

50

Sensory and Motor Mechanisms



▲ **Figure 50.1** Is a star-shaped nose merely decorative?

KEY CONCEPTS

- 50.1 Sensory receptors transduce stimulus energy and transmit signals to the central nervous system
- 50.2 The mechanoreceptors responsible for hearing and equilibrium detect moving fluid or settling particles
- 50.3 Visual receptors in diverse animals depend on light-absorbing pigments
- 50.4 The senses of taste and smell rely on similar sets of sensory receptors
- 50.5 The physical interaction of protein filaments is required for muscle function
- 50.6 Skeletal systems transform muscle contraction into locomotion

OVERVIEW

Sensing and Acting

The face of the star-nosed mole (*Condylura cristata*) is, in a word, astounding (Figure 50.1). Eleven pairs of appendages protrude from its nose, forming a prominent pink star. Although they look a bit like fingers, these appendages are not used in grasping. Nor is the nose used to detect odors. Is the star, then, simply ornamental? No—it has a highly specialized function. Just below its surface lie 25,000 touch-sensitive receptors, more than are found in your whole hand.

Tunneling beneath the wetlands of eastern North America, the virtually blind mole lives in almost total darkness. But as 100,000 neurons relay tactile information from its nose to its brain, the mole finds and captures food with remarkable rapidity: A star-nosed mole can detect and eat prey in as little as 120 milliseconds (msec).

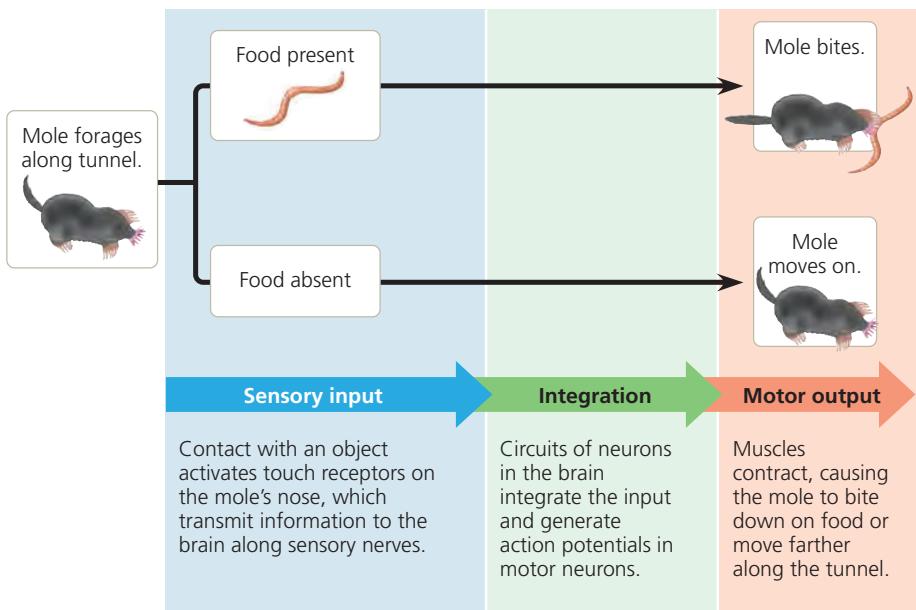
Detecting and processing sensory information and generating motor responses provide the physiological basis for all animal behavior. In this chapter, we will explore the processes of sensing and acting in both vertebrates and invertebrates. We will start with sensory processes that convey information about an animal's external and internal environment to its brain. We will then consider the structure and function of muscles and skeletons that carry out movements as instructed by the brain. Finally, we will investigate various mechanisms of animal movement. These topics will lead us naturally to our discussion of animal behavior in Chapter 51.

CONCEPT 50.1

Sensory receptors transduce stimulus energy and transmit signals to the central nervous system

All sensory processes begin with stimuli, and all stimuli represent forms of energy. A sensory receptor converts stimulus energy to a change in membrane potential and thereby regulates the output of action potentials to the central nervous system (CNS). Activating a sensory receptor does not necessarily require a large amount of stimulus energy. Indeed, some sensory receptors can detect the smallest possible unit of stimulus; most light receptors, for example, can detect a single quantum (photon) of light.

When a stimulus is received and processed by the nervous system, a motor response may be generated. One of the simplest stimulus-response circuits is a reflex, such as the knee-jerk reflex shown in Figure 49.3. Many other behaviors rely on more elaborate processing that involves integration of sensory input. As an example, consider how the star-nosed mole



▲ **Figure 50.2** A simple response pathway: foraging by a star-nosed mole.

forages for food in its tunnel environment (Figure 50.2). When the mole's nose contacts an object in its tunnel, touch receptors in the nose are activated. These receptors transmit sensory information about the object to the mole's brain. Circuits in the brain integrate the input and initiate one of two response pathways, depending on whether food was detected. Motor output commands from the brain sent to skeletal muscles in the body cause the mole either to bite down with its teeth or to continue moving along the tunnel.

With this overview in mind, let's examine the general organization and activity of animal sensory systems.

Sensory Pathways

Sensory pathways have four basic functions: sensory reception, transduction, transmission, and perception.

Sensory Reception and Transduction

A sensory pathway begins with **sensory reception**, the detection of a stimulus by sensory cells. Most sensory cells are specialized neurons or epithelial cells. Some exist singly; others are collected in sensory organs, such as eyes and ears. The term **sensory receptor** is used to describe a sensory cell or organ, as well as the subcellular structure that interacts directly with stimuli. Many sensory receptors detect stimuli from outside the body, such as heat, light, pressure, and chemicals, but there are also receptors for stimuli from within the body, such as blood pressure and body position.

Although animals use a range of sensory receptors to detect widely varying stimuli, the effect in all cases is to open or close ion channels. Thus, for example, ion channels open or close when a substance outside the cell binds to a chemical receptor

in the plasma membrane. The resulting flow of ions across the membrane changes the membrane potential.

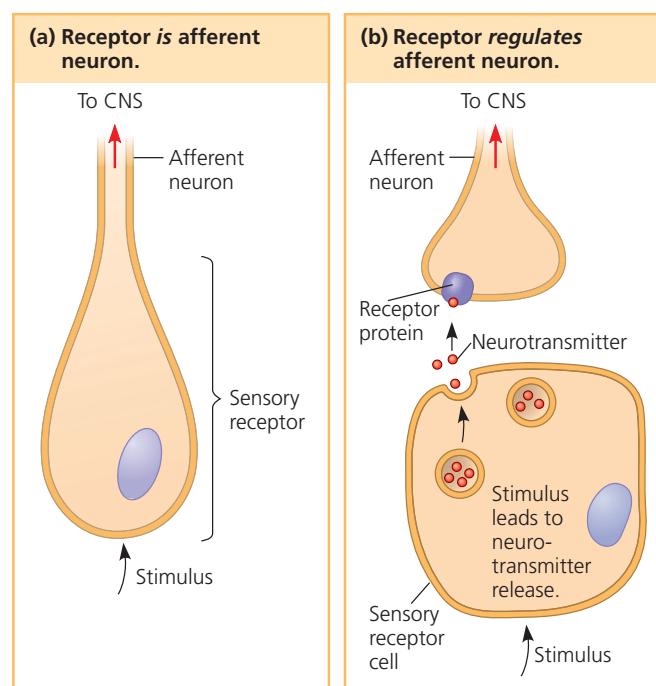
The conversion of a physical or chemical stimulus to a change in the membrane potential of a sensory receptor is called **sensory transduction**, and the change in membrane potential itself is known as a **receptor potential**. Receptor potentials are graded potentials; their magnitude varies with the strength of the stimulus.

Transmission

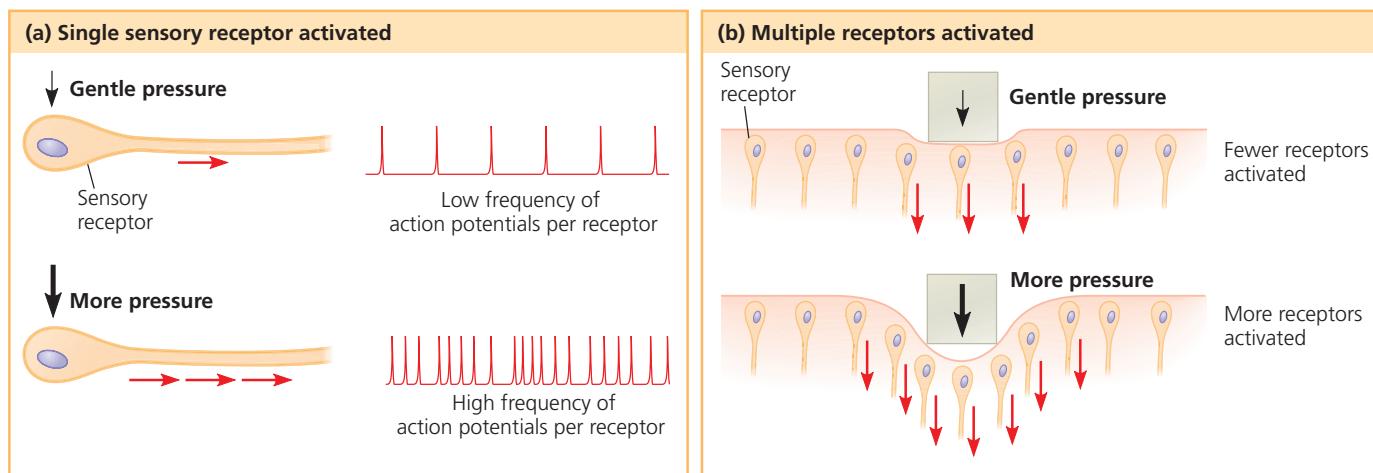
Sensory information travels through the nervous system as nerve impulses, or action potentials. For many sensory receptors, transducing the energy in a stimulus into a receptor potential initiates **transmission** of action potentials to the CNS.

Some sensory receptors are themselves specialized neurons, whereas others are specialized cells that regulate neurons (Figure 50.3). Neurons that act directly as sensory receptors produce action potentials and have an axon that extends into the CNS. Non-neuronal sensory receptor cells form chemical synapses with sensory (afferent) neurons and typically respond to stimuli by increasing the rate at

▼ **Figure 50.3** Classes of sensory receptors.



▼ **Figure 50.4 Coding of stimulus intensity.**



which the afferent neurons produce action potentials. (One exception is in the vertebrate visual system, discussed in Concept 50.3.)

The response of a sensory receptor varies with stimuli of different intensities. The primary difference is the magnitude of the receptor potential, which controls the rate at which action potentials are produced. If the receptor is a sensory neuron, a larger receptor potential results in more frequent action potentials (**Figure 50.4a**). If the receptor is not a sensory neuron, a larger receptor potential causes more neurotransmitter to be released, which usually increases the production of action potentials by the postsynaptic neuron.

Many sensory neurons spontaneously generate action potentials at a low rate. In these neurons, a stimulus does not switch the production of action potentials on or off, but it does change *how often* an action potential is produced. In this manner, such neurons are also able to alert the nervous system to changes in stimulus intensity.

A difference in stimulus strength may not only alter the activity of individual receptors, but also affect the number of receptors that are activated (**Figure 50.4b**). If a stronger stimulus triggers a response by more receptors, more axons transmit action potentials. This increase in the number of axons transmitting action potentials is then decoded by the nervous system as a stronger stimulus.

Processing of sensory information can occur before, during, and after transmission of action potentials to the CNS. In many cases, the *integration* of sensory information begins as soon as the information is received. Receptor potentials produced by stimuli delivered to different parts of a sensory receptor cell are integrated through summation, as are postsynaptic potentials in sensory neurons that form synapses with multiple receptors (see Figure 48.16). As we will discuss shortly, sensory structures such as eyes also provide higher levels of integration, and the brain further processes all incoming signals.

Perception

When action potentials reach the brain via sensory neurons, circuits of neurons process this input, generating the **perception** of the stimuli. Perceptions—such as colors, smells, sounds, and tastes—are constructions formed in the brain and do not exist outside it. So, if a tree falls and no animal is present to hear it, is there a sound? The falling tree certainly produces pressure waves in the air, but if sound is defined as a perception, then there is none unless an animal senses the waves and its brain perceives them.

Action potentials are all-or-none events (see Figure 48.10c). An action potential triggered by light striking the eye has the same properties as an action potential triggered by air vibrating in the ear. How, then, do we distinguish sights, sounds, and other stimuli? The answer lies in the connections that link sensory receptors to the brain. Action potentials from sensory receptors travel along neurons that are dedicated to a particular stimulus; these dedicated neurons synapse with particular neurons in the brain or spinal cord. As a result, the brain distinguishes sensory stimuli such as sight or sound solely by the path to the brain along which the action potentials have traveled.

Amplification and Adaptation

The transduction of stimuli by sensory receptors is subject to two types of modification—amplification and adaptation. **Amplification** refers to the strengthening of a sensory signal during transduction. The effect can be considerable. For example, an action potential conducted from the eye to the human brain has about 100,000 times as much energy as the few photons of light that triggered it.

Amplification that occurs in sensory receptor cells often requires signal transduction pathways involving second messengers. Because these pathways include enzyme-catalyzed reactions, they amplify signal strength through the formation of many product molecules by a single enzyme molecule.

Amplification may also take place in accessory structures of a complex sense organ, as when the pressure associated with sound waves is enhanced by a factor of more than 20 before reaching receptors in the innermost part of the ear.

Upon continued stimulation, many receptors undergo a decrease in responsiveness termed **sensory adaptation** (not to be confused with the evolutionary term *adaptation*). Without sensory adaptation, you would be constantly aware of feeling every beat of your heart and every bit of clothing on your body. Adaptation also enables you to see, hear, and smell changes in the environment that vary widely in stimulus intensity.

Types of Sensory Receptors

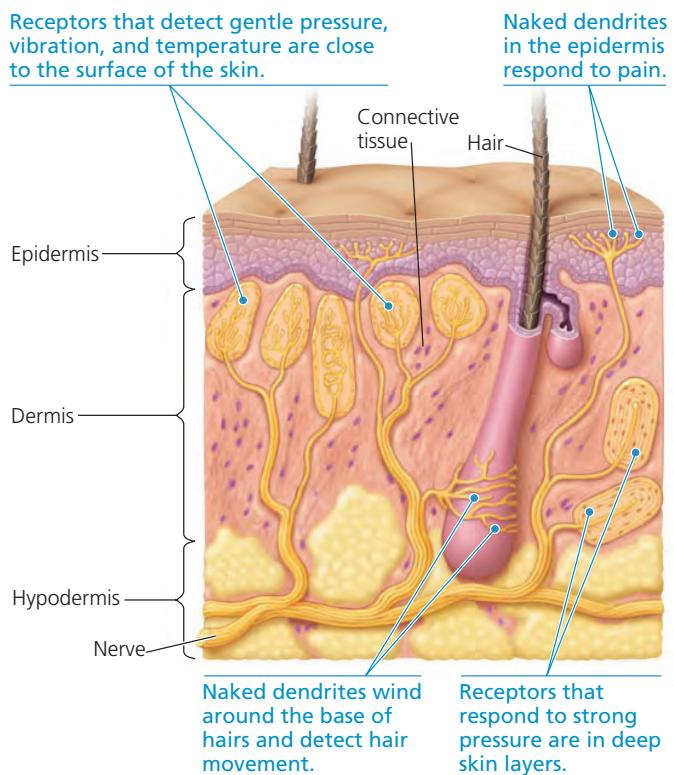
A sensory cell typically has a single type of receptor specific for a particular stimulus, such as light or cold. Often, distinct cells and receptors are responsible for particular qualities of a sensation, such as distinguishing red from blue. Before exploring these specializations, let's consider sensory receptor function at a more basic level. We can classify sensory receptors into five categories based on the nature of the stimuli they transduce: mechanoreceptors, chemoreceptors, electromagnetic receptors, thermoreceptors, and pain receptors.

Mechanoreceptors

Mechanoreceptors sense physical deformation caused by forms of mechanical energy such as pressure, touch, stretch, motion, and sound. Mechanoreceptors typically consist of ion channels that are linked to structures that extend outside the cell, such as "hairs" (cilia), as well as internal cell structures, such as the cytoskeleton. Bending or stretching of the external structure generates tension that alters the permeability of the ion channels. This change in ion permeability alters the membrane potential, resulting in a depolarization or hyperpolarization (see Chapter 48).

The familiar knee-jerk reflex (see Figure 49.3) is triggered by the vertebrate stretch receptor, a mechanoreceptor that detects muscle movement. Vertebrate stretch receptors are dendrites of sensory neurons that spiral around the middle of certain small skeletal muscle fibers. Groups of about 2 to 12 of these fibers, formed into a spindle shape and surrounded by connective tissue, are distributed throughout the muscle, parallel to other muscle fibers. When the muscle is stretched, the spindle fibers are stretched, depolarizing sensory neurons and triggering action potentials that are transmitted to the spinal cord.

The mammalian sense of touch also relies on mechanoreceptors that are the dendrites of sensory neurons. Touch receptors, such as those illustrated in Figure 50.4, are often embedded in layers of connective tissue. The structure of the connective tissue and the location of the receptors dramatically affect the type of mechanical energy (light touch, vibration, or strong pressure) that best stimulates them (Figure 50.5). Receptors that detect a light touch or vibration are close to the surface of the skin; they transduce very slight inputs of mechanical energy into receptor



▲ **Figure 50.5** **Sensory receptors in human skin.** Most receptors in the dermis are encapsulated by connective tissue. Receptors in the epidermis are naked dendrites, as are hair movement receptors that wind around the base of hairs in the dermis.

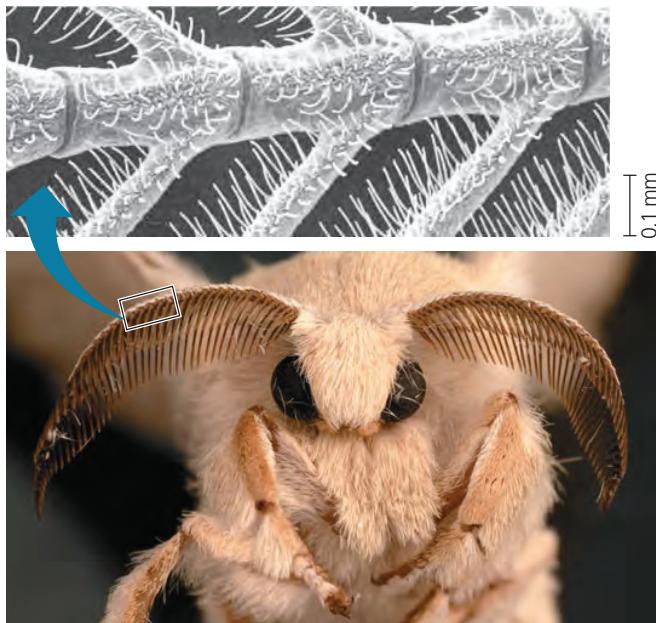
potentials. Receptors that respond to stronger pressure and vibrations are in deep skin layers.

Some animals use mechanoreceptors to literally get a feel for their environment. For example, cats as well as many rodents have extremely sensitive mechanoreceptors at the base of their whiskers. Because deflection of different whiskers triggers action potentials that reach different cells in the brain, an animal's whiskers provide detailed information about nearby objects.

Chemoreceptors

Chemoreceptors include both general receptors—those that transmit information about total solute concentration—and specific receptors—those that respond to individual kinds of molecules. Osmoreceptors in the mammalian brain, for example, detect changes in the total solute concentration of the blood and stimulate thirst when osmolarity increases (see Figure 44.19). Most animals also have receptors for specific molecules, including glucose, oxygen, carbon dioxide, and amino acids.

Two of the most sensitive and specific chemoreceptors known are found in the antennae of the male silkworm moth (Figure 50.6); they detect the two chemical components of the female moth sex pheromone. For pheromones and other molecules detected by chemoreceptors, the stimulus molecule binds to the specific receptor on the membrane of the sensory cell and initiates changes in ion permeability.



▲ Figure 50.6 Chemoreceptors in an insect. The antennae of the male silkworm moth *Bombyx mori* are covered with sensory hairs, visible in the SEM enlargement. The hairs have chemoreceptors that are highly sensitive to the sex pheromone released by the female.

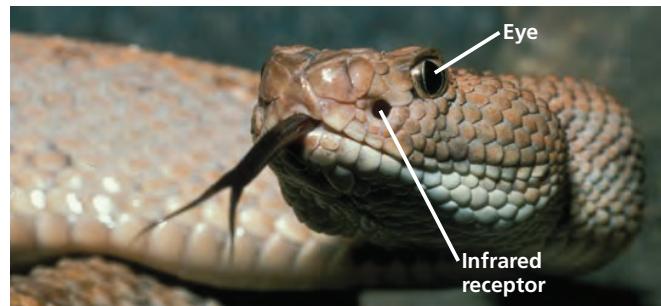
Electromagnetic Receptors

Electromagnetic receptors detect various forms of electromagnetic energy, such as visible light, electricity, and magnetism. For example, snakes have very sensitive infrared receptors that detect the body heat of prey (Figure 50.7a). Similarly, the platypus, a monotreme mammal (see Chapter 34), has electroreceptors on its bill that are thought to detect the electric field generated by the muscles of crustaceans, frogs, small fish, and other prey. In a few cases, the animal detecting an electromagnetic stimulus is also its source: Some fishes generate electric currents and then use their electroreceptors to locate prey or other objects that disturb those currents.

Many animals appear to use Earth's magnetic field lines to orient themselves as they migrate (Figure 50.7b). The iron-containing mineral magnetite is found in many vertebrates (including salmon, pigeons, sea turtles, and humans), in bees, in some molluscs, and in certain protists and prokaryotes that orient to Earth's magnetic field. Once collected by sailors to make compasses for navigation, magnetite may be part of an orienting mechanism in many animals (see Chapter 51).

Thermoreceptors

Thermoreceptors detect heat and cold. Located in the skin and in the anterior hypothalamus, thermoreceptor cells send information to the body's thermostat in the posterior hypothalamus. Our understanding of thermoreception has increased substantially recently, thanks to scientists with an appreciation for fiery foods. Jalapeno and cayenne peppers



(a) This rattlesnake and other pit vipers have a pair of infrared receptors, one anterior to and just below each eye. These organs are sensitive enough to detect the infrared radiation emitted by a warm mouse a meter away. The snake moves its head from side to side until the radiation is detected equally by the two receptors, indicating that the mouse is straight ahead.



(b) Some migrating animals, such as these beluga whales, apparently sense Earth's magnetic field and use the information, along with other cues, for orientation.

▲ Figure 50.7 Specialized electromagnetic receptors.

taste “hot” because they contain a natural product called capsaicin. It turns out that exposing sensory neurons to capsaicin triggers an influx of calcium ions. When scientists identified the receptor protein that binds capsaicin, they made a fascinating discovery: The receptor opens a calcium channel in response not only to capsaicin, but also to high temperatures (42°C or higher). In essence, spicy foods taste “hot” because they activate the same receptors as hot soup and coffee.

Mammals have a number of kinds of thermoreceptors, each specific for a particular temperature range. The capsaicin receptor and at least five other types of thermoreceptors belong to the TRP (transient receptor potential) family of ion channel proteins. Just as the TRP-type receptor specific for high temperature is sensitive to capsaicin, the receptor for temperatures below 28°C can be activated by menthol, a plant product that we perceive to have a “cool” flavor.

Pain Receptors

Extreme pressure or temperature, as well as certain chemicals, can damage animal tissues. To detect stimuli that reflect such noxious (or harmful) conditions, animals rely on **nociceptors** (from the Latin *nocere*, to hurt), also called **pain receptors**. By triggering defensive reactions, such as withdrawal from danger, the perception of pain serves an important function.

In humans, certain naked dendrites act as nociceptors by detecting noxious thermal, mechanical, or chemical stimuli. The capsaicin receptor is thus a thermoreceptor and also a nociceptor. Although nociceptor density is highest in skin, some pain receptors are associated with other organs.

Chemicals produced in an animal's body sometimes enhance the perception of pain. For example, damaged tissues produce prostaglandins, which act as local regulators of inflammation (see Chapter 45). Prostaglandins worsen pain by increasing nociceptor sensitivity to noxious stimuli. Aspirin and ibuprofen reduce pain by inhibiting the synthesis of prostaglandins.

Next we'll turn our focus to sensory systems, beginning with systems for maintaining balance and detecting sound.

CONCEPT CHECK 50.1

- Which one of the five categories of sensory receptors is primarily dedicated to external stimuli?
- Why can eating "hot" peppers cause a person to sweat?
- WHAT IF?** If you stimulated a sensory neuron electrically, how would that stimulation be perceived?

For suggested answers, see Appendix A.

CONCEPT 50.2

The mechanoreceptors responsible for hearing and equilibrium detect moving fluid or settling particles

Hearing and the perception of body equilibrium, or balance, are related in most animals. For both senses, mechanoreceptor cells produce receptor potentials when settling particles or moving fluid causes deflection of cell-surface structures.

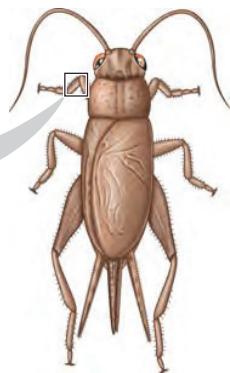
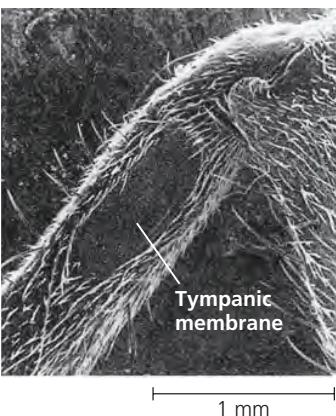
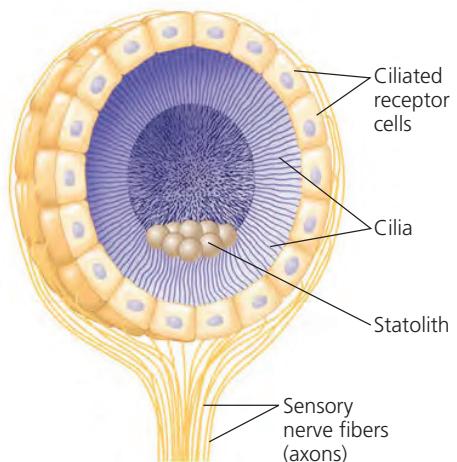
Sensing of Gravity and Sound in Invertebrates

To sense gravity and maintain equilibrium, most invertebrates rely on mechanoreceptors located in organs called **statocysts** (Figure 50.8). In a typical statocyst, a layer of ciliated receptor cells surrounds a chamber that contains one or more **statoliths**, which are grains of sand or other dense granules. When statoliths settle to the low point in the chamber, they stimulate mechanoreceptors in that location. In experiments in which statoliths were replaced with metal shavings, researchers "tricked" crayfish into swimming upside down by using magnets to pull the shavings to the upper end of the statocysts located at the base of their antennae.

Many (perhaps most) insects have body hairs that vibrate in response to sound waves. Hairs of different stiffnesses and lengths vibrate at different frequencies. For example, fine hairs on the antennae of a male mosquito vibrate in a specific way in response to the hum produced by the beating wings

► **Figure 50.8**
The statocyst of an invertebrate.

The settling of statoliths to the low point in the chamber bends cilia on receptor cells in that location, providing the brain with information about the orientation of the body with respect to gravity.



▲ **Figure 50.9** An insect's "ear"—on its leg. The tympanic membrane, visible in this SEM of a cricket's front leg, vibrates in response to sound waves. The vibrations stimulate mechanoreceptors attached to the inside of the tympanic membrane.

of flying females. The importance of this sensory system in the attraction of males to a potential mate can be demonstrated very simply: A tuning fork vibrating at the same frequency as that of a female's wings will itself attract males.

Many insects also detect sound by means of "ears" consisting of a tympanic membrane (eardrum) stretched over an internal air chamber (Figure 50.9). Sound waves vibrate the tympanic membrane, stimulating receptor cells attached to the inside of the membrane and resulting in nerve impulses that are transmitted to the brain. Cockroaches lack such a tympanic membrane, but instead have vibration-sensitive organs located in each leg. These organs can provide enough warning for the insect to avoid being crushed by a descending human foot.

Hearing and Equilibrium in Mammals

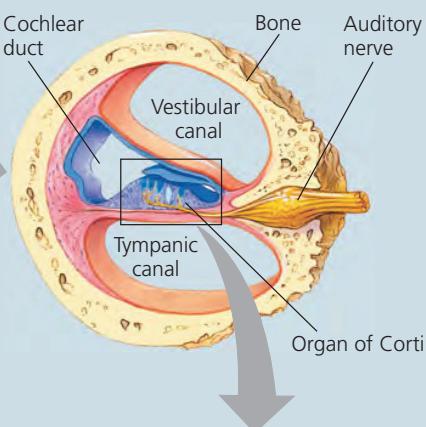
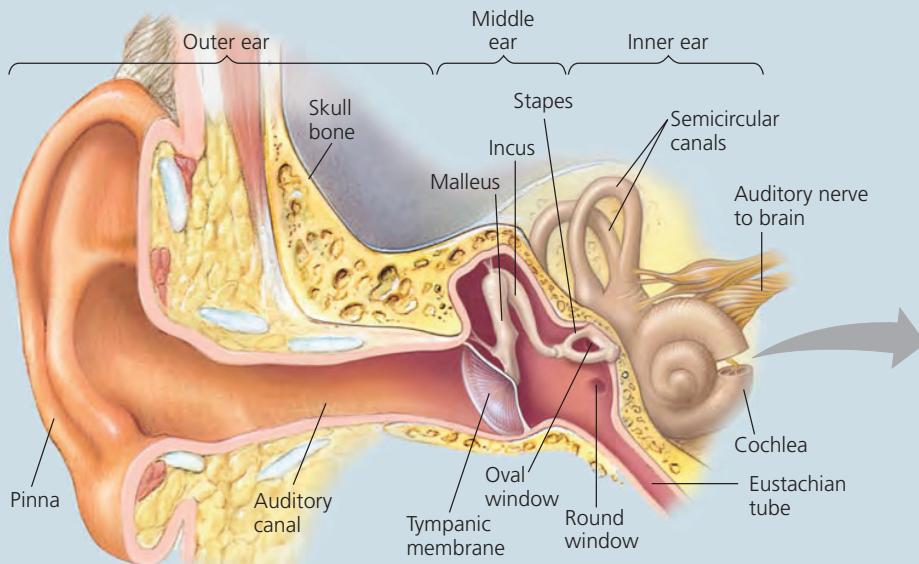
In mammals, as in most other terrestrial vertebrates, the sensory organs for hearing and equilibrium are closely associated. Figure 50.10 explores the structure and function of these organs in the human ear.

▼ Figure 50.10

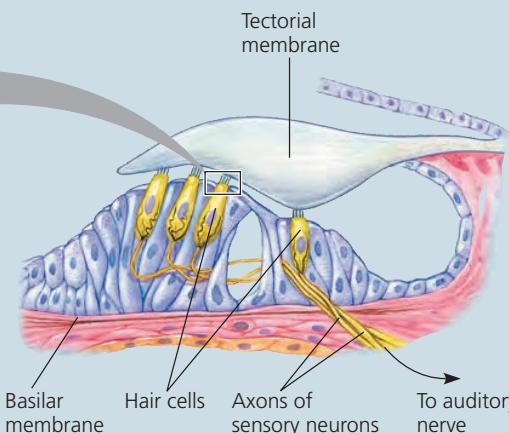
Exploring The Structure of the Human Ear

1 Overview of Ear Structure

The **outer ear** consists of the external pinna and the auditory canal, which collect sound waves and channel them to the **tympanic membrane** (eardrum), which separates the outer ear from the middle ear. In the **middle ear**, three small bones—the malleus (hammer), incus (anvil), and stapes (stirrup)—transmit vibrations to the **oval window**, which is a membrane beneath the stapes. The middle ear also opens into the **Eustachian tube**, which connects to the pharynx and equalizes pressure between the middle ear and the atmosphere. The **inner ear** consists of fluid-filled chambers, including the **semicircular canals**, which function in equilibrium, and the coiled **cochlea** (from the Latin meaning “snail”), a bony chamber that is involved in hearing.



▲ Bundled hairs projecting from a single mammalian hair cell (SEM). Two shorter rows of hairs lie behind the tall hairs in the foreground.



4 Hair Cell

Projecting from each hair cell is a bundle of rod-shaped “hairs,” each containing a core of actin filaments. Vibration of the basilar membrane in response to sound raises and lowers the hair cells, bending the hairs against the surrounding fluid and the tectorial membrane. When the hairs within the bundle are displaced, mechanoreceptors are activated, changing the membrane potential of the hair cell.

3 The Organ of Corti

The floor of the cochlear duct, the basilar membrane, bears the **organ of Corti**, which contains the mechanoreceptors of the ear, hair cells with hairs projecting into the cochlear duct. Many of the hairs are attached to the tectorial membrane, which hangs over the organ of Corti like an awning. Sound waves make the basilar membrane vibrate, which results in bending of the hairs and depolarization of the hair cells.

Hearing

Vibrating objects, such as a plucked guitar string or the vocal cords of your instructor, create pressure waves in the surrounding air. In *hearing*, the ear transduces this mechanical stimulus (pressure waves) into nerve impulses that the brain perceives as sound. To hear music, speech, or other sounds in our environment, we rely on **hair cells**, sensory receptors with hair-like projections on the cell surface that detect motion. Before the vibration waves reach the hair cells, however, they are amplified and transformed by several accessory structures.

The first steps in hearing involve structures in the ear that convert the vibrations of moving air to pressure waves in fluid. Upon reaching the outer ear, moving air causes the tympanic membrane to vibrate. The three bones of the middle ear transmit the vibrations to the oval window, a membrane on the cochlea's surface. When one of those bones, the stapes, vibrates against the oval window, it creates pressure waves in the fluid (called perilymph) inside the cochlea.

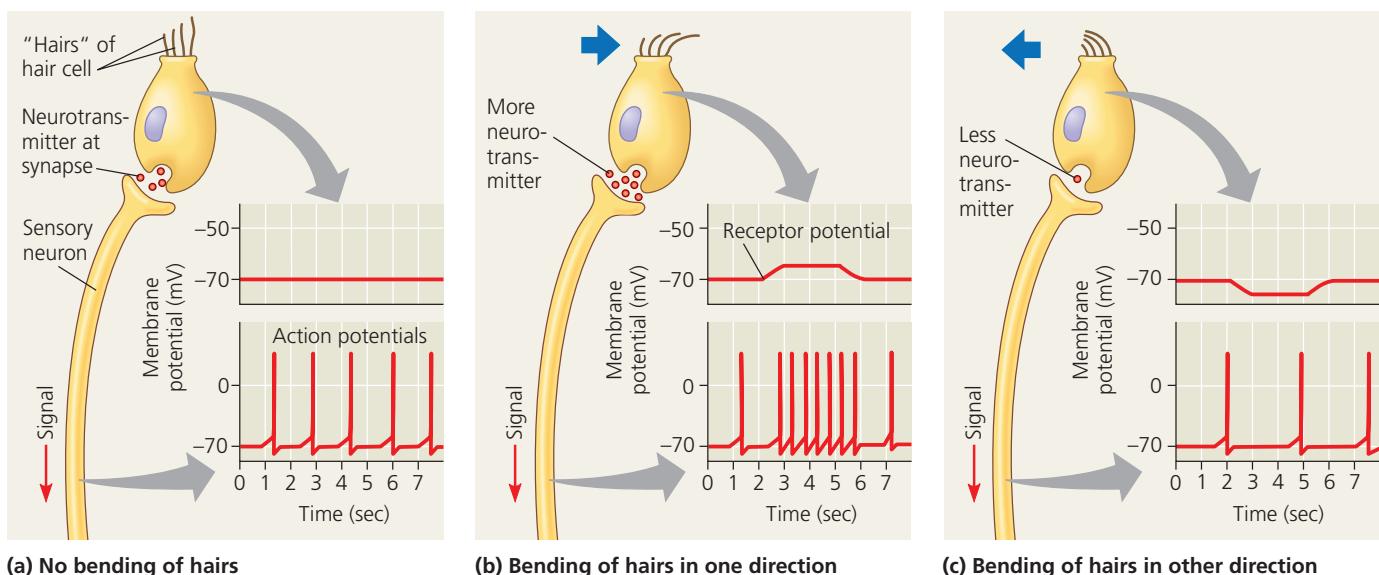
Upon entering the vestibular canal, the pressure waves push down on the cochlear duct and basilar membrane. In response, the basilar membrane and attached hair cells vibrate up and down. The hairs projecting from the moving hair cells are deflected by the tectorial membrane, which lies immediately above in a fixed position (see Figure 50.10). With each vibration, the hairs bend first in one direction and then the other. Mechanoreceptors in the hair cells respond by opening or closing ion channels. As shown in **Figure 50.11**, bending in one direction depolarizes hair cells, increasing neurotransmitter release and the frequency of action potentials directed to the

brain along the auditory nerve. Bending the hairs in the other direction hyperpolarizes hair cells, reducing neurotransmitter release and the frequency of auditory nerve sensations.

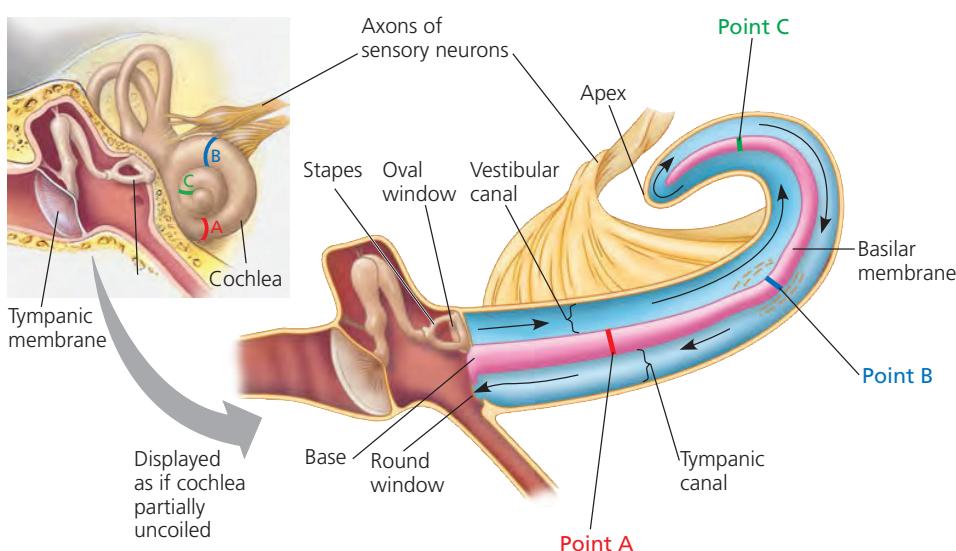
What prevents pressure waves from reverberating within the ear and causing prolonged sensation? Once pressure waves travel through the vestibular canal, they pass around the apex (tip) of the cochlea. The waves then continue through the tympanic canal, dissipating as they strike the **round window** (**Figure 50.12a**). This damping of sound waves resets the apparatus for the next vibrations that arrive.

The ear conveys information to the brain about two important sound variables: volume and pitch. *Volume* (loudness) is determined by the amplitude, or height, of the sound wave. A large-amplitude sound wave causes more vigorous vibration of the basilar membrane, greater bending of the hairs on hair cells, and more action potentials in the sensory neurons. *Pitch* is a function of a sound wave's frequency, the number of vibrations per unit time. High-frequency waves produce high-pitched sounds, whereas low-frequency waves produce low-pitched sounds. Pitch is commonly expressed in cycles per second, or hertz (Hz). Healthy young humans can hear in the range of 20–20,000 Hz; dogs can hear sounds as high as 40,000 Hz; and bats can emit and hear clicking sounds at frequencies above 100,000 Hz, using this ability to locate objects.

The cochlea can distinguish pitch because the basilar membrane is not uniform along its length: It is relatively narrow and stiff at the base of the cochlea near the oval window and wider and more flexible at the apex. Each region of the basilar membrane is tuned to a particular vibration frequency (**Figure 50.12b**). At any instant, the region of the membrane



▲ **Figure 50.11** **Sensory reception by hair cells.** Vertebrate hair cells required for hearing and balance have “hairs” formed into a bundle that bends when surrounding fluid moves. Each hair cell releases an excitatory neurotransmitter at a synapse with a sensory neuron, which conducts action potentials to the CNS. Bending of the bundle in one direction depolarizes the hair cell, causing it to release more neurotransmitter and increasing the frequency of action potentials in the sensory neuron. Bending in the other direction has the opposite effect.



(a) Vibrations of the stapes against the oval window produce pressure waves (black arrows) in the fluid (perilymph; blue) of the cochlea. (For purposes of illustration, the cochlea on the right is drawn partially uncoiled.) The waves travel to the apex via the vestibular canal and back towards the base via the tympanic canal. The energy in the waves causes the basilar membrane (pink) to vibrate, stimulating hair cells (not shown). Because the basilar membrane varies in stiffness along its length, each point along the membrane vibrates maximally in response to waves of a particular frequency.

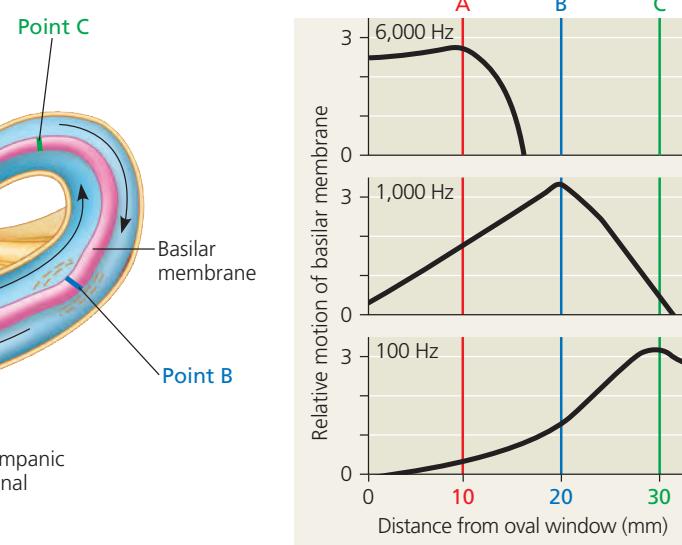
▲ Figure 50.12 Transduction in the cochlea.

? A musical chord consists of several notes, each formed by a sound wave of different frequency. When you hear a chord, where in your body are these notes combined?

vibrating most vigorously triggers the highest frequency of action potentials in the neuronal pathway leading to the brain. There, within the cerebral cortex, the actual perception of pitch occurs. Axons in the auditory nerve project into auditory areas of the cerebral cortex according to the region of the basilar membrane in which the signal originated. When a particular site in our cortex is stimulated, we perceive the sound of a particular pitch.

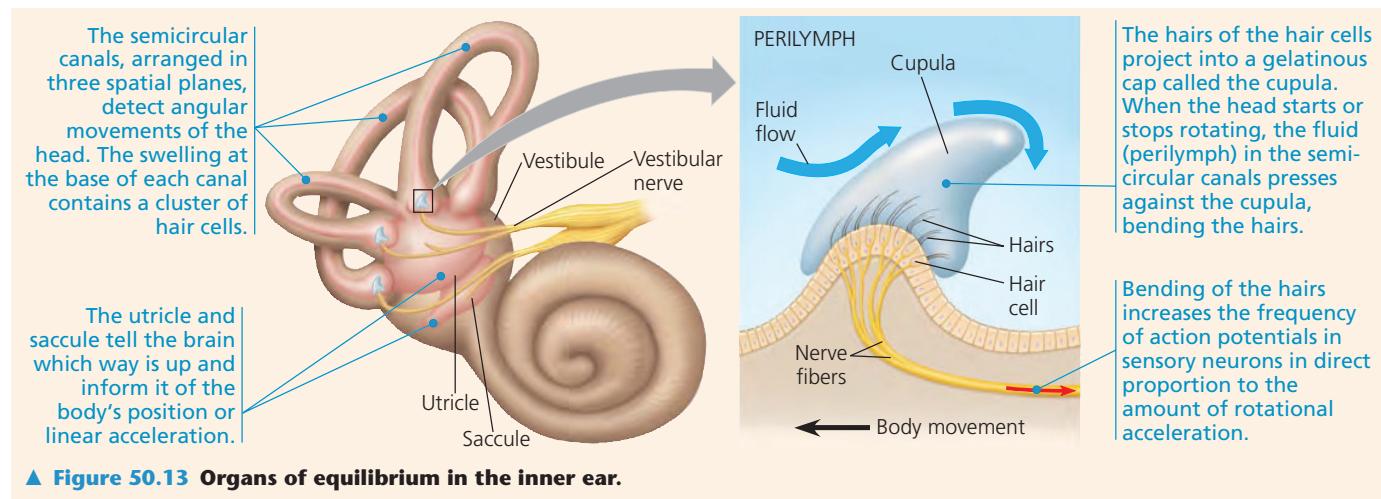
Equilibrium

Several organs in the inner ear of humans and most other mammals detect body movement, position, and balance.



(b) These graphs show the patterns of vibration along the basilar membrane for three different frequencies, high (top), medium (middle), and low (bottom). The higher the frequency, the closer the vibration to the oval window.

Situated in a vestibule behind the oval window, the chambers called the **utricle** and **saccule** allow us to perceive position with respect to gravity or linear movement (Figure 50.13). Each of these chambers contains a sheet of hair cells that project into a gelatinous material. Embedded in this gel are many small calcium carbonate particles called otoliths ("ear stones"). When you tilt your head, the otoliths press on the hairs protruding into the gel. Through the hair cell receptors, this deflection of the hairs is transformed into a change in the output of sensory neurons, signaling the brain that your head is at an angle. The otoliths are also responsible for



▲ Figure 50.13 Organs of equilibrium in the inner ear.

your ability to perceive acceleration, as, for example, when a stationary car in which you are sitting pulls forward. Because the utricle is oriented horizontally and the saccule is positioned vertically, you can detect motion in either the forward-and-back or up-and-down direction.

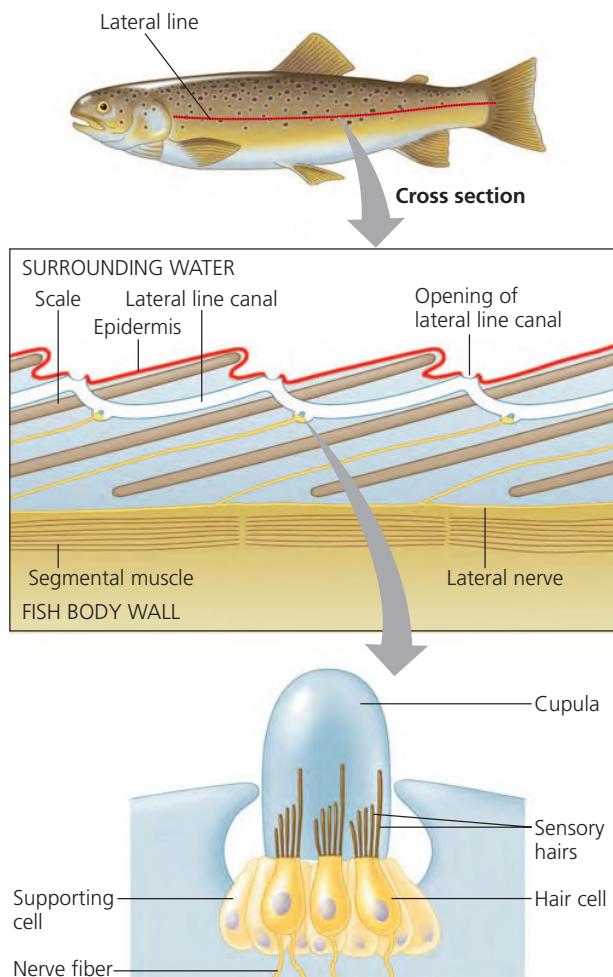
Three semicircular canals connected to the utricle detect turning of the head and other forms of angular acceleration (see Figure 50.11). Within each canal the hair cells form a single cluster, with the hairs projecting into a gelatinous cap called the cupula. Because the three canals are arranged in the three spatial planes, they can detect angular motion of the head in any direction. For example, if you turn your head to the left or right, the fluid within the horizontal canal pushes against the cupula, deflecting the hairs. The brain interprets the resulting changes in impulse production by the sensory neurons as turning of the head. If you spin in place, the fluid and canal eventually come to equilibrium and remain in that state until you stop. At that point, the moving fluid encounters a stationary cupula, triggering the false sensation of angular motion that we call dizziness.

Hearing and Equilibrium in Other Vertebrates

Unlike the mammalian hearing apparatus, the ear of a fish does not open to the outside of the body and has no eardrum or cochlea. The vibrations of the water caused by sound waves are conducted through the skeleton of the head to a pair of inner ears, setting otoliths in motion and stimulating hair cells. The fish's air-filled swim bladder (see Figure 34.16) also vibrates in response to sound. Some fishes, including catfishes and minnows, have a series of bones that conduct vibrations from the swim bladder to the inner ear.

As discussed in Chapter 34, most fishes and aquatic amphibians have a **lateral line system** along both sides of their body (Figure 50.14). The system contains mechanoreceptors that detect low-frequency waves by a mechanism similar to that of the mammalian inner ear. Water from the animal's surroundings enters the lateral line system through numerous pores and flows along a tube past the mechanoreceptors. As in our semicircular canals, receptors are formed from a cluster of hair cells whose hairs are embedded in a gelatinous cap, the cupula. Water movement bends the cupula, leading to depolarization of the hair cells and production of action potentials that are transmitted along the axons of sensory neurons to the brain. In this way, the fish perceives its movement through water or the direction and velocity of water currents flowing over its body. The lateral line system also detects water movements or vibrations generated by prey, predators, and other moving objects.

In terrestrial vertebrates, the inner ear has evolved as the main organ of hearing and equilibrium. Some amphibians have a lateral line system as juveniles, but not as adults living on land. In the ear of a frog or toad, sound vibrations in the air are conducted to the inner ear by a tympanic membrane on



▲ Figure 50.14 The lateral line system in a fish. Water flowing through the system bends hair cells. The hair cells transduce the energy into receptor potentials, triggering action potentials that are conveyed to the brain. The lateral line system enables a fish to monitor water currents, pressure waves produced by moving objects, and low-frequency sounds conducted through the water.

the body surface and a single middle ear bone. Like mammals, birds and other reptiles have a cochlea. However, as in amphibians, sound is conducted from the tympanic membrane to the inner ear of reptiles by a single bone (see Figure 34.37).

CONCEPT CHECK 50.2

- How are statocysts adaptive for animals that burrow underground or live deep in the ocean?
- WHAT IF?** Suppose a series of pressure waves in your cochlea caused a vibration of the basilar membrane that moves gradually from the apex toward the base. How would your brain interpret this stimulus?
- WHAT IF?** If the stapes became fused to the other middle ear bones or to the oval window, how would this condition affect hearing? Explain.

For suggested answers, see Appendix A.

CONCEPT 50.3

Visual receptors in diverse animals depend on light-absorbing pigments

The ability to detect light has a central role in the interaction of nearly all animals with their environment. Although animals use a diverse set of organs for vision, the underlying mechanism for capturing light is the same, suggesting a common evolutionary origin.

Evolution of Visual Perception

EVOLUTION Light detectors in the animal kingdom range from simple clusters of cells that detect only the direction and intensity of light to complex organs that form images. These diverse light detectors all contain **photoreceptors**, cells that contain light-absorbing pigment molecules. Furthermore, the genes that specify where and when photoreceptors arise during embryonic development are shared among animals as diverse as flatworms, annelids, arthropods, and vertebrates. It is thus very probable that the genetic underpinnings of all photoreceptors were already present in the earliest bilaterian animals.

Light-Detecting Organs

Most invertebrates have some kind of light-detecting organ. One of the simplest is that of planarians (Figure 50.15). A pair of ocelli (singular, *ocellus*), which are sometimes called eyespots, are located in the head region. A layer of darkly pigmented cells surrounds the ocelli on three sides, blocking light. Photoreceptors in each ocellus receive light only through the opening where there are no pigmented cells. Because the opening of one ocellus faces left and slightly forward and that of the other ocellus faces right and forward, light shining from one side of the planarian stimulates only the ocellus on that side. The planarian brain compares the rate of action potentials coming from the two ocelli and directs turning movements that minimize the stimulation of both ocelli. The result is that the planarian moves away from the light source until it reaches a shaded location, where a rock or other object is likely to hide the animal from predators.



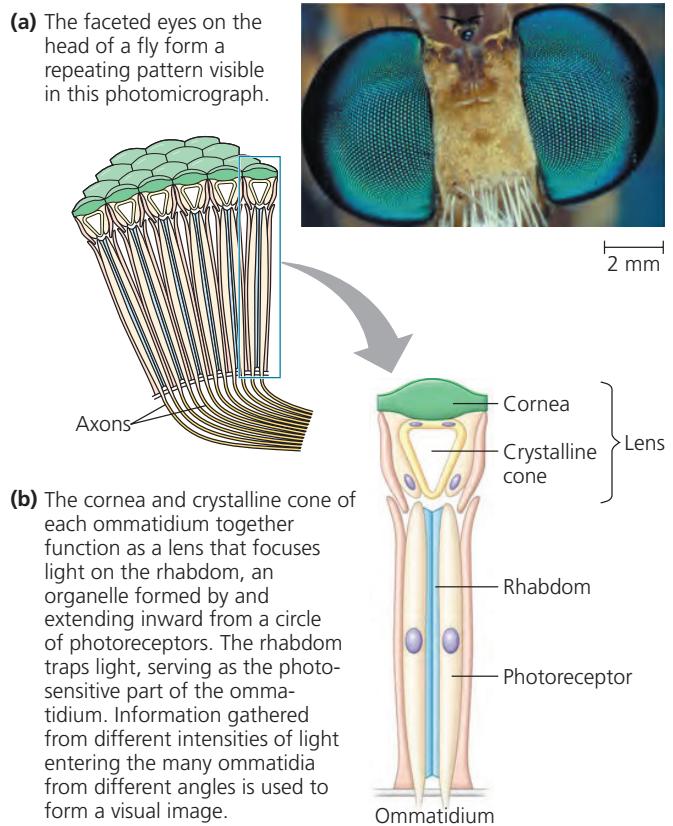
- (a) The planarian's brain directs the body to turn until the sensations from the two ocelli are equal and minimal, causing the animal to move away from light.
- (b) Whereas light striking the front of an ocellus excites the photoreceptors, light striking the back is blocked by the screening pigment. In this way, the ocelli indicate the direction of a light source, triggering the light avoidance behavior.

▲ Figure 50.15 Ocelli and orientation behavior of a planarian.

are located in the head region. A layer of darkly pigmented cells surrounds the ocelli on three sides, blocking light. Photoreceptors in each ocellus receive light only through the opening where there are no pigmented cells. Because the opening of one ocellus faces left and slightly forward and that of the other ocellus faces right and forward, light shining from one side of the planarian stimulates only the ocellus on that side. The planarian brain compares the rate of action potentials coming from the two ocelli and directs turning movements that minimize the stimulation of both ocelli. The result is that the planarian moves away from the light source until it reaches a shaded location, where a rock or other object is likely to hide the animal from predators.

Compound Eyes

Insects and crustaceans (phylum Arthropoda) have compound eyes, as do some polychaete worms (phylum Annelida). A **compound eye** consists of up to several thousand light detectors called **ommatidia** (the “facets” of the eye), each with its own light-focusing lens (Figure 50.16). Each ommatidium detects light from a tiny portion of the visual field. A compound eye is very effective at detecting movement, an important adaptation for flying insects and small animals constantly threatened with predation. Whereas the



▲ Figure 50.16 Compound eyes.

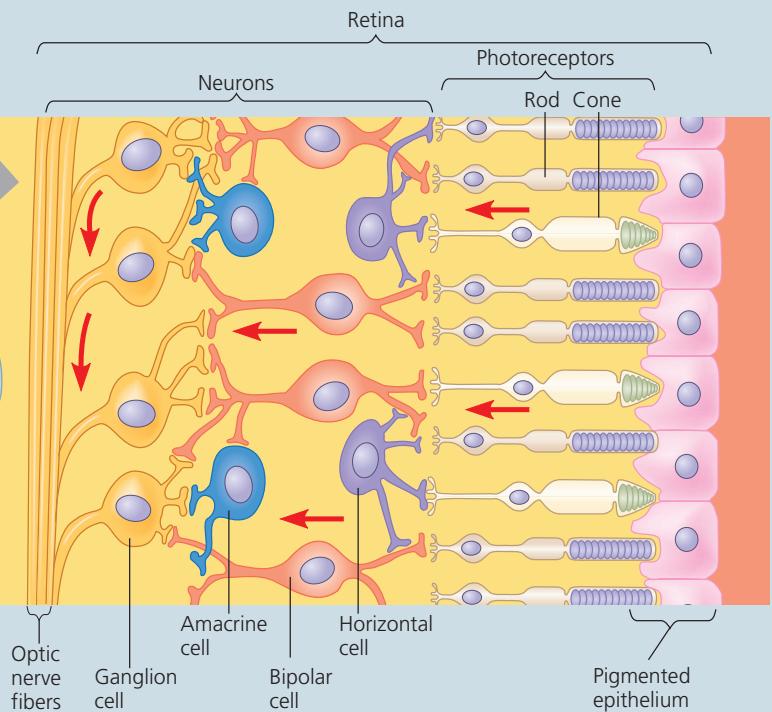
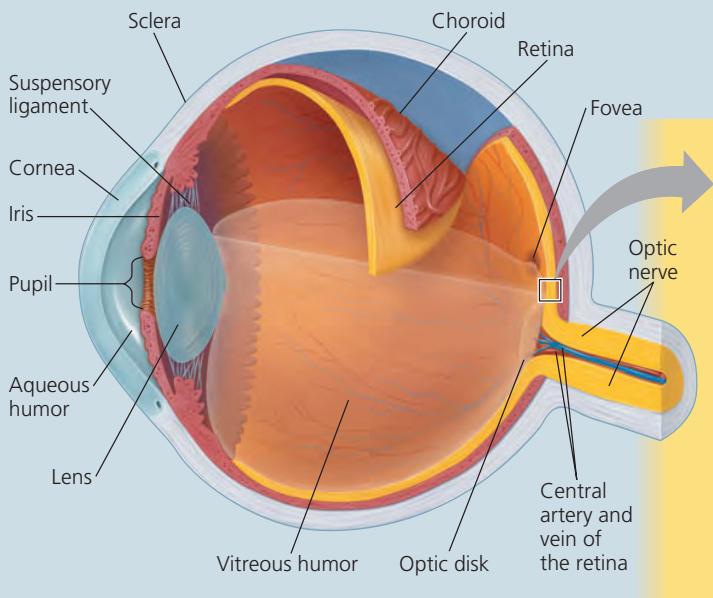
human eye can distinguish only about 50 flashes of light per second, the compound eyes of some insects can detect flickering at six times that rate. (If they slipped into a movie theater, these insects could easily resolve each frame of the film being projected as a separate still image.) Insects also have excellent color vision, and some (including bees) can see into the ultraviolet (UV) range of the electromagnetic spectrum. Because UV light is invisible to humans, we miss seeing differences in the environment that bees and other insects detect. In studying animal behavior, we cannot simply extrapolate our sensory world to other species; different animals have different sensitivities and different brain organizations.

Single-Lens Eyes

Among invertebrates, **single-lens eyes** are found in some jellies and polychaete worms, as well as in spiders and many molluscs. A single-lens eye works somewhat like a camera. The eye of an octopus or squid, for example, has a small opening, the **pupil**, through which light enters. Like a camera's adjustable aperture, the **iris** contracts or expands, changing the

▼ Figure 50.17

Exploring The Structure of the Human Eye



1 Overview of Eye Structure

Starting from the outside, the human eye is surrounded by the conjunctiva, a mucous membrane (not shown); the sclera, a connective tissue; and the choroid, a thin, pigmented layer. At the front, the sclera forms the transparent *cornea* and the choroid forms the colored *iris*. By changing size, the iris regulates the amount of light entering the pupil, the hole in the center of the iris. Just inside the choroid, the neurons and photoreceptors of the **retina** form the innermost layer of the eyeball. The optic nerve exits the eye at the optic disk.

The **lens**, a transparent disk of protein, divides the eye into two cavities. In front of the lens lies the *aqueous humor*, a clear watery substance. Blockage of ducts that drain this fluid can produce glaucoma, a condition in which increased pressure in the eye damages the optic nerve, causing vision loss. Behind the lens lies the jellylike *vitreous humor* (illustrated here in the lower portion of the eyeball).

2 The Retina

Light (coming from left in the above view) strikes the retina, passing through largely transparent layers of neurons before reaching the rods and cones, two types of photoreceptors that differ in shape and in function. The neurons of the retina then relay visual information captured by the photoreceptors to the optic nerve and brain along the pathways shown with red arrows. Each *bipolar cell* receives information from several rods or cones, and each *ganglion cell* gathers input from several bipolar cells. *Horizontal* and *amacrine cells* integrate information across the retina.

One region of the retina, the optic disk, lacks photoreceptors. As a result, this region forms a "blind spot" where light is not detected.

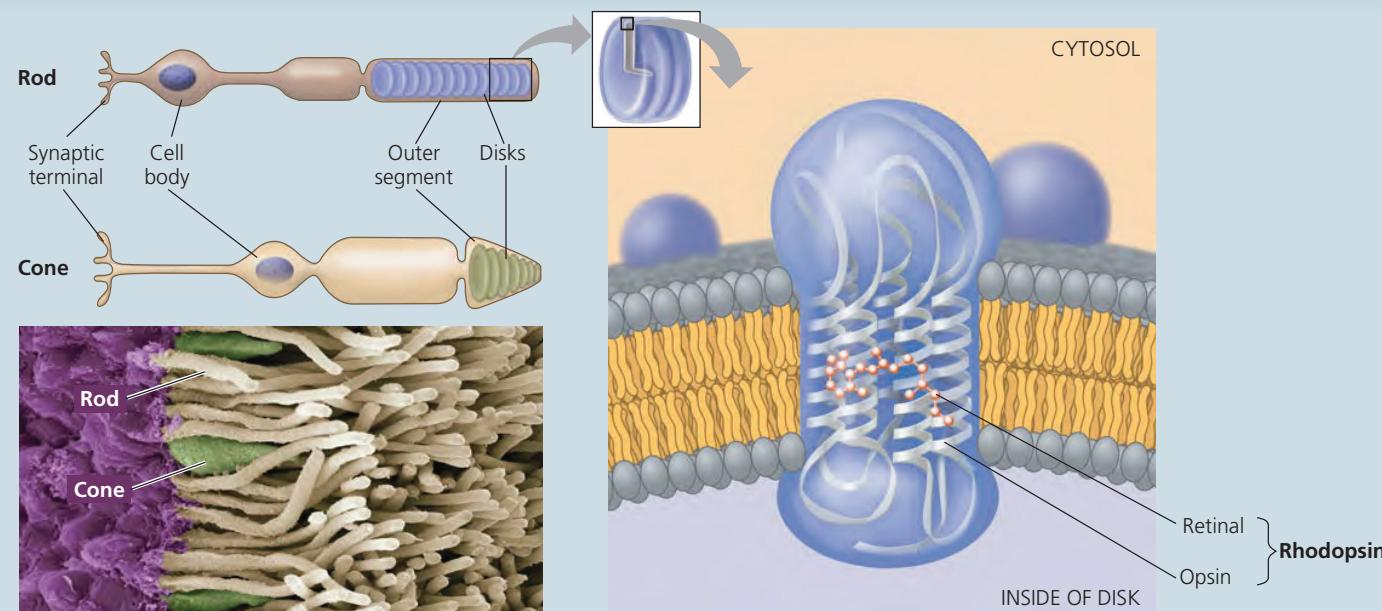
diameter of the pupil to let in more or less light. Behind the pupil, a single lens focuses light on a layer of photoreceptors. Similar to a camera's focusing action, muscles in an invertebrate's single-lens eye move the lens forward or backward, focusing on objects at different distances.

The eyes of all vertebrates have a single lens. In fishes, focusing is as in invertebrates, with the lens moving forward or backward. In other species, including mammals, focusing is achieved by changing the shape of the lens. We will learn about this mechanism, as well as explore visual perception

in much more detail, as we shift our attention to the vertebrate visual system.

The Vertebrate Visual System

The human eye will serve as our model of vision in vertebrates. As detailed in **Figure 50.17**, vision begins when photons of light enter the eye and strike the rods and cones. There the energy of each photon is captured by a shift in configuration of a single chemical bond in retinal.



3 Photoreceptor Cells

Humans have two main types of photoreceptor cells: rods and cones. Within the outer segment of a rod or cone is a stack of membranous disks in which *visual pigments* are embedded. **Rods** are more sensitive to light but do not distinguish colors; they enable us to see at night, but only in black and white. **Cones** provide color vision, but, being less sensitive, contribute very little to night vision. There are three types of cones. Each has a different sensitivity across the visible spectrum, providing an optimal response to red, green, or blue light.

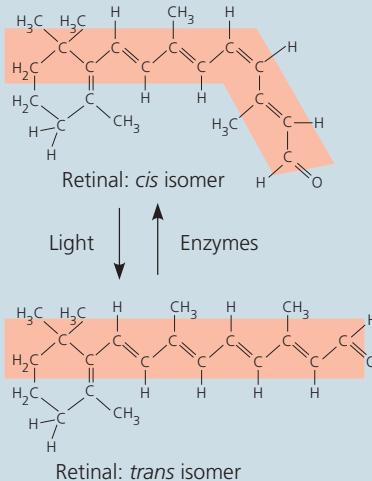
In the colorized SEM shown above, cones (green), rods (light tan), and adjacent neurons (purple) are visible. The pigmented epithelium, which was removed in this preparation, would be to the right.

4 Visual Pigments

Vertebrate visual pigments consist of a light-absorbing molecule called **retinal** (a derivative of vitamin A) bound to a membrane protein called an **opsin**. Seven α helices of each opsin molecule span the disk membrane. The visual pigment of rods, shown here, is called **rhodopsin**.

Retinal exists as two isomers.

Absorption of light shifts one bond in retinal from a *cis* to a *trans* arrangement, converting the molecule from an angled shape to a straight shape. This change in configuration destabilizes and activates the opsin protein to which retinal is bound.



Although light detection in the eye is the first stage in vision, remember that it is actually the brain that “sees.” Thus, to understand vision, we must examine how the capture of light by retinal changes the production of action potentials and then follow these signals to the visual centers of the brain, where images are perceived.

Sensory Transduction in the Eye

The transduction of visual information to the nervous system begins with the light-induced conversion of *cis*-retinal to *trans*-retinal. As shown in **Figure 50.18**, this conversion activates rhodopsin, which activates a G protein, which in turn activates an enzyme that can hydrolyze cyclic GMP. In the dark, cyclic GMP in photoreceptor cells binds to sodium ion (Na^+) channels and keeps them open. When the G protein-dependent pathway is activated, cyclic GMP is broken down, Na^+ channels close, and the cell becomes hyperpolarized.

The signal transduction pathway in photoreceptor cells normally shuts off as enzymes convert retinal back to the *cis* form, returning rhodopsin to its inactive state. In very bright light, however, rhodopsin remains active, and the response in the rods becomes saturated. If the amount of light entering the eyes decreases abruptly, the rods do not regain full responsiveness for several minutes. This is why you are temporarily blinded if you pass quickly from the bright sunshine into a movie theater or other dark environment. (Because light activation changes the color of rhodopsin from

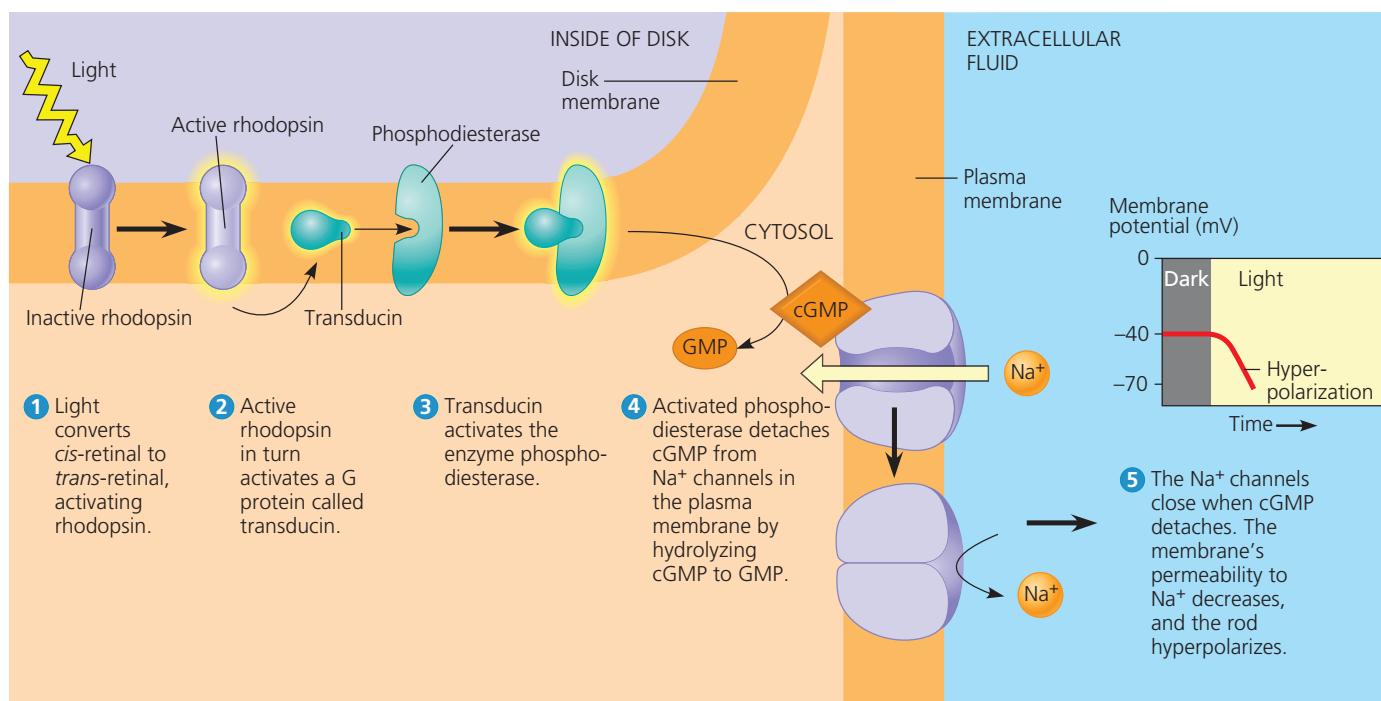
purple to yellow, rods in which the light response is saturated are often described as “bleached.”)

Processing of Visual Information in the Retina

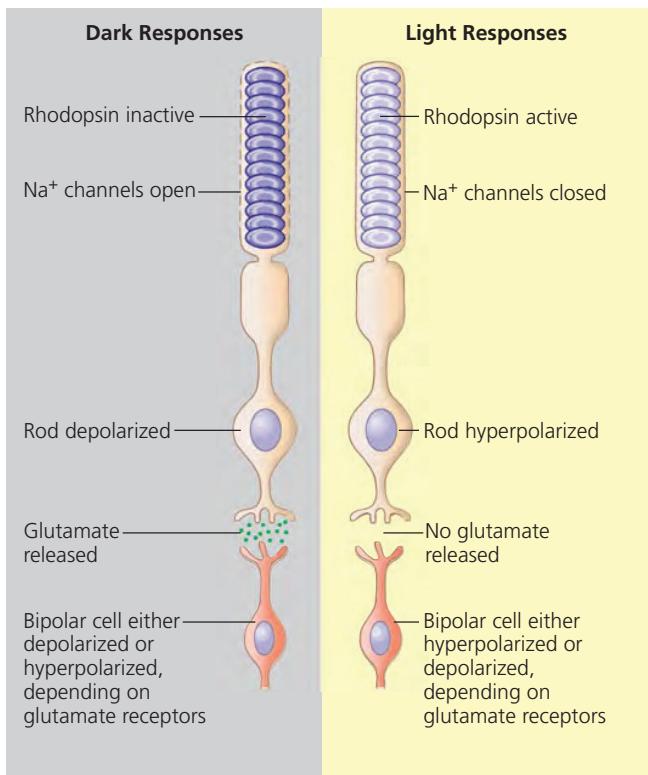
The processing of visual information begins in the retina itself, where both rods and cones form synapses with bipolar cells (**Figure 50.19**). In the dark, rods and cones are depolarized and continually release the neurotransmitter glutamate at these synapses (see Table 48.2). Some bipolar cells depolarize in response to glutamate, whereas others hyperpolarize. Which of the two responses a bipolar cell exhibits depends on the type of glutamate receptor on its surface at the synapse. When light strikes the rods and cones, they hyperpolarize, shutting off their release of glutamate. In response, the bipolar cells that are depolarized by glutamate hyperpolarize, and those that are hyperpolarized by glutamate depolarize.

In addition to bipolar cells, information processing in the retina requires three other types of neurons—ganglion, horizontal, and amacrine cells (see Figure 50.17).

Signals from rods and cones can follow several different pathways in the retina. Some information passes directly from photoreceptors to bipolar cells to ganglion cells. In other cases, horizontal cells carry signals from one rod or cone to other photoreceptors and to several bipolar cells. When an illuminated rod or cone stimulates a horizontal cell, the horizontal cell inhibits more distant photoreceptors and bipolar cells that are not illuminated. The result is



▲ **Figure 50.18 Production of the receptor potential in a rod cell.** In rods (and cones), the receptor potential triggered by light is a hyperpolarization, not a depolarization.



▲ **Figure 50.19** Synaptic activity of rod cells in light and dark.

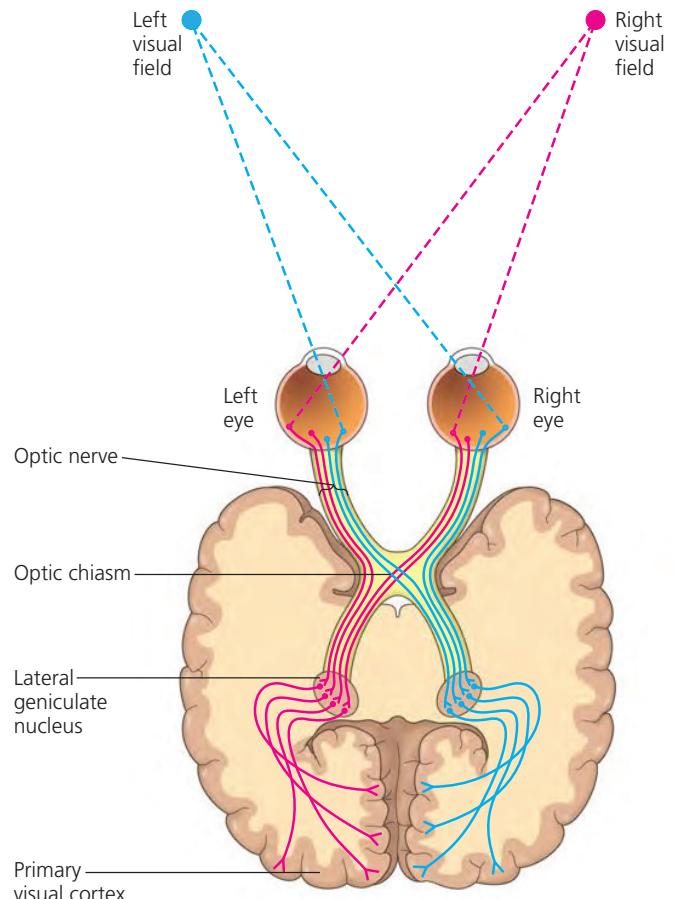
? Like rods, cone cells are depolarized when rhodopsin is inactive. In the case of a cone, why might it be misleading to call this a dark response?

that the region receiving light appears lighter and the dark surroundings even darker. This form of integration, called **lateral inhibition**, sharpens edges and enhances contrast in the image. Amacrine cells distribute some information from one bipolar cell to several ganglion cells. Lateral inhibition is repeated by the interactions of the amacrine cells with the ganglion cells and occurs at all levels of visual processing in the brain.

A single ganglion cell receives information from an array of rods and cones, each of which responds to light coming from a particular location. Together, the rods or cones that feed information to one ganglion cell define a *receptive field*—the part of the visual field to which the ganglion can respond. The fewer rods or cones that supply a single ganglion cell, the smaller the receptive field. A smaller receptive field results in a sharper image, because the information as to where light has struck the retina is more precise. The ganglion cells of the fovea have very small receptive fields, so visual acuity (sharpness) in the fovea is high.

Processing of Visual Information in the Brain

Axons of ganglion cells form the optic nerves that transmit sensations from the eyes to the brain (**Figure 50.20**). The two



▲ **Figure 50.20** Neural pathways for vision. Each optic nerve contains about a million axons that synapse with interneurons in the lateral geniculate nuclei. The nuclei relay sensations to the primary visual cortex, one of many brain centers that cooperate in constructing our visual perceptions.

optic nerves meet at the **optic chiasm** near the center of the base of the cerebral cortex. Axons in the optic nerves are routed at the optic chiasm such that sensations from the left visual field of both eyes are transmitted to the right side of the brain, and sensations from the right visual field are transmitted to the left side of the brain. (Note that each visual field, whether right or left, involves input from both eyes.)

Within the brain, most ganglion cell axons lead to the **lateral geniculate nuclei**, which have axons that reach the **primary visual cortex** in the cerebrum. Additional neurons carry the information to higher-order visual processing and integrating centers elsewhere in the cortex.

Point-by-point information in the visual field is projected along neurons onto the visual cortex. How does the cortex convert a complex set of action potentials representing two-dimensional images focused on the retina to three-dimensional perceptions of our surroundings? Researchers estimate that at least 30% of the cerebral cortex, comprising hundreds of

millions of neurons in perhaps dozens of integrating centers, takes part in formulating what we actually “see.” Determining how these centers integrate such components of our vision as color, motion, depth, shape, and detail is the focus of much exciting research.

Color Vision

Among vertebrates, most fishes, amphibians, and reptiles, including birds, have very good color vision. Humans and other primates also see color well, but are among the minority of mammals with this ability. Many mammals are nocturnal, and having a high proportion of rods in the retina is an adaptation that gives these animals keen night vision. Cats, for instance, are usually most active at night; they have limited color vision and probably see a pastel world during the day.

In humans, the perception of color is based on three types of cones, each with a different visual pigment—red, green, or blue. The three visual pigments, called *photopsins*, are formed from the binding of retinal to three distinct opsin proteins. Slight differences in the opsin proteins are sufficient for each photopsin to absorb light optimally at a different wavelength. Although the visual pigments are designated as red, green, or blue, their absorption spectra in fact overlap. For this reason, the brain’s perception of intermediate hues depends on the differential stimulation of two or more classes of cones. For example, when both red and green cones are stimulated, we may see yellow or orange, depending on which class is more strongly stimulated.

Abnormal color vision typically results from alterations in the genes for one or more photopsin proteins. Because the human genes for the red and green pigments are located on the X chromosome, a single defective copy of either gene can disrupt color vision in males (see Figure 15.7 to review the genetics of sex-linked traits). For this reason, color blindness is more common in males than in females (5–8% of males, fewer than 1% of females) and nearly always disrupts perception of red or green (the gene for blue pigment is on human chromosome 7).

Color blindness is also more common among males than females in squirrel monkeys (*Saimiri sciureus*), providing a good experimental model for studying this disorder. In 2009, researchers studying color blindness in squirrel monkeys made a significant breakthrough in the field of gene therapy (Figure 50.21).

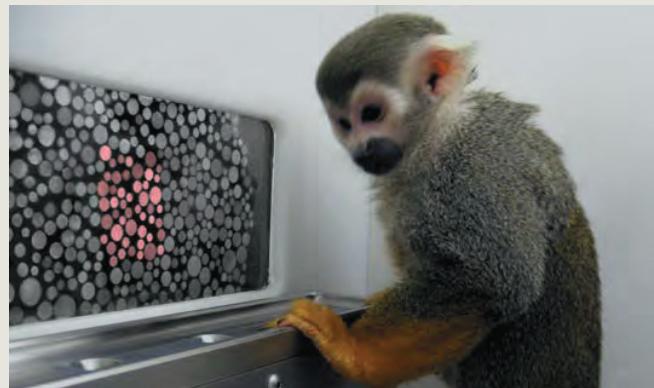
The Visual Field

The brain not only processes visual information, but also controls what information is captured. One important type of control is focusing, which, as noted earlier and illustrated in Figure 50.22, occurs by changing the shape of the lens. When you focus on a close object, your lens becomes almost spherical. When you view a distant object, your lens is flattened. By turning your head and pointing your eyes in a particular direction, your brain also determines what lies in your field of vision.

▼ **Figure 50.21**
IMPACT

Gene Therapy for Vision

Seeking to learn whether a defect in color vision could be remedied in an adult animal, researchers chose to study squirrel monkeys, which have only two opsin genes. The opsin encoded by one gene is sensitive to blue light, while the other opsin is sensitive to either red or green light, depending on the allele. Because the red/green opsin gene is X-linked, all males have only the red-sensitive or the green-sensitive version and are red-green color-blind. In a gene therapy experiment, researchers injected a virus containing the gene for the missing version into the retina of adult male monkeys. After 20 weeks, the new opsin allele was being expressed in cones and the monkeys had begun to distinguish red from green in a field of colored dots.



WHY IT MATTERS These experiments demonstrate that the neural circuits required to process visual information can be generated or activated even in adults, opening up the possibility for treating a range of vision disorders by gene therapy. Indeed, gene therapy has already been used to treat Leber’s congenital amaurosis (LCA), an inherited retinal degenerative disease that causes severe loss of vision at birth. After using gene therapy to restore vision in dogs and mice with LCA, researchers successfully treated the disease in humans by injecting the functional LCA gene in a viral vector.

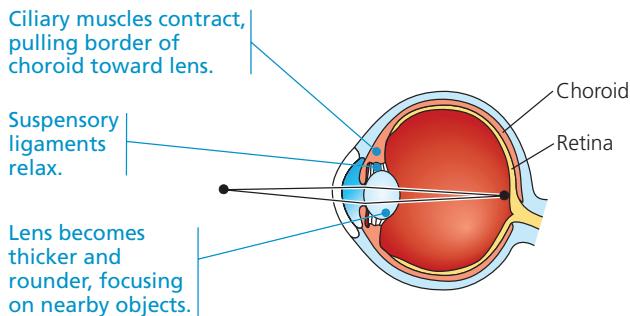
FURTHER READING F. P. M. Cremers and R. W. J. Collin, Promises and challenges of genetic therapy for blindness, *The Lancet* 374:1569–1570 (2009).

MAKE CONNECTIONS Red-green color blindness is X-linked in squirrel monkeys and humans (see Figure 15.7, p. 291). Why is the inheritance pattern in humans not apparent in squirrel monkeys?

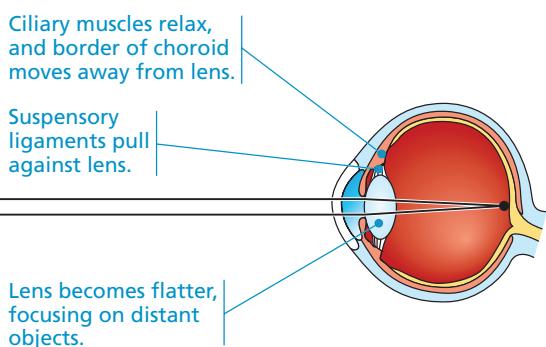
Although our peripheral vision allows us to see objects over a nearly 180° range, the distribution of photoreceptors across the eye limits both what we see and how well we see it. Overall, the human retina contains about 125 million rods and about 6 million cones. At the **fovea**, the center of the visual field, there are no rods but a very high density of cones—about 150,000 cones per square millimeter. The ratio of rods to cones increases with distance from the fovea, with the peripheral regions having only rods. In daylight, you achieve your sharpest vision by looking directly at an object, such that light shines on the tightly packed cones in your fovea.

▼ **Figure 50.22 Focusing in the mammalian eye.** Ciliary muscles control the shape of the lens, which bends light and focuses it on the retina. The thicker the lens, the more sharply the light is bent.

(a) Near vision (accommodation)



(b) Distance vision



At night, looking directly at a dimly lit object is ineffective, since the rods—the more sensitive light receptors—are found outside the fovea. Thus, for example, you see a dim star best by focusing on a point just to one side of it.

CONCEPT CHECK 50.3

1. Contrast the light-detecting organs of planarians and flies. How is each organ adaptive for the lifestyle of the animal?
2. In a condition called presbyopia, the eyes' lenses lose much of their elasticity and maintain a flat shape. Explain how this condition affects a person's vision.
3. **WHAT IF?** If you perceive an object floating across your field of view, how might you determine whether the image represents a real object rather than a disturbance in your eye or in a neural circuit of your brain?
4. **MAKE CONNECTIONS** Compare the function of retinal in the eye with that of the pigment chlorophyll in a plant photosystem (see Concept 10.2, pp. 190–194).

For suggested answers, see Appendix A.

CONCEPT 50.4

The senses of taste and smell rely on similar sets of sensory receptors

Many animals use their chemical senses to find mates (as when male silk moths respond to pheromones emitted by females), to recognize territory that has been marked by some chemical substance (as when dogs and cats sniff boundaries that have been staked out by their spraying neighbors), and to help navigate during migration (as when salmon use the unique scent of their streams of origin to return there for breeding). Animals such as ants and bees that live in large social groups rely extensively on chemical “conversation.” In all animals, chemical senses are important in feeding behavior. For example, a hydra retracts its tentacles toward its mouth when it detects the compound glutathione, which is released from prey captured by the tentacles.

The perceptions of **gustation** (taste) and **olfaction** (smell) both depend on chemoreceptors that detect specific chemicals in the environment. In the case of terrestrial animals, taste is the detection of chemicals called **tastants** that are present in a solution, and smell is the detection of **odorants** that are carried through the air. There is no distinction between taste and smell in aquatic animals.

The taste receptors of insects are located within sensory hairs located on the feet and in mouthparts. These animals use their sense of taste to select food. A tasting hair contains several chemoreceptors, each especially responsive to a particular class of tastant, such as sugar or salt. Insects are also capable of smelling airborne odorants using olfactory hairs, usually located on their antennae (see Figure 50.6). The chemical DEET (*N,N*-diethyl-meta-toluamide), sold as an insect “repellant,” actually protects against bites by blocking the olfactory receptor in mosquitoes that detects human scent.

Taste in Mammals

Humans and other mammals recognize five types of tastants. Four represent the familiar taste perceptions—sweet, sour, salty, and bitter. The fifth, called umami (Japanese for “delicious”), is elicited by the amino acid glutamate. Often used as a flavor enhancer, monosodium glutamate (MSG) occurs naturally in foods such as meat and aged cheese, imparting a quality sometimes described as savory. Researchers have identified the receptor proteins for all of the tastes except salty.

For decades, many researchers assumed that a taste cell could have more than one type of receptor. An alternative idea is that each taste cell has a single receptor type, programming the cell to recognize only one of the five tastes. Which hypothesis is correct? In 2005, scientists at the University of California, San Diego, used a cloned bitter taste receptor to genetically

▼ Figure 50.23

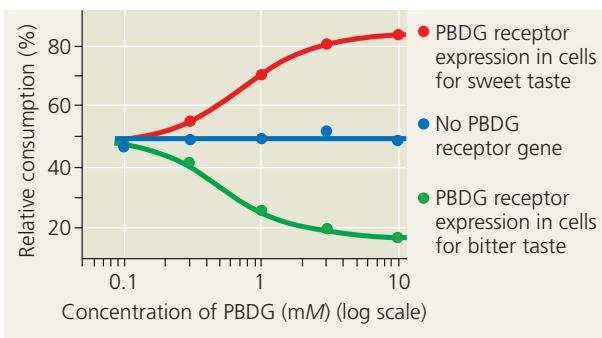
INQUIRY

How do mammals detect different tastes?

EXPERIMENT To investigate the basis of mammalian taste perception, Ken Mueller, Nick Ryba, and Charles Zuker used a chemical called phenyl- β -D-glucopyranoside (PBDG). Humans find the taste of PBDG extremely bitter. Mice, however, appear to lack a receptor for PBDG. Whereas mice avoid drinking water containing other bitter tastants, they show no aversion to water that contains PBDG.

Using a molecular cloning strategy, Mueller generated mice that made the human PBDG receptor in cells that normally make either a sweet receptor or a bitter receptor. The mice were given a choice of two bottles, one filled with pure water and one filled with water containing PBDG at varying concentrations. The researchers then observed whether the mice had an attraction or an aversion to PBDG.

RESULTS



$$\text{Relative consumption} = (\text{Fluid intake from bottle containing PBDG} \div \text{Total fluid intake}) \times 100\%$$

CONCLUSION The researchers found that the presence of a bitter receptor in sweet taste cells is sufficient to cause mice to be attracted to a bitter chemical. They concluded that the mammalian brain must therefore perceive sweet or bitter taste solely on the basis of which sensory neurons are activated.

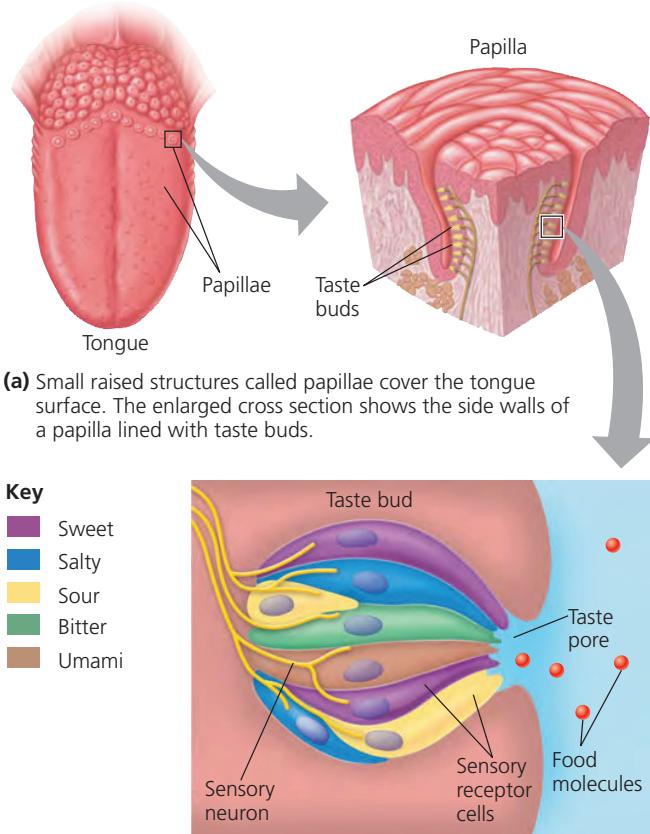
SOURCE K. L. Mueller et al., The receptors and coding logic for bitter taste, *Nature* 434:225–229 (2005).

WHAT IF? Suppose instead of the PBDG receptor the researchers had used a receptor specific for a sweetener that humans crave but mice ignore. How would the results of the experiment have differed?

reprogram gustation in a mouse (Figure 50.23). Based on these and other studies, the researchers concluded that an individual taste cell expresses a single receptor type and detects tastants representing only one of the five tastes.

The receptor cells for taste in mammals are modified epithelial cells organized into **taste buds**, which are scattered in several areas of the tongue and mouth (Figure 50.24). Most taste buds on the tongue are associated with nipple-shaped projections called papillae. Any region of the tongue with taste buds can detect any of the five types of taste. (The frequently reproduced “taste maps” of the tongue are thus not accurate.)

Taste receptors fall into two categories, each evolutionarily related to receptors for other senses. The sensation of sweet,



(b) Taste buds in all regions of the tongue contain sensory receptor cells specific for each of the five taste types.

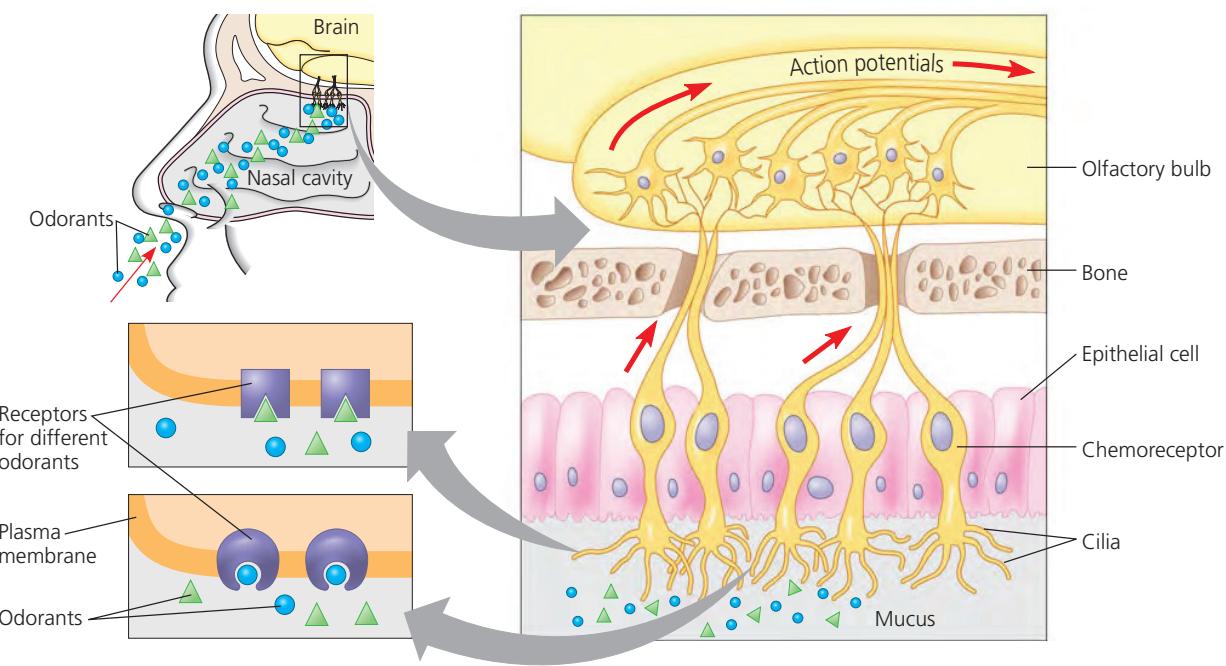
▲ Figure 50.24 Human taste receptors.

sweet, and umami, and bitter tastes requires a G protein-coupled receptor, or GPCR (see Figure 11.7). In humans, there are more than 30 different receptors for bitter taste, each able to recognize multiple bitter tastants. In contrast, humans have one type of sweet receptor and one type of umami receptor, each assembled from a different pair of GPCR proteins. Other GPCR proteins are critical for the sense of smell, as we will discuss shortly.

Unlike the other identified taste receptors, the receptor for sour tastants belongs to the TRP family (see p. 1089). Formed from a pair of TRP proteins, the sour receptor is similar to the capsaicin receptor and other thermoreceptor proteins. In taste buds, the TRP proteins of the sour receptor assemble into a channel in the plasma membrane of the taste cell. Binding of an acid or other sour-tasting substance to the receptor triggers a change in the ion channel. Depolarization occurs, activating a sensory neuron.

Smell in Humans

In olfaction, unlike gustation, the sensory cells are neurons. Olfactory receptor cells line the upper portion of the nasal cavity and send impulses along their axons directly to the olfactory bulb of the brain (Figure 50.25). The receptive ends



▲ Figure 50.25 Smell in humans. Odorant molecules bind to specific receptor proteins in the plasma membrane of olfactory receptor cells, triggering action potentials.

WHAT IF? If you spray an “air freshener” in a musty room, would you be affecting detection, transmission, or perception of the odorants responsible for the musty smell?

of the cells contain cilia that extend into the layer of mucus coating the nasal cavity. When an odorant diffuses into this region, it binds to a specific GPCR protein called an odorant receptor (OR) on the plasma membrane of the olfactory cilia. These events trigger signal transduction leading to the production of cyclic AMP. In olfactory cells, cyclic AMP opens channels in the plasma membrane that are permeable to both Na^+ and Ca^{2+} . The flow of these ions into the receptor cell leads to depolarization of the membrane, generating action potentials.

Humans can distinguish thousands of different odors, each caused by a structurally distinct odorant. This level of sensory discrimination requires many different ORs. In 1991, Richard Axel and Linda Buck, working at Columbia University, discovered a family of more than 1,000 OR genes—about 3% of all human genes. Each olfactory receptor cell appears to express one OR gene. Cells selective for different odorants are interspersed in the nasal cavity. Those cells that express the same OR gene transmit action potentials to the same small region of the olfactory bulb. In 2004, Axel and Buck shared a Nobel Prize for their studies of the gene family and receptors that function in olfaction.

Although the receptors and brain pathways for taste and smell are independent, the two senses do interact. Indeed, much of the complex flavor humans experience when eating is due to our sense of smell. If the olfactory system is blocked, as occurs when you have a head cold, the perception of taste is sharply reduced.

CONCEPT CHECK 50.4

- Explain why some taste receptor cells and all olfactory receptor cells use G protein-coupled receptors, yet only olfactory receptor cells produce action potentials.
- Pathways involving G proteins provide an opportunity for an increase in signal strength in the course of signal transduction, a change referred to as amplification. How might this be beneficial in olfaction?
- WHAT IF?** If you discovered a mutation in mice that disrupted the ability to taste sweet, bitter, and umami, but not sour or salty, what might you predict about where this mutation acts in the signaling pathways used by these receptors?

For suggested answers, see Appendix A.

CONCEPT 50.5

The physical interaction of protein filaments is required for muscle function

Throughout our discussion of sensory mechanisms, we have seen how sensory inputs to the nervous system result in specific behaviors: the touch-guided foraging of a star-nosed mole, the upside-down swimming of a crayfish with manipulated

statocysts, and the light-avoiding maneuvers of planarians. Underlying the diverse forms of behavior in animals are common fundamental mechanisms: Feeding, swimming, and crawling all require muscle activity in response to nervous system input.

Muscle cell function relies on microfilaments, which are the actin components of the cytoskeleton. Recall from Chapter 6 that microfilaments, like microtubules, function in cell motility. Muscle contraction is the product of microfilament movement powered by chemical energy; muscle extension occurs only passively. To understand how microfilaments contribute to muscle contraction, we must analyze the structure of muscles and muscle fibers. We will begin by examining vertebrate skeletal muscle and then turn our attention to other types of muscle.

Vertebrate Skeletal Muscle

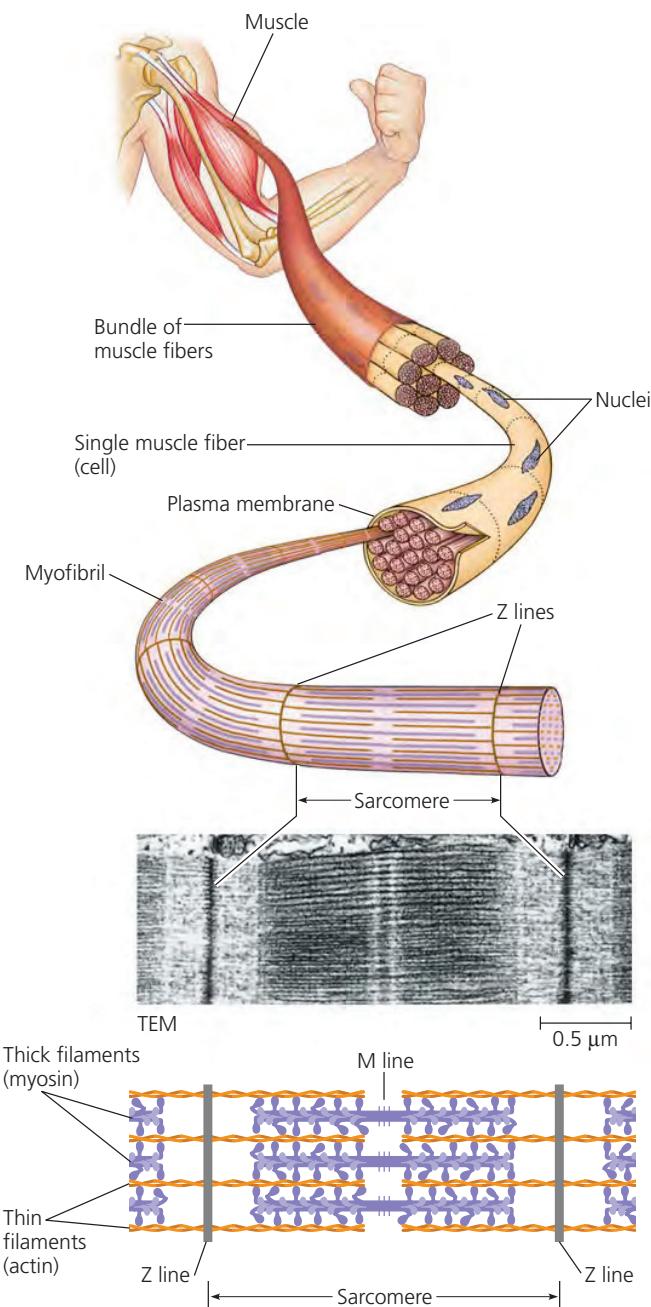
Vertebrate **skeletal muscle**, which moves bones and body, is characterized by a hierarchy of smaller and smaller units (**Figure 50.26**). Most skeletal muscles consist of a bundle of long fibers running parallel to the length of the muscle. Each fiber is a single cell. A muscle fiber, or cell, contains multiple nuclei, reflecting its formation by the fusion of many embryonic cells. Inside the fiber lies a bundle of smaller **myofibrils** arranged longitudinally. The myofibrils, in turn, are composed of thin filaments and thick filaments. **Thin filaments** consist of two strands of actin and two strands of a regulatory protein (not shown here) coiled around one another. **Thick filaments** are staggered arrays of myosin molecules.

Skeletal muscle is also called **striated muscle** because the regular arrangement of the filaments creates a pattern of light and dark bands. Each repeating unit is a **sarcomere**, the basic contractile unit of the muscle. The borders of the sarcomere are lined up in adjacent myofibrils and contribute to the striations visible with a light microscope. Thin filaments are attached at the Z lines and project toward the center of the sarcomere, while thick filaments are attached at the M lines centered in the sarcomere. In a muscle fiber at rest, thick and thin filaments only partially overlap. Near the edge of the sarcomere there are only thin filaments, whereas the zone in the center contains only thick filaments. This arrangement is the key to how the sarcomere, and hence the whole muscle, contracts.

The Sliding-Filament Model of Muscle Contraction

We can explain much of what happens during the contraction of a whole muscle by focusing on the contraction of a single sarcomere (**Figure 50.27**). According to the **sliding-filament model**, the filaments do not change in length when the sarcomere shortens. Instead, the thin and thick filaments slide past each other, increasing their overlap.

The longitudinal sliding of the filaments relies on the interaction of actin and myosin. Each myosin molecule has a long “tail” region and a globular “head” region. The tail adheres to the tails of other myosin molecules that form the thick filament. The head, which extends to the side, can bind



▲ Figure 50.26 The structure of skeletal muscle.

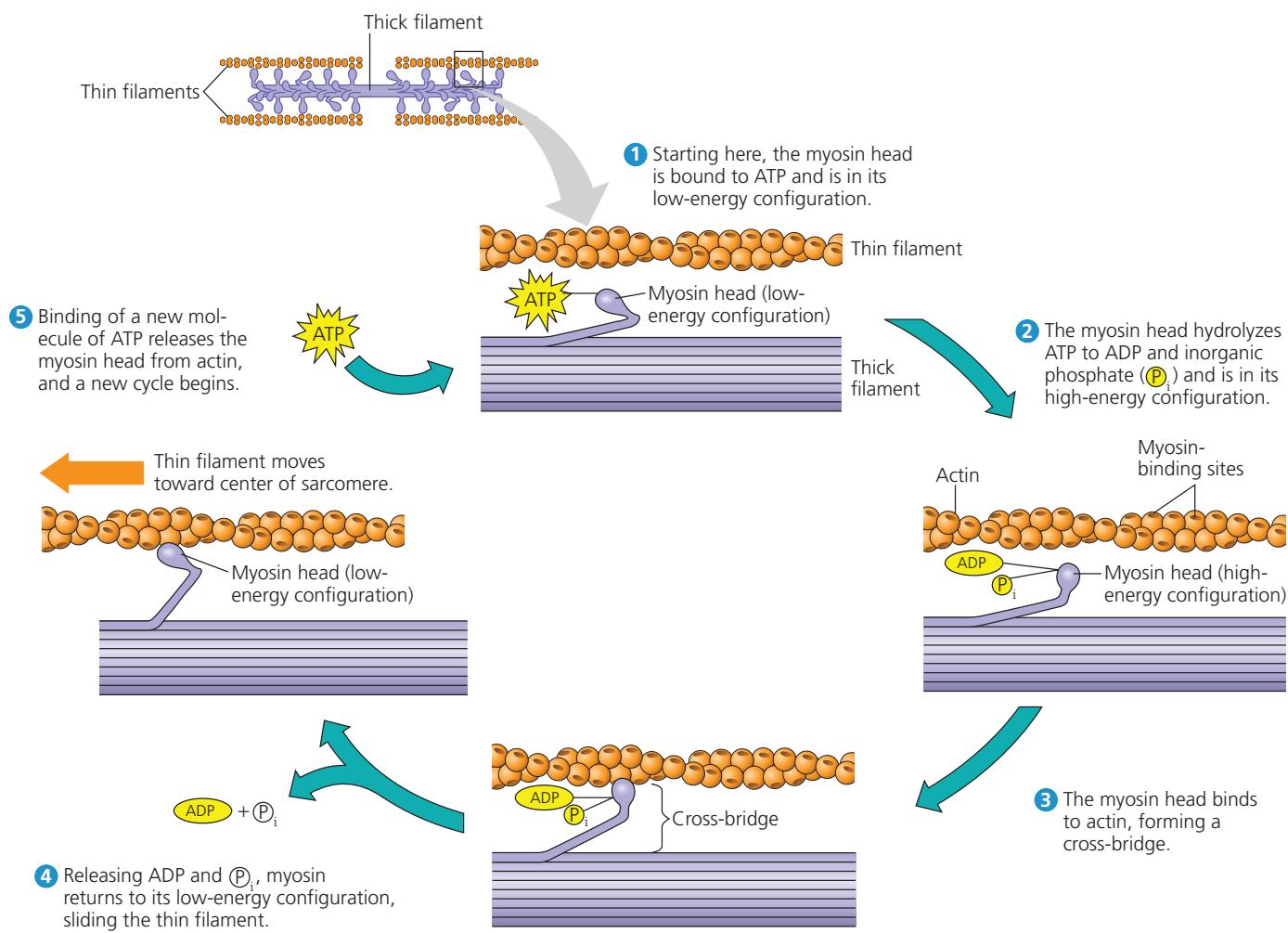
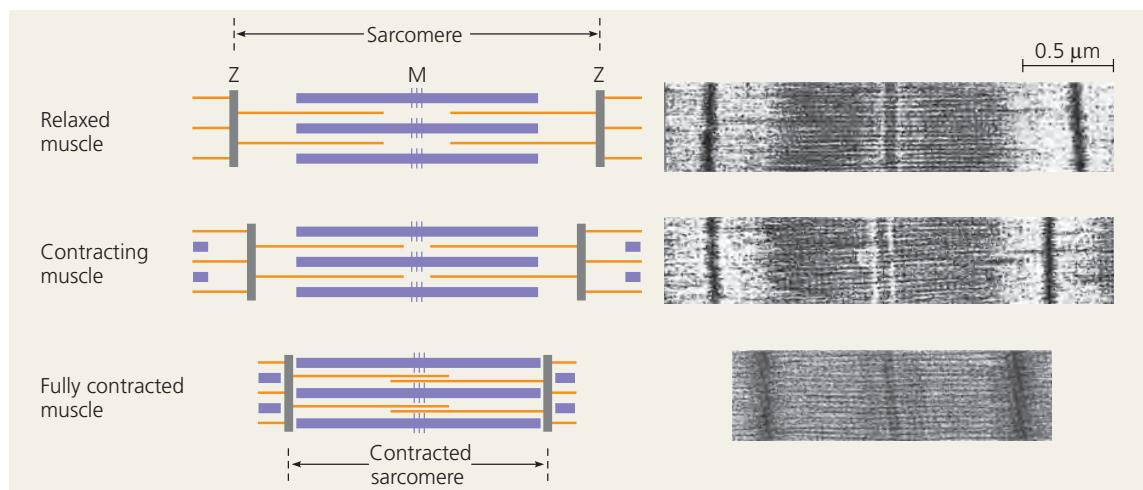
ATP and hydrolyze it to ADP and inorganic phosphate. As shown in **Figure 50.28**, hydrolysis of ATP converts myosin to a high-energy form. This form of myosin binds to actin, forms a cross-bridge, and pulls the thin filament toward the center of the sarcomere. The cross-bridge is broken when a new molecule of ATP binds to the myosin head.

Muscle contraction requires repeated cycles of binding and release. In each cycle, the myosin head freed from a cross-bridge cleaves the newly bound ATP and binds again to actin. Because the thin filament moved toward the center of

► **Figure 50.27**

The sliding-filament model of muscle contraction.

The drawings on the left show that the lengths of the thick (myosin) filaments (purple) and thin (actin) filaments (orange) remain the same as a muscle fiber contracts.



▲ **Figure 50.28** Myosin-actin interactions underlying muscle fiber contraction.

? When ATP binds, what prevents the filaments from sliding back into their original positions?



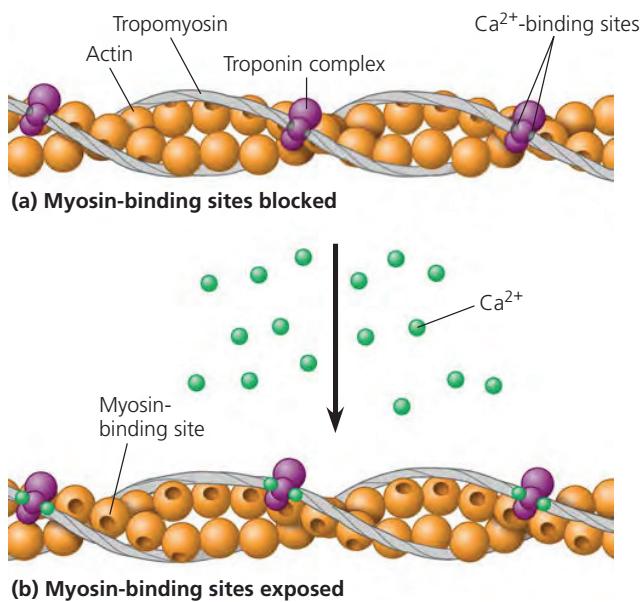
BioFlix Visit the Study Area at www.masteringbiology.com for the BioFlix® 3-D Animation on Muscle Contraction.

the sarcomere in the previous cycle, the myosin head now attaches to a new binding site farther along the thin filament. Each of the approximately 350 heads of a thick filament forms and re-forms about five cross-bridges per second, driving filaments past each other.

A typical muscle fiber at rest contains only enough ATP for a few contractions. To power repetitive contractions, the muscle cell relies on two other storage compounds: creatine phosphate and glycogen. Transfer of a phosphate group from creatine phosphate to ADP in an enzyme-catalyzed reaction synthesizes additional ATP. In this way, the resting supply of creatine phosphate can sustain contractions for about 15 seconds. ATP stores are also replenished when glycogen is broken down to glucose, which can be used to generate ATP, by either aerobic respiration or glycolysis (and lactic acid fermentation; see Chapter 9). Using a typical muscle fiber's glycogen store, glycolysis can support about 1 minute of sustained contraction, whereas aerobic respiration can power contractions for nearly an hour.

The Role of Calcium and Regulatory Proteins

Calcium ions (Ca^{2+}) and proteins bound to actin play crucial roles in both muscle cell contraction and relaxation. **Tropomyosin**, a regulatory protein, and the **troponin complex**, a set of additional regulatory proteins, are bound to the actin strands of thin filaments. In a muscle fiber at rest, tropomyosin covers the myosin-binding sites along the thin filament, preventing actin and myosin from interacting (Figure 50.29a). When Ca^{2+} accumulates in the cytosol, it



▲ Figure 50.29 The role of regulatory proteins and calcium in muscle fiber contraction. Each thin filament consists of two strands of actin, tropomyosin, and the troponin complex.

binds to the troponin complex, causing tropomyosin bound along the actin strands to shift position and expose the myosin-binding sites on the thin filament (Figure 50.29b). Thus, when the Ca^{2+} concentration rises in the cytosol, the thin and thick filaments slide past each other, and the muscle fiber contracts. When the Ca^{2+} concentration falls, the binding sites are covered, and contraction stops.

Motor neurons cause muscle contraction by triggering the release of Ca^{2+} into the cytosol of muscle cells with which they form synapses. This regulation of Ca^{2+} concentration is a multistep process involving a network of membranes and compartments within the muscle cell. As you read the following description, refer to the overview and diagram in Figure 50.30.

The arrival of an action potential at the synaptic terminal of a motor neuron causes release of the neurotransmitter acetylcholine. Binding of acetylcholine to receptors on the muscle fiber leads to a depolarization, triggering an action potential. Within the muscle fiber, the action potential spreads deep into the interior, following infoldings of the plasma membrane called **transverse (T) tubules**. The T tubules make close contact with the **sarcoplasmic reticulum (SR)**, a specialized endoplasmic reticulum. As the action potential spreads along the T tubules, it triggers changes in the SR, opening Ca^{2+} channels. Calcium ions stored in the interior of the SR flow through these open channels into the cytosol and bind to the troponin complex, initiating contraction of the muscle fiber.

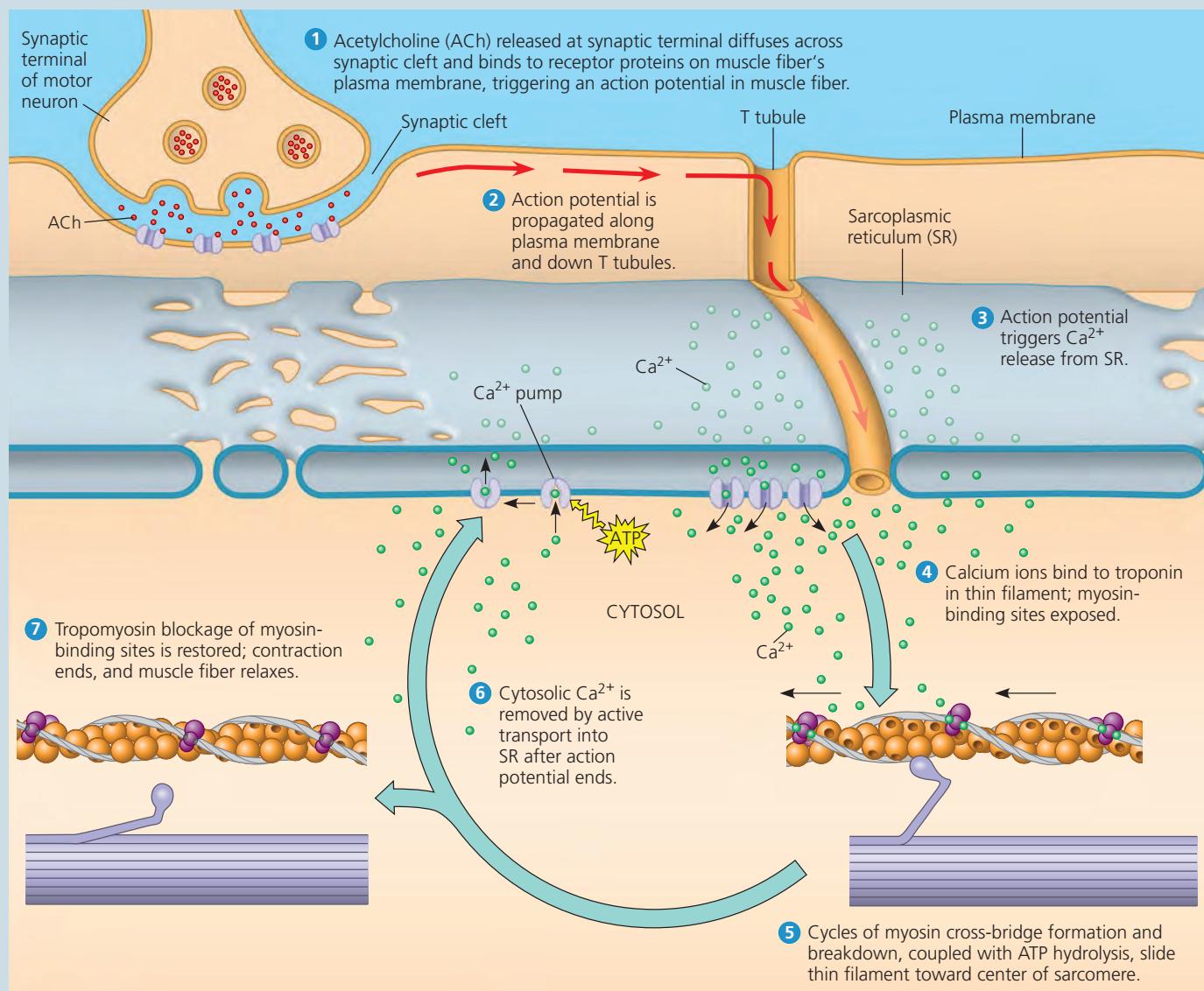
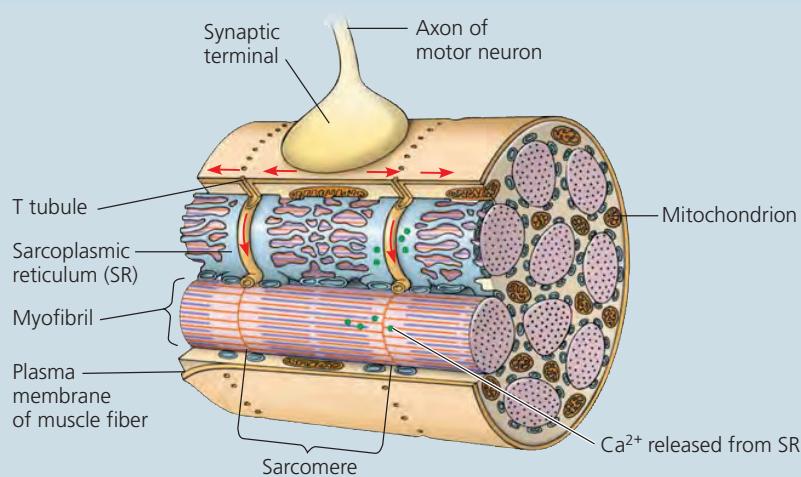
When motor neuron input stops, the muscle cell relaxes. As it relaxes, the filaments slide back to their starting position. During this phase, proteins in the cell reset the muscle for the next cycle of contraction. Relaxation begins as transport proteins in the SR pump Ca^{2+} in from the cytosol. When the Ca^{2+} concentration in the cytosol drops to a low level, the regulatory proteins bound to the thin filament shift back to their starting position, once again blocking the myosin-binding sites. At the same time, the Ca^{2+} pumped from the cytosol accumulates in the SR, providing the stores needed to respond to the next action potential.

Several diseases cause paralysis by interfering with the excitation of skeletal muscle fibers by motor neurons. In amyotrophic lateral sclerosis (ALS), also called Lou Gehrig's disease, motor neurons in the spinal cord and brainstem degenerate, and the muscle fibers with which they synapse atrophy. ALS is progressive and usually fatal within five years after symptoms appear; currently there is no cure or treatment. Myasthenia gravis is an autoimmune disease in which a person produces antibodies to the acetylcholine receptors on skeletal muscle fibers. As the number of these receptors decreases, synaptic transmission between motor neurons and muscle fibers declines. Fortunately, effective treatments are available for myasthenia gravis.

▼ Figure 50.30

Exploring The Regulation of Skeletal Muscle Contraction

The electrical, chemical, and molecular events regulating skeletal muscle contraction are shown in a cutaway view of a muscle cell and in the enlarged diagram below. Action potentials (red arrows) triggered by the motor neuron sweep across the muscle fiber and into it along the transverse (T) tubules, initiating the movements of calcium (green dots) that regulate muscle activity.



Nervous Control of Muscle Tension

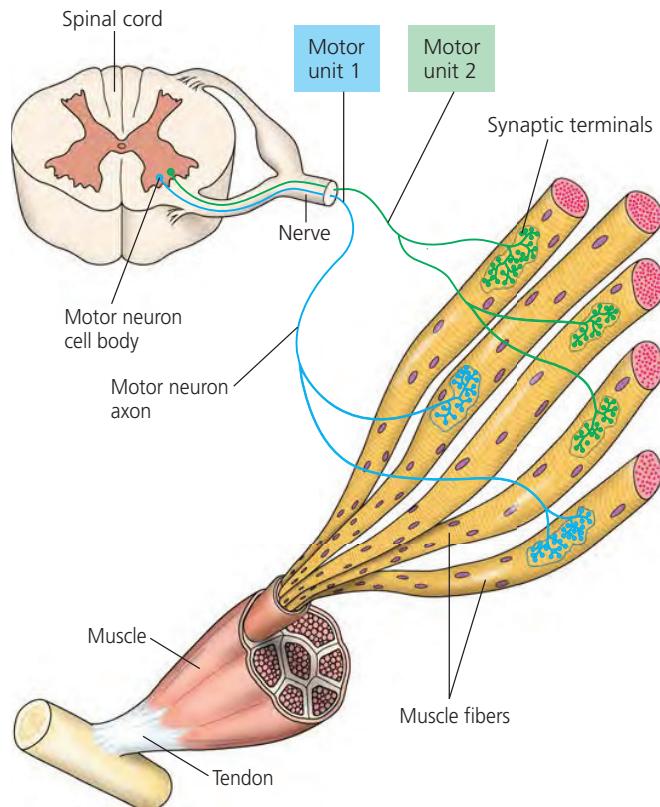
Whereas contraction of a single skeletal muscle fiber is a brief all-or-none twitch, contraction of a whole muscle, such as the biceps in your upper arm, is graded; you can voluntarily alter the extent and strength of its contraction. There are two basic mechanisms by which the nervous system produces graded contractions of whole muscles: (1) by varying the number of muscle fibers that contract and (2) by varying the rate at which muscle fibers are stimulated. Let's consider each mechanism in turn.

In vertebrates, each branched motor neuron may form synapses with many skeletal muscle fibers, although each fiber is controlled by only one motor neuron. For the whole muscle, there may be hundreds of motor neurons, each with its own pool of muscle fibers. A **motor unit** consists of a single motor neuron and all the muscle fibers it controls (**Figure 50.31**). When a motor neuron produces an action potential, all the muscle fibers in its motor unit contract as a group. The strength of the resulting contraction depends on how many muscle fibers the motor neuron controls.

In most muscles, the number of muscle fibers in different motor units ranges from a few to hundreds. The nervous system can thus regulate the strength of contraction in a muscle by determining how many motor units are activated at a given instant and by selecting large or small motor units to activate. The force (tension) developed by a muscle progressively increases as more and more of the motor neurons controlling the muscle are activated, a process called *recruitment* of motor neurons. Depending on the number of motor neurons your brain recruits and the size of their motor units, you can lift a fork or something much heavier, like your biology textbook.

Some muscles, especially those that hold up the body and maintain posture, are almost always partially contracted. In such muscles, the nervous system may alternate activation among the motor units, reducing the length of time any one set of fibers is contracted. Prolonged contraction can result in muscle fatigue due to the depletion of ATP and dissipation of ion gradients required for normal electrical signaling. Although accumulation of lactate (see Figure 9.17) may also contribute to muscle fatigue, recent research actually points to a beneficial effect of lactate on muscle function.

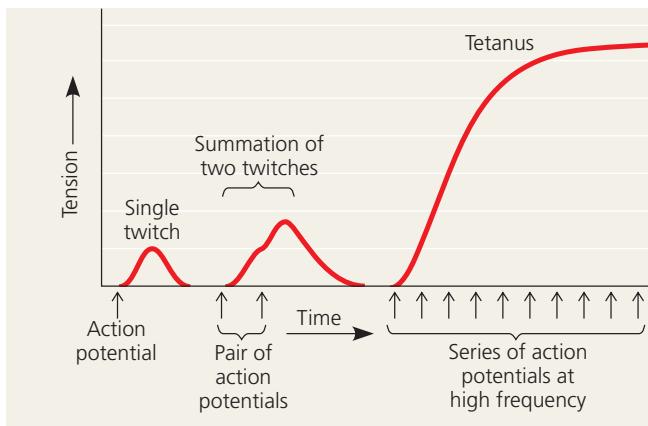
The nervous system regulates muscle contraction not only by controlling which motor units are activated, but also by varying the rate of muscle fiber stimulation. A single action potential produces a twitch lasting about 100 msec or less. If a second action potential arrives before the muscle fiber has completely relaxed, the two twitches add together, resulting in greater tension (**Figure 50.32**). Further summation occurs as the rate of stimulation increases. When the rate is so high that the muscle fiber cannot relax at all between stimuli, the twitches fuse into one smooth, sustained



▲ Figure 50.31 Motor units in a vertebrate skeletal muscle. Each muscle fiber (cell) forms synapses with only one motor neuron, but each motor neuron typically synapses with many muscle fibers. A motor neuron and all the muscle fibers it controls constitute a motor unit.

contraction called **tetanus**. Motor neurons usually deliver their action potentials in rapid-fire volleys, and the resulting summation of tension results in the smooth contraction typical of tetanus rather than the jerky actions of individual twitches. (Although a smooth, sustained contraction is part of normal muscle function, tetanus is also the name of a disease of uncontrolled muscle contraction caused by a bacterial toxin.)

The increase in tension during summation and tetanus occurs because skeletal muscle fibers are connected to bones via tendons and connective tissues. When a muscle fiber contracts, it stretches these elastic structures, which then transmit tension to the bones. In a single twitch, the muscle fiber begins to relax before the elastic structures are fully stretched. During summation, however, the high-frequency action potentials maintain an elevated concentration of Ca^{2+} in the muscle fiber's cytosol, prolonging cross-bridge cycling and causing greater stretching of the elastic structures. During tetanus, the elastic structures are fully stretched, and all of the tension generated by the muscle fiber is transmitted to the bones.



▲ **Figure 50.32 Summation of twitches.** This graph illustrates how the number of action potentials in a short period of time influences the tension developed in a muscle fiber.

? How could the nervous system cause a skeletal muscle to produce the most forceful contraction it is capable of?

Types of Skeletal Muscle Fibers

Our discussion to this point has focused on the general properties of vertebrate skeletal muscles. There are, however, several distinct types of skeletal muscle fibers, each of which is adapted to a particular set of functions. Scientists typically classify these varied fiber types either by the source of ATP used to power muscle activity or by the speed of muscle contraction. We'll consider each of the two classification schemes.

Oxidative and Glycolytic Fibers Fibers that rely mostly on aerobic respiration are called oxidative fibers. Such fibers are specialized in ways that enable them to make use of a steady energy supply: They have many mitochondria, a rich blood supply, and a large amount of an oxygen-storing protein called **myoglobin**. A brownish red pigment, myoglobin binds oxygen more tightly than does hemoglobin, enabling oxidative fiber to extract oxygen from the blood efficiently. In contrast to oxidative fibers, glycolytic fibers use glycolysis as their primary source of ATP. They have a larger diameter and less myoglobin than oxidative fibers and thus fatigue much more readily. These different fiber types are readily apparent in the muscle of poultry and fish: The dark meat is made up of oxidative fibers rich in myoglobin, and the light meat is composed of glycolytic fibers.

Fast-Twitch and Slow-Twitch Fibers Muscle fibers vary in the speed with which they contract: **Fast-twitch fibers** develop tension two to three times faster than **slow-twitch fibers**. Fast fibers enable brief, rapid, powerful contractions. Slow fibers, often found in muscles that maintain posture, can sustain long contractions. A slow fiber has less sarcoplasmic reticulum and pumps Ca^{2+} more slowly than a fast fiber. Because

Ca^{2+} remains in the cytosol longer, a muscle twitch in a slow fiber lasts about five times as long as one in a fast fiber.

The difference in contraction speed between slow-twitch and fast-twitch fibers mainly reflects the rate at which their myosin heads hydrolyze ATP. However, there isn't a one-to-one relationship between contraction speed and ATP source. Whereas all slow-twitch fibers are oxidative, fast-twitch fibers can be either glycolytic or oxidative.

Most human skeletal muscles contain both fast- and slow-twitch fibers, although the muscles of the eye and hand are exclusively fast-twitch. In a muscle that has a mixture of fast and slow fibers, the relative proportions of each are genetically determined. However, if such a muscle is used repeatedly for activities requiring high endurance, some fast glycolytic fibers can develop into fast oxidative fibers. Because fast oxidative fibers fatigue more slowly than fast glycolytic fibers, the result will be a muscle that is more resistant to fatigue.

Some vertebrates have skeletal muscle fibers that twitch at rates far faster than any human muscle. For example, superfast muscles produce a rattlesnake's rattle and a dove's coo. The fastest such muscles, however, surround the gas-filled swim bladder inside the male toadfish (Figure 50.33). In producing its characteristic "boat whistle" mating call, the toadfish can contract and relax these muscles more than 200 times per second!

Other Types of Muscle

Although all muscles share the same fundamental mechanism of contraction—actin and myosin filaments sliding past each other—there are many different types of muscle. Vertebrates, for example, have cardiac muscle and smooth muscle in addition to skeletal muscle (see Figure 40.5).



▲ **Figure 50.33 Specialization of skeletal muscles.** The male toadfish (*Opsanus tau*) uses superfast muscles to produce its mating call.

Vertebrate **cardiac muscle** is found in only one part of the body: the heart. Like skeletal muscle, cardiac muscle is striated. However, structural differences between skeletal and cardiac muscle fibers result in differences in their electrical and membrane properties. Whereas skeletal muscle fibers do not produce action potentials unless stimulated by a motor neuron, cardiac muscle cells have ion channels in their plasma membrane that cause rhythmic depolarizations, triggering action potentials without input from the nervous system. Action potentials of cardiac muscle cells last up to 20 times longer than those of the skeletal muscle fibers. Plasma membranes of adjacent cardiac muscle cells interlock at specialized regions called **intercalated disks**, where gap junctions (see Figure 6.32) provide direct electrical coupling between the cells. Thus, the action potential generated by specialized cells in one part of the heart spreads to all other cardiac muscle cells, causing the whole heart to contract. A long refractory period prevents summation and tetanus.

Smooth muscle in vertebrates is found mainly in the walls of hollow organs, such as blood vessels and organs of the digestive tract. Smooth muscle cells lack striations because their actin and myosin filaments are not regularly arrayed along the length of the cell. Instead, the thick filaments are scattered throughout the cytoplasm, and the thin filaments are attached to structures called dense bodies, some of which are tethered to the plasma membrane. There is less myosin than in striated muscle fibers, and the myosin is not associated with specific actin strands. Some smooth muscle cells contract only when stimulated by neurons of the autonomic nervous system. Others can generate action potentials without input from neurons—they are electrically coupled to one another. Smooth muscles contract and relax more slowly than striated muscles.

Although Ca^{2+} regulates smooth muscle contraction, the mechanism for regulation is different from that in skeletal and cardiac muscle. Smooth muscle cells have no troponin complex or T tubules, and their sarcoplasmic reticulum is not well developed. During an action potential, Ca^{2+} enters the cytosol mainly through the plasma membrane. Calcium ions cause contraction by binding to the protein calmodulin, which activates an enzyme that phosphorylates the myosin head, enabling cross-bridge activity.

Invertebrates have muscle cells similar to vertebrate skeletal and smooth muscle cells, and arthropod skeletal muscles are nearly identical to those of vertebrates. However, because the flight muscles of insects are capable of independent, rhythmic contraction, the wings of some insects can actually beat faster than action potentials can arrive from the central nervous system. Another interesting evolutionary adaptation has been discovered in the muscles that hold a clam's shell closed. The thick filaments in these muscles contain a protein called paramyosin that enables the muscles to remain contracted for as long as a month with only a low rate of energy consumption.

CONCEPT CHECK 50.5

1. Contrast the role of Ca^{2+} in the contraction of a skeletal muscle fiber and a smooth muscle cell.
2. **WHAT IF?** Why are the muscles of an animal that has recently died likely to be stiff?
3. **MAKE CONNECTIONS** How does the activity of tropomyosin and troponin in muscle contraction compare with the activity of a competitive inhibitor in enzyme action? (See Figure 8.17, p. 156.)

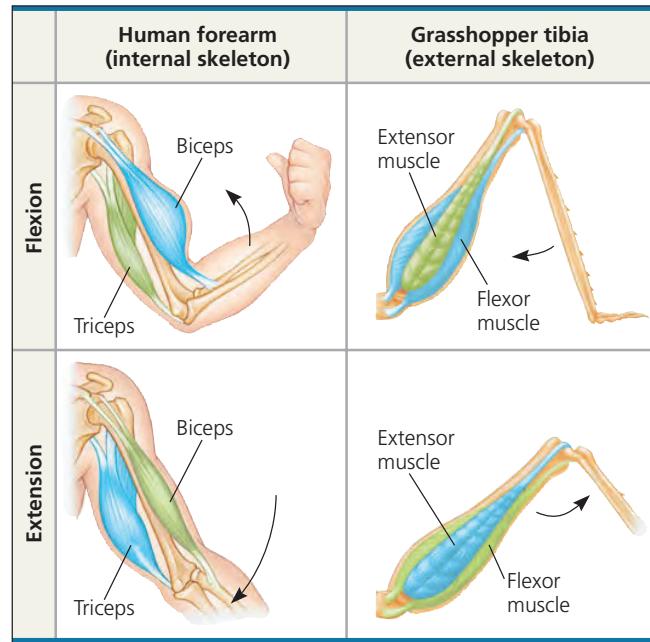
For suggested answers, see Appendix A.

CONCEPT 50.6

Skeletal systems transform muscle contraction into locomotion

Converting muscle contraction to movement requires a skeleton—a rigid structure to which muscles can attach. An animal changes its rigidity, shape, or location by contracting muscles connecting two parts of its skeleton.

Because muscles exert force only during contraction, moving a body part back and forth typically requires two muscles attached to the same section of the skeleton. We can see such an arrangement of muscles in the upper portion of a human arm or grasshopper leg (Figure 50.34). Although we call such



Key ■ Contracting muscle ■ Relaxing muscle

▲ **Figure 50.34 The interaction of muscles and skeletons in movement.** Back-and-forth movement of a body part is generally accomplished by antagonistic muscles. This arrangement works with either an internal skeleton, as in mammals, or an external skeleton, as in insects.

muscles an antagonistic pair, their function is actually cooperative, coordinated by the nervous system. For example, when you extend your arm, motor neurons trigger your triceps muscle to contract while the absence of neuronal input allows your biceps to relax.

Vital for movement, the skeletons of animals also function in support and protection. Most land animals would collapse if they had no skeleton to support their mass. Even an animal living in water would be formless without a framework to maintain its shape. In many animals, a hard skeleton also protects soft tissues. For example, the vertebrate skull protects the brain, and the ribs of terrestrial vertebrates form a cage around the heart, lungs, and other internal organs.

Types of Skeletal Systems

Although we tend to think of skeletons only as interconnected sets of bones, skeletons come in many different forms. Hardened support structures can be external (as in exoskeletons), internal (as in endoskeletons), or even absent (as in fluid-based, or hydrostatic, skeletons).

Hydrostatic Skeletons

A **hydrostatic skeleton** consists of fluid held under pressure in a closed body compartment. This is the main type of skeleton in most cnidarians, flatworms, nematodes, and annelids (see Chapter 33). These animals control their form and movement by using muscles to change the shape of fluid-filled compartments. Among the cnidarians, for example, a hydra elongates by closing its mouth and using contractile cells in its body wall to constrict its central gastrovascular cavity. Because water cannot be compressed very much, decreasing the diameter of the cavity forces the cavity to become longer.

Worms use hydrostatic skeletons in diverse ways to move through their environment. In planarians and other flatworms, movement results mainly from muscles in the body wall exerting localized forces against the interstitial fluid. In nematodes (roundworms), longitudinal muscles contracting around the fluid-filled body cavity move the animal forward by undulations, or wavelike motions. In earthworms and many other annelids, circular and longitudinal muscles act together to change the shape of individual fluid-filled segments, which are divided by septa. These shape changes bring about **peristalsis**, a movement produced by rhythmic waves of muscle contractions passing from front to back (**Figure 50.35**).

Hydrostatic skeletons are well suited for life in aquatic environments. On land, they provide support for crawling and burrowing and may cushion internal organs from shocks. However, a hydrostatic skeleton cannot support walking or running, in which an animal's body is held off the ground.

Exoskeletons

The clam shell you find on a beach once served as an **exoskeleton**, a hard encasement deposited on an animal's

▲ **Figure 50.35 Crawling by peristalsis.** Contraction of the longitudinal muscles thickens and shortens the earthworm; contraction of the circular muscles constricts and elongates it.

attached to knobs and plates of the cuticle that extend into the interior of the body. With each growth spurt, an arthropod must shed its exoskeleton (molt) and produce a larger one.

Endoskeletons

Animals ranging from sponges to mammals have a hardened internal skeleton, or **endoskeleton**, buried within their soft tissues. In sponges, the endoskeleton consists of hard needle-like structures of inorganic material (see Figure 33.4) or fibers made of protein. Echinoderms' bodies are reinforced by ossicles, hard plates composed of magnesium carbonate and calcium carbonate crystals. Whereas the ossicles of sea urchins

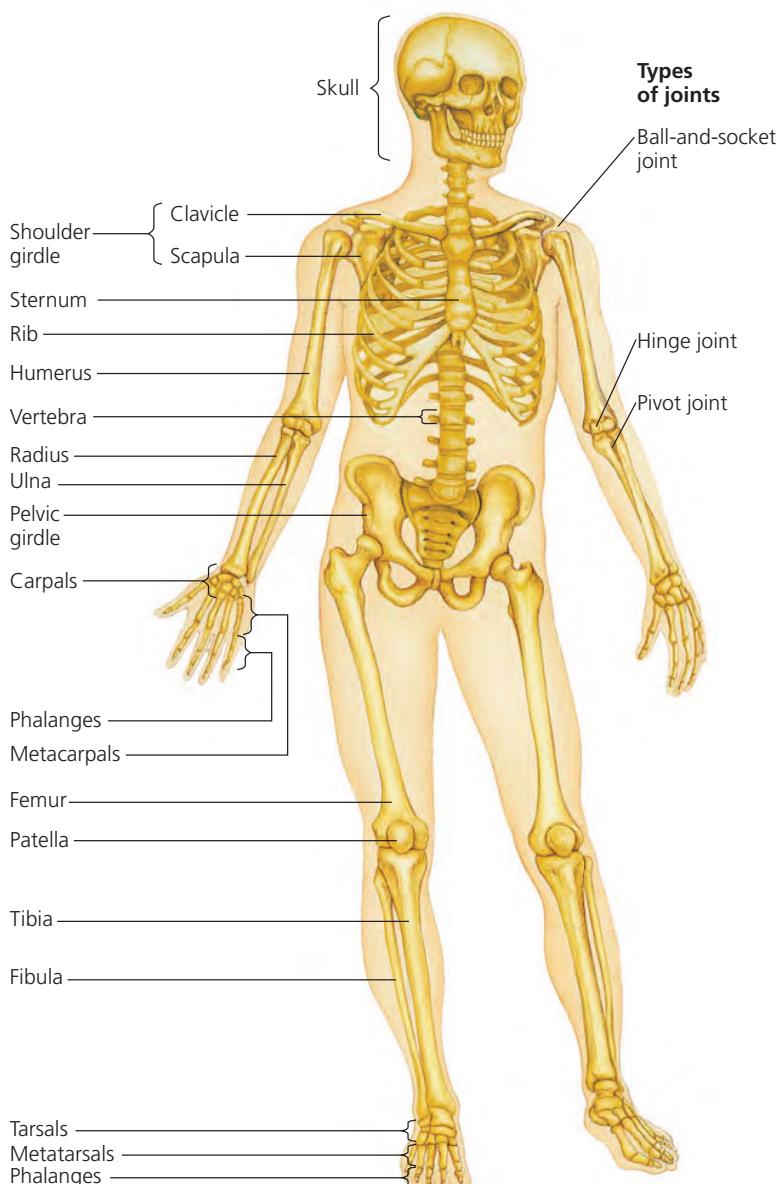
are tightly bound, the ossicles of sea stars are more loosely linked, allowing a sea star to change the shape of its arms.

Chordates have an endoskeleton consisting of cartilage, bone, or some combination of these materials (see Figure 40.5). The mammalian skeleton is built from more than 200 bones, some fused together and others connected at joints by ligaments that allow freedom of movement (**Figures 50.36** and **50.37**).

Size and Scale of Skeletons

An exoskeleton needs to cover and protect an animal's body, but how thick does an endoskeleton need to be? We can begin to answer this question by applying ideas from civil

▼ **Figure 50.36** Bones and joints of the human skeleton.



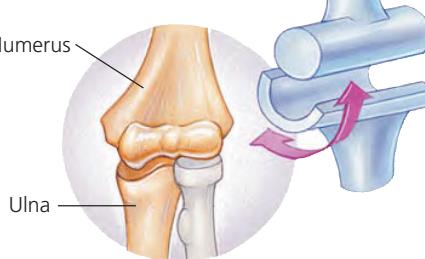
▼ **Figure 50.37** Types of joints.

Ball-and-socket joint



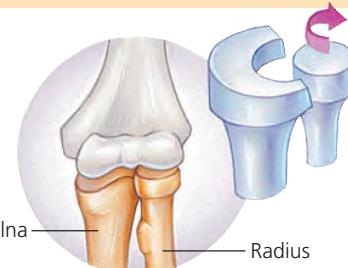
Ball-and-socket joints are found where the humerus contacts the shoulder girdle and where the femur contacts the pelvic girdle. These joints enable the arms and legs to rotate and move in several planes.

Hinge joint



Hinge joints, such as between the humerus and the head of the ulna, restrict movement to a single plane.

Pivot joint



Pivot joints enable rotating the forearm at the elbow and turning the head from side to side.

engineering. For example, the weight of a building increases with the cube of its dimensions. However, the strength of a building support depends on its cross-sectional area, which only increases with the square of its diameter. We can thus predict that if we scaled up a mouse to the size of an elephant, the legs of the giant mouse would be too thin to support its weight. Indeed, large animals do have very different body proportions from those of small animals.

In applying the building analogy, we might also predict that the size of leg bones should be directly proportional to the strain imposed by body weight. However, our prediction would be inaccurate, in part because animal bodies are complex and nonrigid. In supporting body weight, it turns out that body posture—the position of the legs relative to the main body—is more important than leg size, at least in mammals and birds. Muscles and tendons (connective tissue that joins muscle to bone) hold the legs of large mammals relatively straight and positioned under the body and actually bear most of the load.

Types of Locomotion

Movement is a hallmark of animals. Even animals fixed to a surface move their body parts: Sponges use beating flagella to generate water currents that draw and trap small food particles, and sessile cnidarians wave tentacles that capture prey (see Chapter 33). Most animals, however, are mobile and spend a considerable portion of their time and energy actively searching for food, escaping from danger, and seeking mates. These activities involve **locomotion**, or active travel from place to place.

Friction and gravity tend to keep an animal stationary and thus oppose locomotion. To move, an animal must expend energy to overcome these two forces. As we will see next, the amount of energy required to oppose friction or gravity is often reduced by an animal body plan adapted for movement in a particular environment.

Locomotion on Land

On land, a walking, running, hopping, or crawling animal must be able to support itself and move against gravity, but air poses relatively little resistance, at least at moderate speeds. When a land animal walks, runs, or hops, its leg muscles expend energy both to propel it and to keep it from falling down. With each step, the animal's leg muscles must overcome inertia by accelerating a leg from a standing start. For moving on land, powerful muscles and strong skeletal support are more important than a streamlined shape.

Diverse adaptations for traveling on land have evolved in various vertebrates. For example, kangaroos have large, powerful muscles in their hind legs, suitable for locomotion by hopping (**Figure 50.38**). As a kangaroo lands after each leap, tendons in its hind legs momentarily store energy. The farther the animal hops, the more energy its tendons store. Analogous to the energy in a compressed spring, the energy stored in the tendons is available for the next jump and



▲ **Figure 50.38 Energy-efficient locomotion on land.**

Members of the kangaroo family travel from place to place mainly by leaping on their large hind legs. Kinetic energy momentarily stored in tendons after each leap provides a boost for the next leap. In fact, a large kangaroo hopping at 30 km/hr uses no more energy per minute than it does at 6 km/hr. The large tail helps balance the kangaroo when it leaps as well as when it sits.

reduces the total amount of energy the animal must expend to travel. The legs of an insect, dog, or human also retain some energy during walking or running, although a considerably smaller share than those of a kangaroo.

Maintaining balance is another prerequisite for walking, running, or hopping. A kangaroo's large tail helps balance its body during leaps and also forms a stable tripod with its hind legs when the animal sits or moves slowly. Illustrating the same principle, a walking cat, dog, or horse keeps three feet on the ground. Bipedal animals, such as humans and birds, keep part of at least one foot on the ground when walking. When an animal runs, all four feet (or both feet for bipeds) may be off the ground briefly, but at running speeds it is momentum more than foot contact that keeps the body upright.

Crawling poses a very different situation. Because much of its body is in contact with the ground, a crawling animal must exert considerable effort to overcome friction. You have read how earthworms crawl by peristalsis. Many snakes crawl by undulating their entire body from side to side. Assisted by large, movable scales on its underside, a snake's body pushes against the ground, propelling the animal forward. Boa constrictors and pythons creep straight forward, driven by muscles that lift belly scales off the ground, tilt the scales forward, and then push them backward against the ground.

Swimming

Because most animals are reasonably buoyant in water, overcoming gravity is less of a problem for swimming animals than for species that move on land or through the air. On the other hand, water is a much denser and more viscous medium than air, and thus drag (friction) is a major problem for aquatic animals. A sleek, fusiform (torpedo-like) shape is a common adaptation of fast swimmers (see Figure 40.2).

Although most animal phyla include species that swim, swimming occurs in diverse ways. For instance, many insects and four-legged vertebrates use their legs as oars to push against the water. Squids, scallops, and some cnidarians are jet-propelled, taking in water and squirting it out in bursts. Sharks and bony fishes swim by moving their body and tail from side to side, while whales and dolphins move by undulating their body and tail up and down.

Flying

Active flight (in contrast to gliding downward from a tree) has evolved in only a few animal groups: insects, reptiles (including birds), and, among the mammals, bats. One group of flying reptiles, the pterosaurs, died out millions of years ago, leaving birds and bats as the only flying vertebrates.

Gravity poses a major problem for a flying animal because its wings must develop enough lift to overcome gravity's downward force. The key to flight is wing shape. All wings are airfoils—structures whose shape alters air currents in a way that helps animals or airplanes stay aloft. As for the body to which the wings attach, a fusiform shape helps reduce drag in air as it does in water.

Flying animals are relatively light, with body masses ranging from less than a gram for some insects to about 20 kg for the largest flying birds. Many flying animals have structural adaptations that contribute to low body mass. Birds, for example, have no urinary bladder or teeth and have relatively large bones with air-filled regions that help lessen the bird's weight (see Chapter 34).

Energy Costs of Locomotion

During the 1960s, three scientists at Duke University became interested in the bioenergetics of locomotion. Physiologists typically determine an animal's rate of energy use during locomotion by measuring oxygen consumption or carbon dioxide production (see Chapter 40). To apply such a strategy to flight, Vance Tucker trained parakeets to fly in a wind tunnel while wearing a face mask (Figure 50.39). By connecting



▲ **Figure 50.39 Measuring energy usage during flight.**

The tube connected to the plastic face mask collects the gases this parakeet exhales during flight in a wind tunnel.

the mask to a tube that collected the air the bird exhaled as it flew, he could measure rates of gas exchange and calculate energy expenditure. In the meantime, Dick Taylor and Knut Schmidt-Nielsen measured energy consumption at rest and during locomotion for animals of widely varying body sizes. Schmidt-Nielsen then calculated an energy cost for locomotion: the amount of fuel it takes to transport a given amount of body weight over a set distance.

Schmidt-Nielsen's analysis demonstrated that the energy cost of locomotion depends on the mode of locomotion and the environment (Figure 50.40). Swimming is the most energy-efficient mode of locomotion (assuming that an animal has adaptations that facilitate swimming). Running animals generally expend more energy per meter traveled than equivalently sized swimming animals, partly because running and walking require energy to overcome gravity. If we compare

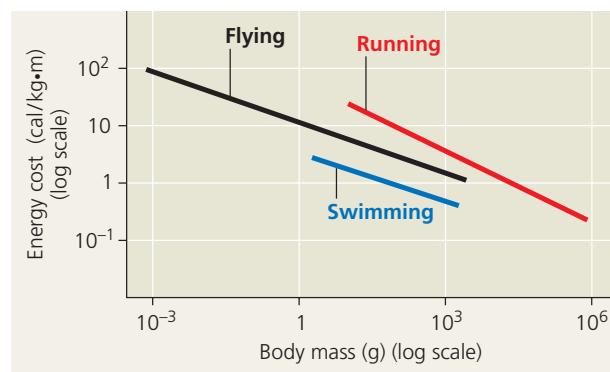
▼ **Figure 50.40**

INQUIRY

What are the energy costs of locomotion?

EXPERIMENT Knut Schmidt-Nielsen wondered whether there were general principles governing the energy costs of different types of locomotion among diverse animal species. To answer this question, he drew on his own studies as well as the scientific literature for measurements made when animals swam in water flumes, ran on treadmills, or flew in wind tunnels. He converted all of these data to a common set of units and graphed the results.

RESULTS



This graph plots the energy cost, in calories per kilogram of body mass per meter traveled, against body mass for animals specialized for running, flying, and swimming. Note that both axes are plotted on logarithmic scales.

CONCLUSION For most animals of a given body mass, swimming is the most energy-efficient and running the least energy-efficient mode of locomotion. In addition, a small animal typically expends more energy per kilogram of body mass than a large animal, regardless of the type of locomotion used.

SOURCE K. Schmidt-Nielsen, Locomotion: Energy cost of swimming, flying, and running, *Science* 177:222–228 (1972).

WHAT IF? If you plotted the efficiency of a duck as a swimmer on this graph, where might you expect it to fall, and why?

the energy consumption per minute rather than per meter, we find that flying animals use more energy than swimming or running animals with the same body mass.

Figure 50.40 also reveals that a larger animal travels more efficiently than a smaller animal adapted to the same mode of transport. This relationship of size to energy expenditure during locomotion is apparent in the downward slope of each line on the graph. For example, a 450-kg horse expends less energy *per kilogram of body mass* than a 4-kg cat running the same distance. Of course, the total amount of energy expended in locomotion is greater for the larger animal.

Energy from food that is used for locomotion is unavailable for other activities, such as growth and reproduction. Thus, structural and behavioral adaptations that maximize the efficiency of locomotion increase an organism's evolutionary fitness.

Although we have discussed sensory receptors and muscles separately in this chapter, they are part of a single integrated

system linking brain, body, and the external world. An animal's behavior is the product of this system. In Chapter 51, we'll discuss behavior in the context of animal form and function and also link it to ecology, the study of how organisms interact with their environment.

CONCEPT CHECK 50.6

1. In what way are septa an important feature of the earthworm skeleton?
2. Contrast swimming and flying in terms of the main problems they pose and the adaptations that allow animals to overcome those problems.
3. **WHAT IF?** When using your arms to lower yourself into a chair, you bend your arms without using your biceps. Explain how this is possible. (*Hint:* Think about gravity as an antagonistic force.)

For suggested answers, see Appendix A.

50 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

CONCEPT 50.1

Sensory receptors transduce stimulus energy and transmit signals to the central nervous system (pp. 1085–1090)

- **Sensory receptors** are usually specialized neurons or epithelial cells that detect external or internal stimuli. The detection of a stimulus by sensory cells precedes **sensory transduction**, the change in the membrane potential of a sensory receptor in response to a stimulus. The resulting receptor potential controls **transmission** of action potentials to the CNS, where sensory information is integrated to generate perceptions. The frequency of action potentials in an axon and the number of axons activated determine stimulus strength. The identity of the axon carrying the signal encodes the nature or quality of the stimulus. Signal transduction pathways in receptor cells often amplify the signal, which causes the receptor cell either to produce action potentials or to release neurotransmitter at a synapse with a sensory neuron.
- There are five basic types of sensory receptors.

Mechanoreceptors respond to stimuli such as pressure, touch, stretch, motion, and sound. **Chemoreceptors** detect either total solute concentrations or specific molecules.

Electromagnetic receptors detect different forms of electromagnetic radiation. Various types of **thermoreceptors** signal surface and core temperatures of the body. Pain is detected by a group of **nociceptors** that respond to excess heat, pressure, or specific classes of chemicals.

? To simplify the classification of sensory receptors, why might it make sense to eliminate nociceptors as a distinct class?

CONCEPT 50.2

The mechanoreceptors responsible for hearing and equilibrium detect moving fluid or settling particles (pp. 1090–1094)

- Most invertebrates sense their orientation with respect to gravity by means of **statocysts**. Specialized **hair cells** form the basis for hearing and balance in mammals and for detection of water movement in fishes and aquatic amphibians. In mammals, the **timpanic membrane** (eardrum) transmits sound waves to three small bones of the middle ear, which transmit the waves through the oval window to the fluid in the coiled **cochlea** of the inner ear. Pressure waves in the fluid vibrate the **basilar membrane**, depolarizing hair cells and triggering action potentials that travel via the auditory nerve to the brain. Each region of the basilar membrane vibrates most vigorously at a particular frequency and leads to excitation of a specific auditory area of the cerebral cortex. Receptors in the inner ear function in balance and equilibrium.

? What quality of sound determines the direction of displacement of a particular hair cell in the ear, and how is that quality encoded in signals sent to the brain?

CONCEPT 50.3

Visual receptors in diverse animals depend on light-absorbing pigments (pp. 1095–1101)

- Invertebrates have varied light detectors, including simple light-sensitive eyespots, image-forming compound eyes, and single-lens eyes. In the vertebrate eye, a single lens is used to focus light on **photoreceptors** in the **retina**. Both **rods** and **cones** contain a pigment, **retinal**, bonded to a protein (opsin).

Absorption of light by retinal triggers a signal transduction pathway that hyperpolarizes the photoreceptors, causing them to release less neurotransmitter. Synapses transmit information from photoreceptors to cells that integrate information and convey it to the brain along axons that form the optic nerve.

? How does processing of sensory information sent to the vertebrate brain in vision differ from that in hearing or olfaction?

CONCEPT 50.4

The senses of taste and smell rely on similar sets of sensory receptors (pp. 1101–1103)

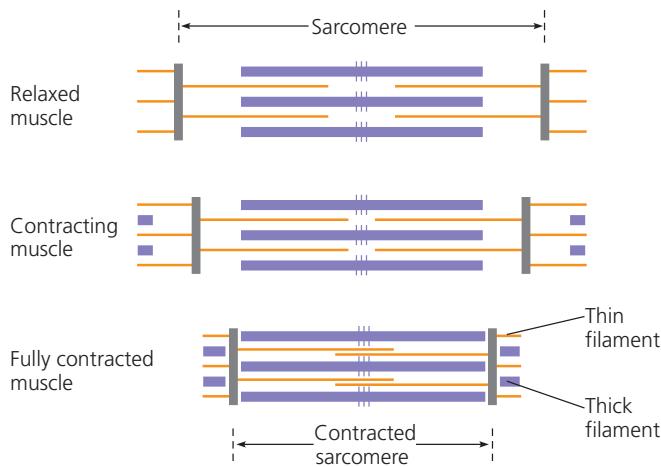
- Both taste (**gustation**) and smell (**olfaction**) depend on the stimulation of chemoreceptors by small dissolved molecules that bind to proteins on the plasma membrane. In humans, sensory cells within taste buds express a single receptor type specific for one of the five taste perceptions—sweet, sour, salty, bitter, and umami (elicited by glutamate). Olfactory receptor cells line the upper part of the nasal cavity and extend axons to the olfactory bulb of the brain. More than 1,000 genes code for membrane proteins that bind to specific classes of odorants, and each receptor cell appears to express only one of those genes.

? Why do foods taste bland when you have a head cold?

CONCEPT 50.5

The physical interaction of protein filaments is required for muscle function (pp. 1103–1110)

- The muscle cells (fibers) of vertebrate skeletal muscle contain myofibrils composed of **thin filaments** of (mostly) actin and **thick filaments** of myosin. Together with accessory proteins, these filaments are organized into repeating units called **sarcomeres**. Myosin heads, energized by the hydrolysis of ATP, bind to the thin filaments, forming cross-bridges, then release upon binding ATP anew. As this cycle repeats, the thick and thin filaments slide past each other, shortening the sarcomere and contracting the muscle fiber.



- Motor neurons release acetylcholine, triggering action potentials that penetrate the muscle fiber along the T tubules and stimulate the release of Ca^{2+} from the **sarcoplasmic reticulum**. When the Ca^{2+} binds the **troponin complex**, **tropomyosin** repositions on the thin filaments, exposing the

myosin-binding sites on actin and thus initiating cross-bridge formation. A **motor unit** consists of a motor neuron and the muscle fibers it controls. Recruiting multiple motor units results in stronger contractions. A twitch results from a single action potential in a motor neuron. Skeletal muscle fibers can be slow-twitch or fast-twitch and oxidative or glycolytic.

- Cardiac muscle, found only in the heart, consists of striated cells that are electrically connected by intercalated disks and that can generate action potentials without input from neurons. In smooth muscles, contractions are slow and may be initiated by the muscles themselves or by stimulation from neurons in the autonomic nervous system.

? What are two major functions of ATP hydrolysis in skeletal muscle activity?

CONCEPT 50.6

Skeletal systems transform muscle contraction into locomotion (pp. 1110–1115)

- Skeletal muscles, often in antagonistic pairs, bring about movement by contracting and pulling against the skeleton. Skeletons may be **hydrostatic** and maintained by fluid pressure, as in worms; hardened into **exoskeletons**, as in insects; or in the form of **endoskeletons**, as in vertebrates.
- Each form of **locomotion**—swimming, movement on land, or flying—presents a particular challenge. For example, swimmers need to overcome friction, but face less of a challenge from gravity than do animals that move on land or fly. Animals specialized for swimming expend less energy per distance traveled than similarly sized animals specialized for flying or running. For any of the three major modes of locomotion, larger animals are more efficient than smaller ones.

? Explain how microscopic and macroscopic anchoring of muscle filaments enables you to bend your elbow.

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

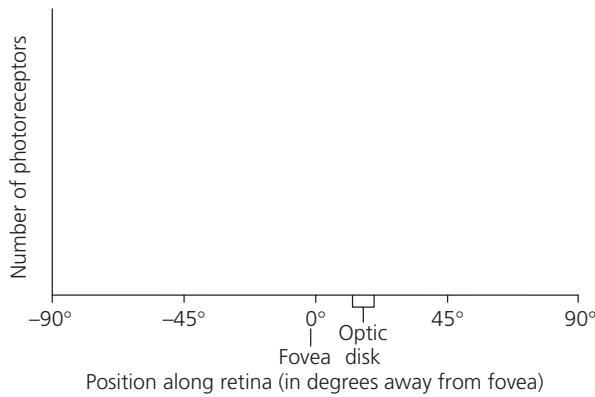
- Which of the following sensory receptors is *incorrectly* paired with its category?
 - hair cell—mechanoreceptor
 - muscle spindle—mechanoreceptor
 - taste receptor—chemoreceptor
 - rod—electromagnetic receptor
 - olfactory receptor—electromagnetic receptor
- The middle ear converts
 - air pressure waves to fluid pressure waves.
 - fluid pressure waves to air pressure waves.
 - air pressure waves to nerve impulses.
 - fluid pressure waves to nerve impulses.
 - pressure waves to hair cell movements.
- During the contraction of a vertebrate skeletal muscle fiber, calcium ions
 - break cross-bridges by acting as a cofactor in the hydrolysis of ATP.
 - bind with troponin, changing its shape so that the myosin-binding sites on actin are exposed.
 - transmit action potentials from the motor neuron to the muscle fiber.
 - spread action potentials through the T tubules.
 - re-establish the polarization of the plasma membrane following an action potential.

LEVEL 2: APPLICATION/ANALYSIS

4. Which sensory distinction is *not* encoded by a difference in neuron identity?
 - a. white and red
 - b. red and green
 - c. loud and faint
 - d. salty and sweet
 - e. spicy and cool
5. The transduction of sound waves into action potentials takes place
 - a. within the tectorial membrane as it is stimulated by the hair cells.
 - b. when hair cells are bent against the tectorial membrane, causing them to depolarize and release neurotransmitter that stimulates sensory neurons.
 - c. as the basilar membrane becomes more permeable to sodium ions and depolarizes, initiating an action potential in a sensory neuron.
 - d. as the basilar membrane vibrates at different frequencies in response to the varying volume of sounds.
 - e. within the middle ear as the vibrations are amplified by the malleus, incus, and stapes.

LEVEL 3: SYNTHESIS/EVALUATION

6. Although some sharks close their eyes just before they bite, their bites are on target. Researchers have noted that sharks often misdirect their bites at metal objects and that they can find batteries buried under sand. This evidence suggests that sharks keep track of their prey during the split second before they bite in the same way that
 - a. a rattlesnake finds a mouse in its burrow.
 - b. a male silkworm moth locates a mate.
 - c. a bat finds moths in the dark.
 - d. a platypus locates its prey in a muddy river.
 - e. a flatworm avoids light places.
7. **DRAW IT** Based on the information in the text, fill in the following graph. Use one line for rods and another line for cones.



8. EVOLUTION CONNECTION

In general, locomotion on land requires more energy than locomotion in water. By integrating what you have learned about animal form and function in Unit 7, discuss some of the evolutionary adaptations of mammals that support the high energy requirements for moving on land.

9. SCIENTIFIC INQUIRY

Although skeletal muscles generally fatigue fairly rapidly, clam shell muscles have a protein called paramyosin that allows them to sustain contraction for up to a month. From your knowledge of the cellular mechanism of contraction, propose a hypothesis to explain how paramyosin might work. How would you test your hypothesis experimentally?

10. WRITE ABOUT A THEME

Structure and Function In a short essay (100–150 words), describe at least three ways in which the structure of the lens of the human eye is well adapted to its function in vision.

For selected answers, see Appendix A.

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