs of the neuromast cells, producing a generator potential. The generator potential causes an action potential in the sensory neuron.

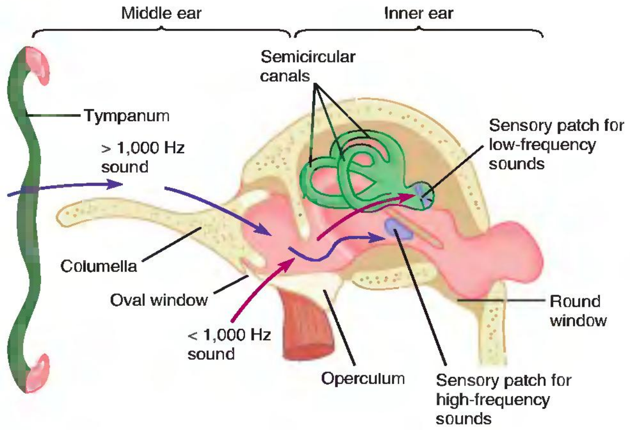

FIGURE 24.20

Ear of an Anuran (Posterior View). Red arrows show the pathway of low-frequency sounds, via the operculum. Dark-blue arrows show the pathway of high-frequency sounds, via the columella (stapes).

The sense of equilibrium and balance in amphibians involves the semicircular canals. These canals help detect rotational movements and gravity. Since the semicircular canals have a similar function in all vertebrates, they are discussed later in this section in information about the human ear.

The structures of reptilian ears vary. For example, the ears of snakes lack a middle-ear cavity and a tympanum. A bone of the jaw articulates with the stapes and receives vibrations of the substratum. In other reptiles, a tympanum may be on the surface or in a small depression in the head. The inner ear of reptiles is similar to that of amphibians.

Hearing is well developed in most birds. Loose, delicate feathers cover the external ear opening. Middle- and inner-ear structures are similar to those of mammals.

Auditory senses were also important to the early mammals. Adaptations include an ear flap (the auricle) and the auditory tube (external auditory canal), leading to the tympanum that directs sounds to the middle ear. In mammals, the long, coiled, sensory structure of the inner ear that contains receptors for sound is the cochlea. *This structure provides more surface area for receptor cells and gives mammals greater sensitivity to pitch and volume than is present in other animals.* Since the structure

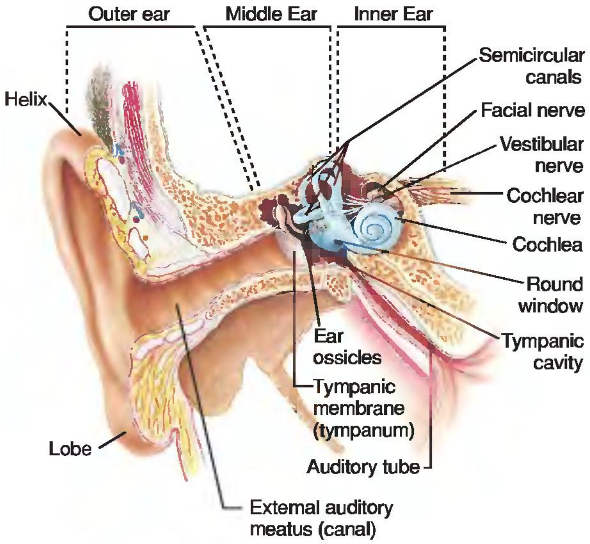

FIGURE 24.21

Anatomy of the Human Ear. Note the outer, middle, and inner regions. The inner ear includes the semicircular canals, which are involved with equilibrium, and the cochlea, which is involved with hearing.

and function of all mammal ears are basically the same, the familiar human ear is a good example.

The human ear has three divisions: the outer, middle, and inner ear. The outer ear consists of the auricle and external auditory canal (figure 24.21). The middle ear begins at the tympanic membrane (tympanum or eardrum) and ends inside the skull, where two small membranous openings, the oval and round windows, are located. Three small ossicles are between the tympanic membrane and the oval window. They include the malleus (hammer), incus (anvil), and stapes (stirrup), so named for their shapes. The malleus adheres to the tympanic membrane and connects to the incus. The incus connects to the stapes, which adheres to the oval window. The auditory (eustachian) tube extends from the middle ear to the nasopharynx and equalizes air pressure between the middle ear and the throat.

The inner ear has three components. The first two, the vestibule and the semicircular canals, are concerned with equilibrium, and the third, the cochlea, is involved with hearing. The semicircular canals are arranged so that one is in each dimension of space. The process of hearing can be summarized as follows:

1. Sound waves enter the outer ear and create pressure waves that reach the tympanic membrane.
2. Air molecules under pressure vibrate the tympanic membrane. The vibrations move the malleus on the other side of the membrane.
3. The handle of the malleus articulates with the incus, vibrating it.
4. The vibrating incus moves the stapes back and forth against the oval window.
5. The movements of the oval window set up pressure changes that vibrate the fluid in the inner ear. These vibrations are transmitted to the basilar membrane, causing it to ripple.
6. Receptor hair cells of the organ of Corti that are in contact with the overlying tectorial membrane are bent, causing a generator potential, which leads to an action potential that travels along the vestibulocochlear nerve to the brain for interpretation.
7. Vibrations in the cochlear fluid dissipate as a result of movements of the round window.

Humans are not able to hear low-pitched sounds, below 20 cycles per second, although some other vertebrates can. Young children can hear high-pitched sounds up to 20,000 cycles per second, but this ability decreases with age. Other vertebrates can hear sounds at much higher frequencies. For example, dogs can easily detect sounds of 40,000 cycles per second. Thus, dogs can hear sounds from a high-pitched dog whistle that seems silent to humans.

The sense of equilibrium (balance) can be divided into two separate senses. Static equilibrium refers to sensing movement in one plane (either vertical or horizontal), and dynamic equilibrium refers to sensing angular and/or rotational movement.

When the body is still, the otoliths in the semicircular canals rest on hair cells (figure 24.22*a*). When the head or body moves horizontally, or vertically, the granules are displaced, causing the gelatinous material to sag (figure 24.22*b*). This displacement bends the hairs slightly so that hair cells initiate a generator potential and then an action potential. Continuous movement of the fluid in the semicircular canals may cause motion sickness or seasickness in humans.

HEARING AND EQUILIBRIUM IN WATER

In bony fishes, receptors for equilibrium, balance, and hearing are in the inner ear, and their functions are similar to those of other vertebrates (figure 24.23). For example, semicircular canals detect rotational movements, and other sensory patches help with equilibrium and balance by detecting the direction of gravitational pull. Since fishes lack the outer and/or middle ear found in other vertebrates, vibrations pass from the water through the bones of the skull to the inner ear. A few fishes have chains of bony ossicles (modifications of vertebrae) that pass between the swim bladder and the back of the skull. Vibrations that strike the fishes are thus amplified by the swim bladder and sent through the ossicles to the skull.

SKIN SENSORS OF DAMAGING STIMULI

Pain receptors are bare sensory nerve endings that are present throughout the body of mammals, except for the brain and intestines. These nerve endings are also called **nociceptors** (L. *no-cere*,

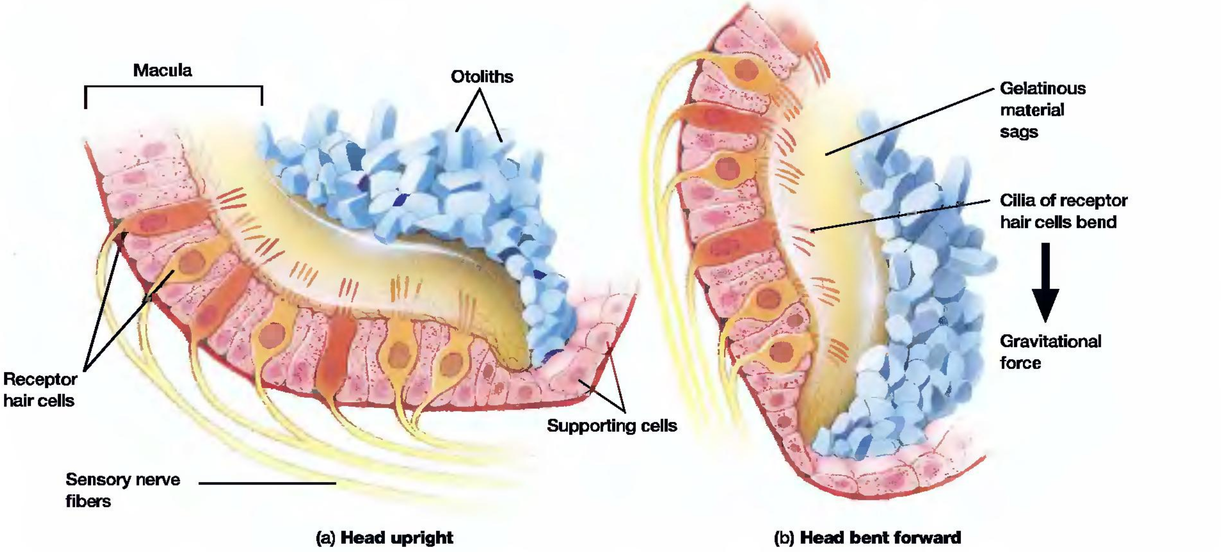

FIGURE 24.22

Static Equilibrium (Balance). Receptor hair cells in the utricle and saccule respond to sideways or up or down movement. *(a)* When the head is upright, otoliths are balanced directly over the cilia of receptor hair cells. *(b)* When the head bends forward, the otoliths shift, and the cilia of hair cells bend. This bending of hairs initiates a generator potential.

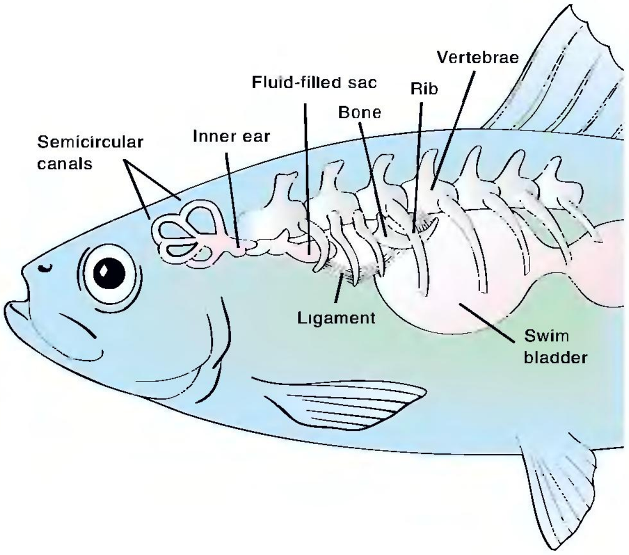

FIGURE 24.23

Inner Ear of a Bony Fish. Sound waves that enter the pharynx are transmitted to gas in the swim bladder, causing it to expand and contract at frequencies and amplitudes corresponding to the incoming sound waves. Contacting the swim bladder is a bone that is suspended by ligaments and vibrates at the same frequency. The vibrations pass forward along a chain of bones (ossicles) and then to a fluid-filled sac connected directly to the inner ear.

to injure + receptor). Severe heat, cold, irritating chemicals, and strong mechanical stimuli (e.g., penetration) may elicit a response from nociceptors that the brain interprets as pain or itching. Details of the structure and physiology of pain receptors, however, are unknown.

SKIN SENSORS OF HEAT AND COLD

Sensors of temperature (thermoreceptors) are also bare sensory nerve endings. Thermoreceptors may be present in either the epidermis or dermis. Mammals have a distinctly different distribution of areas sensitive to either cold or warm. These areas are called cold or warm spots. A spot refers to a small area of the skin that, when stimulated, yields a temperature sensation of warmth or cold. Cold receptors in the skin respond to temperatures below skin temperature, and heat receptors respond to temperatures above skin temperature. Materials coming into contact with the skin need not be warm or cold to produce temperature sensations. For example, when metal is placed on the skin, it absorbs heat and you feel a sense of coldness. Wood placed on the skin absorbs less heat and, therefore, feels warmer than metal.

The ability to detect changes in temperature has become well developed in a number of animals. For example, rattlesnakes and other pit vipers have heat-sensitive **pit organs** on each side of the face between the eye and nostril (figure 24.24). These depressions are lined with sensory epithelium containing receptor cells that respond to temperatures (infrared thermal regulation) different from the snakes' surroundings. Snakes use these pit organs to locate warm-blooded prey.

FIGURE 24.24

Thermoreception. A rattlesnake *(Crotalus vergrandis)* has a pit organ between each eye and nostril that detects heat and allows the snake to locate warm prey in the dark.

SKIN SENSORS OF MECHANICAL STIMULI

Many animals rely on tactile (pertaining to touch) stimuli to obtain information about their environment. Mechanical sensory receptors in vertebrate skin detect stimuli that the brain interprets as light touch, touch-pressure, and vibration.

Light touch is perceived when the skin is touched, but not strongly deformed. Receptors of light touch include **bare sensory nerve endings** and **tactile (Meissner's) corpuscles** (figure 24.25). Bare sensory nerve endings are the most widely distributed receptors in the vertebrate body, and are involved with pain and thermal stimuli, as well as light touch. The **bulbs of Krause** are mechanoreceptors, found in the dermis in certain parts of the body, that respond to some physical stimuli, such as position changes. Other receptors for touch-pressure are **Pacinian corpuscles** and the **organs of Ruffini.**

Many mammals have specially adapted sensory hairs called **vibrissae** (sing., vibrissa) on their wrists, snouts, and eyebrows (e.g., cat whiskers). Around the base of each vibrissa is a blood sinus. Nerves that border the sinus carry impulses from several kinds of mechanoreceptors to the brain for interpretation.

SONAR

Bats, shrews, several cave-dwelling birds (oilbird, cave swiftlet), whales, and dolphins can determine distance and depth by a form of echolocation called **sonar (biosonar).** These animals emit high-frequency sounds and then determine how long it takes for the sounds to return after bouncing off objects in the environment. For example, some bats emit clicks that last from 2 to 3 milliseconds and are repeated several hundred times per second. The returning echo created when a moth or other insect flies past the bat can provide enough information for the bat to locate and catch its prey. Overall, the three-dimensional imaging achieved with this auditory sonar system is quite sophisticated.

SMELL

The sense of smell, or **olfaction** (L. *olere*, to smell + *facere*, to make), is due to olfactory neurons (receptor cells) in the roof of the vertebrate nasal cavity (figure 24.26). These cells, which are specialized endings of the fibers that make up the olfactory nerve, lie among supporting epithelial cells. They are densely packed; for example, a dog has up to 40 million olfactory receptor cells per square centimeter. Each olfactory cell ends in a tuft of cilia containing receptor sites for various chemicals.

Several theories have been proposed to explain how odors are perceived. The most likely one is that odor molecules physically interacr with protein receptors on the receptor-plasma membrane. Such an interaction somehow alters membrane permeability and leads to a generator potential.

In most fishes, openings (external nares) in the snout lead to the olfactory receptors. Recent research has revealed that some fishes rely heavily on their sense of smell. For example, salmon and lampreys return to spawn in the same streams in which they hatched years earlier. Their migrations to these streams often involve distances of hundreds of miles and are guided by the fishes' perception of characteristic odors of their spawning stream.

Olfaction is an important sense for many amphibians. It is used in mate recognition, as well as in detecting noxious chemicals and locating food.

Olfactory senses are better developed in reptiles than in amphibians. In addition to having more olfactory epithelium, most reptiles (except crocodilians) possess blind-ending pouches that open into the mouth. These pouches, called **Jacobson's (vomeronasal) organs,** are best developed in snakes and lizards (figure 24.27). The protrusible, forked tongues of snakes and lizards are accessory olfactory organs used to sample airborne chemicals. A snake's tongue flicks out and then moves to the Jacobson's organs, which perceive odor molecules. Turtles and the tuatara use Jacobson's organs to taste objects held in the mouth.

Olfaction apparently plays a minor role in the lives of most birds. External nares open near the base of the beak, but the olfactory epithelium is poorly developed. Vultures are exceptions, in that they locate dead and dying prey largely by smell.

Many mammals can perceive olfactory stimuli over long distances during either the day or night. They use the stimuli to locate food, recognize members of the same species, and avoid predators.

TASTE

The receptors for taste, or **gustation** (L. *gustus*, taste), are chemoreceptors. They may be on the body surface of an animal or in the mouth and throat. For example, the surface of the mammalian tongue is covered with many small protuberances called

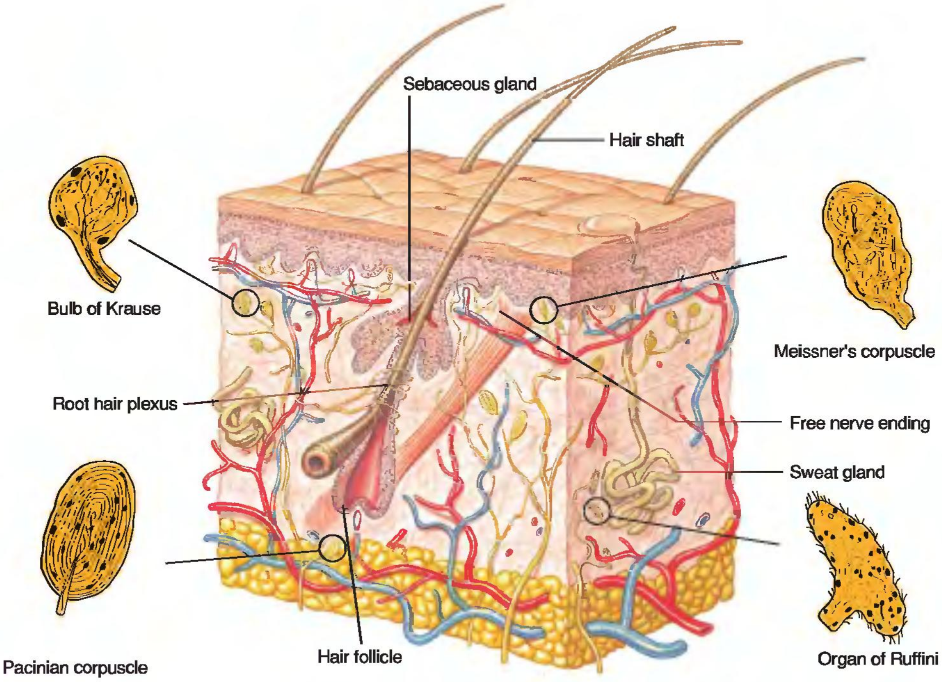

FIGURE 24.25

Different Sensory Receptors to Mechanical Stimuli. Sensory receptors in the skin for light touch (Meissner's corpuscles), touch-pressure (organs of Ruffini and Pacinian corpuscles), position (bulbs of Krause), and pain (free nerve endings).

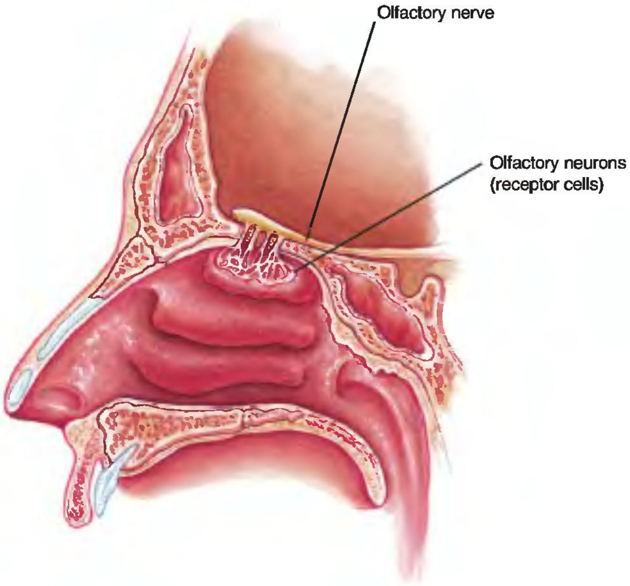

FIGURE 24.26

Smell. Position of olfactory receptors in a human nasal passageway. Columnar epithelial cells support the receptor cells, which have hair-like processes (analogous to dendrites) projecting into the nasal cavity. When chemicals in the air stimulate these receptor cells, the olfactory nerves conduct nerve impulses to the brain.

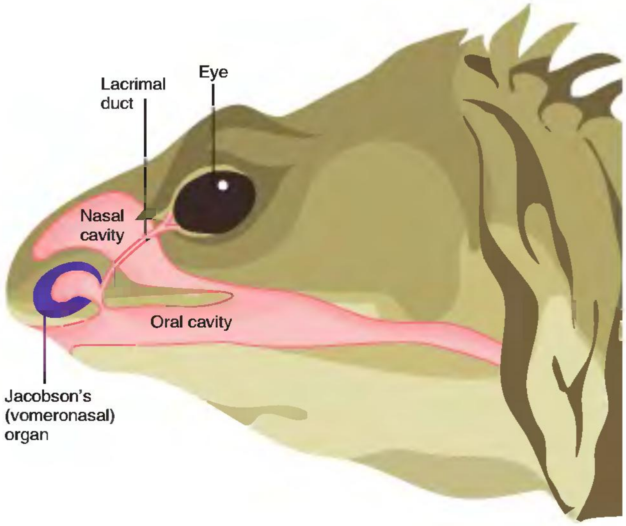

FIGURE 24.27

Smell. Anatomic relationships of Jacobson's (vomeronasal) organ in a generalized lizard. Only the left organ alongside the nasal cavity is shown. Jacobson's organ is a spherical structure, with the ventral side invaginated into a sphere the shape of a mushroom. A narrow duct connects the interior of Jacobson's organ to the oral cavity. In many lizards, fluid draining from the eye via the lacrimal duct may bring odoriferous molecules into contact with the sensory epithelium of Jacobson's organ.

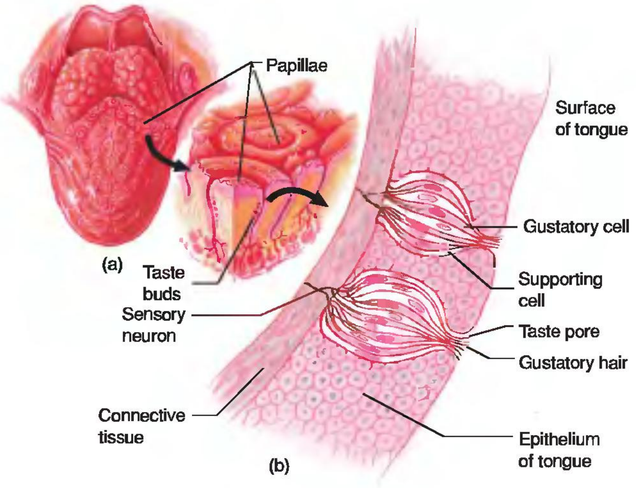

FIGURE 24.28

Taste. *(a)* Surface view of the human tongue, showing the many papillae and the numerous taste buds between papillae. *(b)* Supporting cells encapsulate the gustatory cell and its associated gustatory hair.

papillae (sing., papilla). Papillae give the tongue its "bumpy" appearance (figure 24.28*a*). In the crevices between the papillae are thousands of specialized receptors called **taste buds** (figure 24.28*b*). Taste buds are barrel-shaped clusters of chemoreceptor cells called gustatory cells and supporting cells arranged like alternating segments of an orange. Extending from each receptor cell are gustatory hairs that project through a tiny opening called the taste pore. Sensory neurons are associated with the basal ends of the gustatory cells.

The four generally recognized taste sensations are sweet (sugars), sour (acids), bitter (alkaloids), and salty (electrolytes). The exact mechanism(s) that stimulate a chemoreceptor taste cell are not known. One theory is that different types of gustatory stimuli cause proteins on the surface of the receptor-cell plasma membrane to change the permeability of the membrane—in effect, "opening and closing gates" to chemical stimuli and causing a generator potential.

Vertebrates other than mammals may have taste buds on other parts of the body. For example, reptiles and birds do not usually have taste buds on the tongue; instead, most taste buds are in the pharynx. In fishes and amphibians, taste buds may also be found in the skin. For example, a sturgeon's taste buds are abundant on its head projection, which is called the rostrum. As the sturgeon glides over the bottom, it can obtain a foretaste of potential food before the mouth reaches the food. In other fishes, taste buds are widely distributed in the roof, side walls, and floor of the pharynx, where they monitor the incoming flow of water. In fishes that feed on the bottom (catfish, carp, suckers), taste buds are distributed over the entire surface of the head and body to the tip of the tail. They are also abundant on the barbels ("whiskers") of catfish.

VISION

Vision (photoreception) is the primary sense that vertebrates in a light-filled environment use, and consequently, their photoreceptive structures are well developed. Most vertebrates have eyes capable of forming visual images. As figure 24.29 indicates, the eyeball has a lens, a sclera (the tough outer coat), a choroid layer (a thin middle layer), and an inner retina containing many light-sensitive receptor cells (photoreceptors). The transparent cornea is continuous with the sclera and covers the front of the eyeball. Choroid tissue also extends to the front of the eyeball to form the iris, ciliary body, and suspensory ligaments. The colored iris is heavily endowed with light-screening pigments, and it has radial and circular smooth muscles for regulating the amount of light entering the pupil. A clear fluid (aqueous humor) fills the anterior and posterior chambers, which lie between the lens and the cornea. The lens is behind the iris, and a jellylike vitreous body fills the vitreous chamber behind the lens. The moist mucous membrane that covers the eyeball is the conjunctiva.

Vertebrates can adjust their vision for light coming from either close-up or distant objects. This process of focusing light rays precisely on the retina is called **accommodation.** Vertebrates rely on the coordinated stretching and relaxation of the eye muscles and fibers (the ciliary body and suspensory ligaments) that attach to the lens for accommodation.

The eyes of fishes are similar in most aspects of structure and function to those in other vertebrates. However, fish eyes are lidless, and the lens is rounded and close to the cornea. Focusing requires moving the lens forward or backward.

Vision is one of the most important senses in amphibians because they are primarily sight feeders. ***A** number of adaptations allow the eyes of amphibians to function in terrestrial environments.* For example, the eyes of some amphibians (e.g., anurans, salamanders) are close together on the front of the head and provide the binocular vision and well-developed depth perception necessary for capturing prey. Other amphibians with smaller and more lateral eyes (e.g., some salamanders) lack binocular vision. However, their more laterally placed eyes permit these animals to see well off to their sides. The transparent **nictitating membrane** (an "inner eyelid") is movable and cleans and protects the eye.

Vision is the dominant sense in most reptiles, and their eyes are similar to those of amphibians. Upper and lower eyelids, a nictitating membrane, and a blood sinus protect and cleanse the surface of the eye. In snakes and some lizards, the upper and lower eyelids fuse in the embryo to form a protective window of clear skin called the spectacle. Some reptiles possess a **median (parietal) eye** that develops from outgrowths of the roof of the optic tectum (midbrain) (figure 24.30). In the tuatara, the median eye is complete with a lens, nerve, and retina. In other reptiles, the median eye is less developed. Skin covers median eyes, which probably cannot form images. They can, however, differentiate light and dark periods and are used in orientation to the sun.

Vision is an important sense for most birds. The structure of the bird eye is similar to that of other vertebrates *(see figure 24.29)*. Birds have a unique, double-focusing mechanism. Padlike

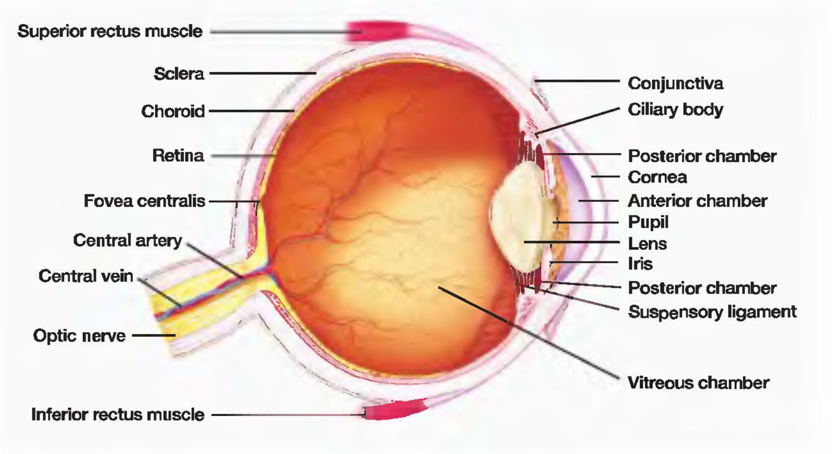

FIGURE 24.29

Internal Anatomy of the Human Eyeball. Light passes through the transparent cornea. The lens focuses the light on the rear surface of the eye, the retina, at the fovea centralis. The retina is rich in rods and cones.

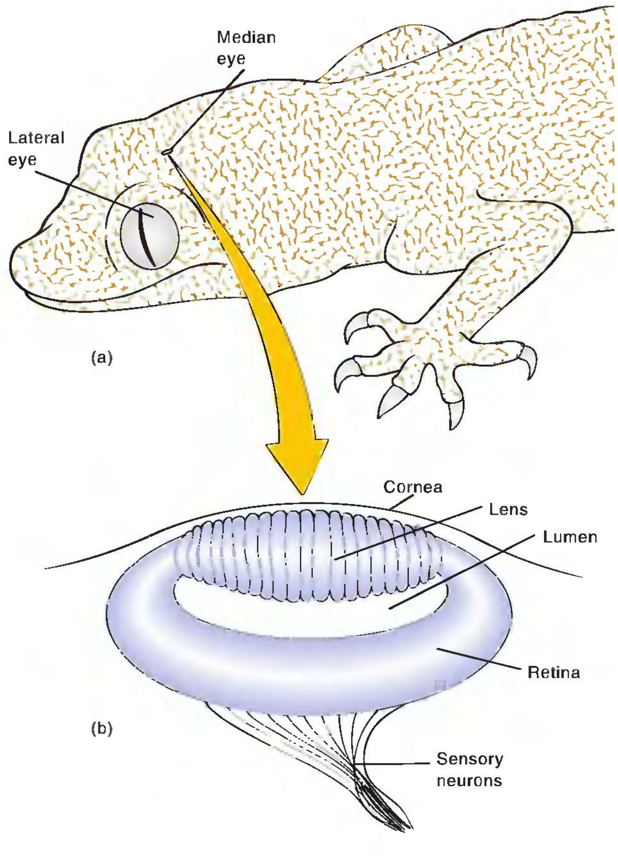

FIGURE 24.30

Median Eye of Reptiles. *(a)* Median eye in a reptile and its relationship to the lateral eyes (dorsal view). *(b)* Sagittal section of the median eye.

structures control the curvature of the lens, and ciliary muscles change the curvature of the cornea. Double, nearly instantaneous focusing allows an osprey, or other bird of prey, to focus on a fish throughout a brief, but breathtakingly fast, descent. Like reptiles, birds have a nictitating membrane that is drawn over the eyeball surface to cleanse and protect it.

In all vertebrates, the retina is well developed. Its basement layer is composed of pigmented epithelium that covers the choroid layer. Nervous tissue that contains photoreceptors lies on this basement layer. The photoreceptors are called **rod** and **cone cells** because of their shape. Rods are sensitive to dim light, whereas cones respond to high-intensity light and are involved in color perception.

When a pigment **(rhodopsin)** in a rod cell absorbs light energy, the energy that this reaction releases triggers the generator potential in an axon and then an action potential that leaves the eyeball via the optic nerve. When the photoreceptor cells are not being stimulated (i.e., in the dark), vitamin A and energy from ATP convert rhodopsin back to its light-sensitive form.

Nineteenth-century poet Leigh Hunt said, "Colors are the smiles of Nature." How does an animal distinguish one smile from another? The answer lies to a great extent in the three types of cone-shaped, color-sensitive cells in the retinas of the eyes of primates, birds, reptiles, and fishes. Each type of cone cell responds differently to light reflected from a colored object, depending on whether the cells have red-, green-, or blue-absorbing pigments. The pigments are light-absorbing proteins that are particularly sensitive to either the long-wavelength (red), intermediate-wavelength (green), or short-wavelength (blue) region of the visible spectrum. The retinal nerves translate the relative amounts of light that each type of cone absorbs into generator potentials that are then transmitted as a nerve impulse to the brain, where the overall pattern evokes the sensation of a specific hue.