A greater horseshoe bat *(Rhinolophus ferrumequinum)* hunting a moth. The bat uses its sensory system to pursue prey, and the moth uses its sensory system in attempting to evade capture.

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39 Sensory Systems

STUDY PLAN

39.1 Overview of Sensory Receptors and Pathways
- Five basic types of receptors are common to almost all animals
- Afferent neurons link receptors to the CNS
- Many receptor systems reduce their response when stimuli remain constant

39.2 Mechanoreceptors and the Tactile and Spatial Senses
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39.3 Mechanoreceptors and Hearing
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- Human ears are representative of the auditory structures of mammals
- Many vertebrates keep track of obstacles and prey by echolocation

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- Vision involves detection and perception of radiant energy
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- The retina of mammals and birds contains rods and cones and a complex network of neurons
- Three kinds of opsin pigments underlie color vision
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- Invertebrates have either the same or different receptors for taste and smell
- Taste and smell receptors are differentiated in terrestrial animals
- In vertebrates, taste receptors are located in taste buds
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- Nociceptors protect animals from potentially damaging stimuli

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- Magnetoreceptors are used for navigation
- Electroreceptors are used for location of prey or for communication

WHY IT MATTERS

An insectivorous bat leaves its cave after a good day's sleep to look for food. As it flies, the bat emits a steady stream of ultrasonic clicking noises. Receptors in the bat's ears detect echoes of the clicks bouncing off objects in the environment and send signals to the brain, where they are integrated into a sound map that the animal uses to avoid trees and other obstacles. This ability to detect objects by *echolocation* is so keenly developed that a bat can detect and avoid a thin wire in the dark.

Besides recognizing obstacles, the bat's sensory system is keenly tuned to the distinctive pattern of echoes reflected by the fluttering wings of its favorite food, a moth. Although the slow-flying moth would seem doomed to become a meal for the foraging bat, natural selection has provided some species of moths with an astoundingly sensitive and efficient auditory sense as well as a programmed escape mechanism. On each side of its abdomen is an "ear," a thin membrane that resonates at the frequencies of the clicks emitted by the bat. The moth's ears register the clicks while the bat is still about 30 m away and initiate a response that turns its flight path directly away from the source of the clicks, giving the moth an early advantage in the nocturnal dance of life and death.

In spite of the moth's evasive turn, the bat's random flight pattern carries it in the direction of its prey. At a distance of about 6 m, when echoes from the moth begin to register in the bat's auditory system, the bat increases the frequency of its clicks, enabling it to pinpoint the moth's position.

The moth has not exhausted its evasive tactics, however. As the bat closes in, the increased frequency of the clicks sets off another programmed response that alters the moth's flight into sudden loops and turns, ending with a closed-wing, vertical fall toward the ground. After dropping a few feet, the moth resumes its fluttering flight.

Although the moth escapes for a moment, the bat also alters its path, turning back toward the moth as its echolocation again locks on the prey. The contest goes on, but the bat's sensory system finally leads it to intercept the moth an instant before its vertical drop, and the bat retires to a branch to eat its meal.

Natural selection has produced highly adaptive sensory receptors in moths, bats, and all other animals. These systems, the subject of this chapter, provide animals with a steady stream of information about their internal and external environments. After integrating the information in the central nervous system (CNS), animals respond in ways that enable them to survive and reproduce. We begin this chapter with a survey of animal sensory systems and the ways in which they work.

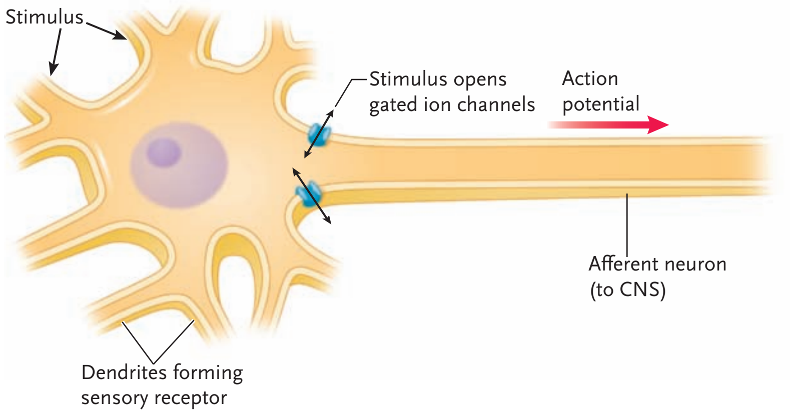
39.1 Overview of Sensory Receptors and Pathways

Information about an animal's external and internal environments is picked up by **sensory receptors,** formed by the dendrites of afferent neurons, or by specialized receptor cells making synapses with afferent neurons **(Figure 39.1).** The receptors associated with eyes, ears, skin, and other surface organs detect stimuli from the external environment. Sensory receptors associated with internal organs detect stimuli arising in the body interior.

Sensory receptors respond to stimuli by undergoing a change in membrane potential, caused in most receptors by changes in the rate at which channels conduct positive ions such as Na^+, K^+, or Ca^{2+} across the plasma membrane. Examples of stimuli are light, heat, sound waves, mechanical stress, and chemicals; the conversion of a stimulus into a change in membrane potential is called **sensory transduction.** The change in membrane potential may generate one or more action potentials, which travel along the axon of an afferent neuron to reach the interneuron networks of the CNS. These interneurons integrate the action potentials, and the brain formulates a compensating response, that is, a response appropriate for the stimulus (see Section 38.3). In animals with complex nervous systems, the

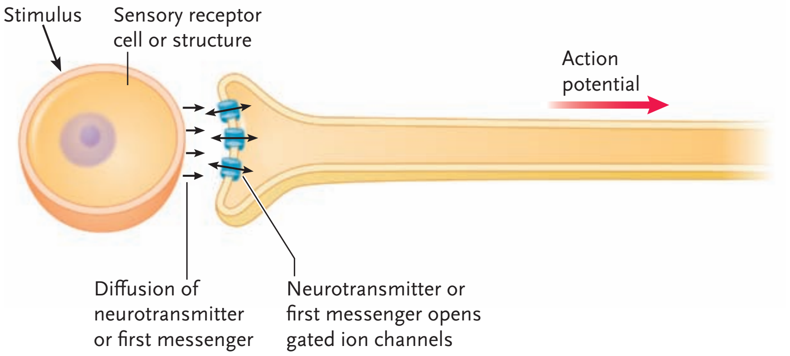
Figure 39.1
Sensory receptors, formed **(a)** by the dendrites of an afferent neuron or **(b)** by a separate cell or structure that communicates with an afferent neuron via a neurotransmitter.

a. Sensory receptor formed by dendrites of an afferent neuron



In sensory receptors formed by the dendrites of afferent neurons, a stimulus causes a change in membrane potential that generates action potentials in the axon of the neuron. Temperature and pain receptors are among the receptors of this type.

b. Sensory receptor formed by a cell that synapses with an afferent neuron



In sensory receptors consisting of separate cells, a stimulus causes a change in membrane potential that releases a neurotransmitter from the cell. The neurotransmitter triggers an action potential in the axon of a nearby afferent neuron. Mechanoreceptors, photoreceptors, and chemoreceptors are examples of receptors of this type.

interneuron networks may also produce an awareness of a stimulus in the form of a conscious sensation or perception.

Five Basic Types of Receptors Are Common to Almost All Animals

Many sensory receptors are positioned individually in body tissues. Others are part of complex sensory organs, such as the eyes or ears, that are specialized for reception of physical or chemical stimuli. Commonly, sensory receptors are classified into five major types, based on the type of stimulus that each detects:

1. **Mechanoreceptors** detect mechanical energy, such as changes in pressure, body position, or acceleration. The auditory receptors in the ears are examples of mechanoreceptors.
2. **Photoreceptors** detect the energy of light. In vertebrates, photoreceptors are mostly located in the retina of the eye.
3. **Chemoreceptors** detect specific molecules, or chemical conditions such as acidity. The taste buds on the tongue are examples of chemoreceptors.
4. **Thermoreceptors** detect the flow of heat energy. Receptors of this type are located in the skin, where they detect changes in the temperature of the body surface.
5. **Nociceptors** detect tissue damage or noxious chemicals; their activity registers as pain. Pain receptors are located in the skin, and also in some internal organs.

In addition to these major types, some animals have receptors that can detect electrical or magnetic fields.

Although humans are traditionally said to have five senses—vision, hearing, taste, smell, and touch—our sensory receptors actually detect more than twice as many kinds of environmental stimuli. Among these are external heat, internal temperature, gravity, acceleration, the positions of muscles and joints, body balance, internal pH, and the internal concentration of substances such as oxygen, carbon dioxide, salts, and glucose.

Afferent Neurons Link Receptors to the CNS

Sensory pathways begin at a sensory receptor and proceed by afferent neurons to the CNS. Because of its wiring, each type of receptor produces a specific kind of response. For example, action potentials arising in the retina of the eye travel along the optic nerve to the visual cortex, where they are interpreted by the brain as differences in the pattern, color, and intensity of light. If you receive a blow to the eye, the stimulus is still interpreted in the visual cortex as differences in the color and intensity of light detected by the eyes—you “see stars”—even though the stimulus is mechanical.

One way in which the intensity and extent of a stimulus is registered is by the frequency (number per unit time) of action potentials traveling along each axon of an afferent pathway. That is, the stronger the stimulus, the more frequently afferent neurons fire action potentials (see Section 37.2). A light touch to the hand, for example, causes action potentials to flow at low frequencies along the axons leading to the primary somatosensory area of the cerebral cortex. As the pressure increases, the number of action potentials per second rises in proportion; in the brain, the increase is interpreted as greater pressure on the hand. Maximum stimulus input is interpreted as pain in the sensory cortex.

The second way in which the intensity and extent of a stimulus is registered is by the number of afferent neurons that the stimulus activates to generate action potentials in the pathway. This way reflects the number of afferent neurons carrying signals from a stimulated region to the brain. The more sensory receptors that are activated, the more axons carry information to the brain. A light touch activates a relatively small number of receptors in a small area near the surface of the finger, for example. As the pressure increases, the resulting indentation of the finger’s surface increases in area and depth, activating more receptors. In the appropriate somatosensory area of the brain, the larger number of axons carrying action potentials is interpreted as an increase in pressure spread over a greater area of the finger.

Many Receptor Systems Reduce Their Response When Stimuli Remain Constant

In many systems, the effect of a stimulus is reduced if it continues at a constant level. The reduction, called **sensory adaptation**, reduces the frequency of action potentials generated in afferent neurons when the intensity of a stimulus remains constant. Some receptors adapt quickly and broadly; other receptors adapt only slightly.

For example, when you go to bed, you are initially aware of the touch and pressure of the covers on your skin. Within a few minutes, the sensations lessen or are lost even though your position remains the same. The loss reflects adaptation of mechanoreceptors in your skin. If you move, so that the stimulus changes, the mechanoreceptors again become active. In contrast, nociceptors adapt only slightly, or not at all, to painful stimuli.

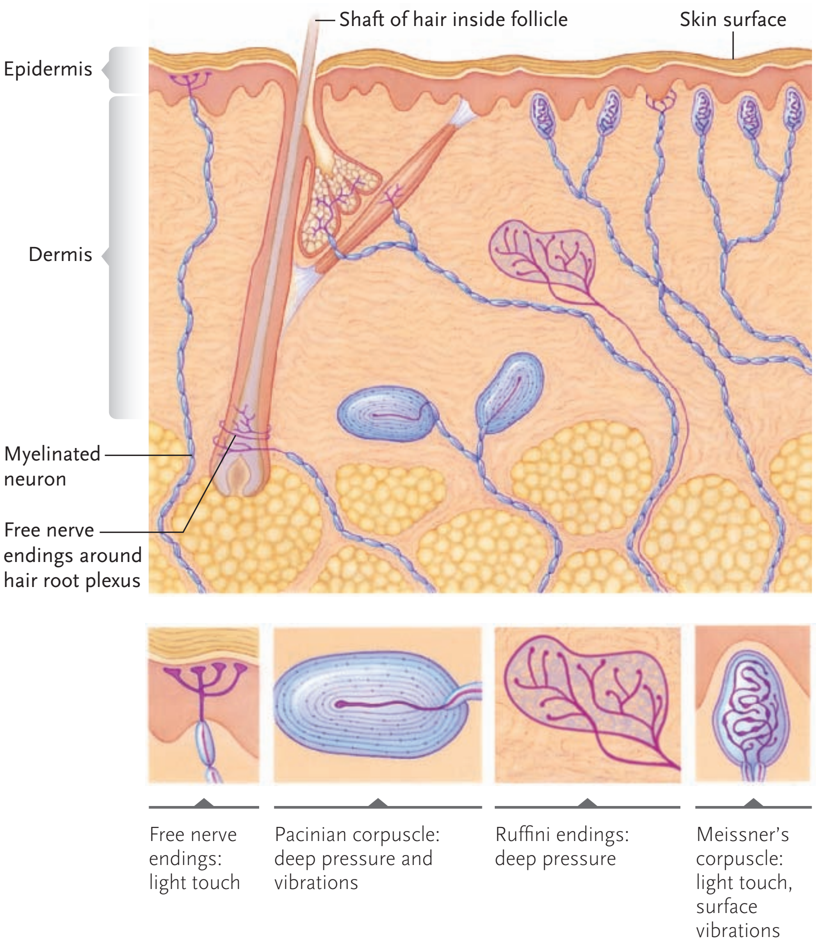
In some sensory receptors, biochemical changes in the receptor cell contribute to adaptation. For example, when you move from a dark movie theater into bright sunshine, the photoreceptors of the eye adapt to bright light partly through breakdown of some of the pigments that absorb light.

Sensory adaptation is crucial to animal survival. The adaptation of photoreceptors in our eyes keeps us from being blinded indefinitely as we pass from a darkened room into bright sunlight. Sensory adaptation also increases the sensitivity of receptor systems to *changes* in environmental stimuli, which may be more important to survival than keeping track of environmental factors that remain constant. You may have noticed a cat sitting motionless, focused on its prey, a mouse. As long as the environmental stimuli are constant, the cat's position remains fixed. However, if the mouse moves, the cat will respond rapidly and attempt to capture and kill it.

Many prey animals take advantage of adaptation in predators as a means for concealment or defense. These animals instinctively become motionless when they sense a predator in their environment, which frequently allows them to remain undetected by the adapted senses of their predator.

Nonadapting receptors, such as those detecting pain, are also essential for survival. Pain signals a potential danger to some part of the body, and the signals are maintained until a response by the animal compensates for the stimulus causing the pain.

We now examine the individual receptor types and their characteristics.



Free nerve endings: light touch

Pacinian corpuscle: deep pressure and vibrations

Ruffini endings: deep pressure

Meissner's corpuscle: light touch, surface vibrations

Figure 39.2
Types of mechanoreceptors detecting tactile stimuli in human skin.

Study Break

1. Define sensory transduction.
2. Sensory receptors send signals to the CNS in the same way. How are stimuli of different kinds perceived as being different?

39.2 Mechanoreceptors and the Tactile and Spatial Senses

Mechanical stimuli such as touch and pressure are detected by mechanoreceptors. The mechanical forces of a stimulus distort proteins in the plasma membrane of receptors, altering the flow of ions through the membrane. The changed ion flows generate action potentials in afferent neurons leading to the CNS. Sensory information from the receptors informs the brain of the body's contact with objects in the environment, provides information on the movement, position, and balance of body parts, and underlies the sense of hearing.

Receptors for Touch and Pressure Occur throughout the Body

In vertebrates, mechanoreceptors detecting touch and pressure are embedded in the skin and other surface tissues, in skeletal muscles, in the walls of blood vessels, and in internal organs. In humans, touch receptors in the skin are concentrated in greatest numbers in the fingertips, lips, and tip of the tongue, giving these regions the greatest sensitivity to mechanical stimuli. In other areas, such as the skin of the back, arms, and legs, the receptors are more widely spaced.

You can compare the spacing of receptors by pressing two toothpicks lightly against a fingertip and then against the skin of your arm or leg. On your fingertip, the toothpicks can be quite close together—separated by only a millimeter or so—and still be discerned as two separate points. On your arm or leg, they must be nearly 5 cm (almost 2 inches) apart to be distinguished.

Human skin contains several types of touch and pressure receptors **(Figure 39.2).** Some are free nerve endings, the dendrites of afferent neurons with no specialized structures surrounding them. Others, such as Pacinian corpuscles, have structures surrounding the nerve endings that contribute to reception of stimuli. Free nerve endings wrapped around hair follicles respond when the hair is bent, making you instantly aware, for example, of a spider exploring your arm or leg.

Proprioceptors Provide Information about Movements and Position of the Body

Mechanoreceptors called **proprioceptors** (*proprius* = one's own) detect stimuli that are used in the CNS to maintain body balance and equilibrium and to monitor the position of the head and limbs. The activity of these receptors allows you to touch the tip of your nose with your eyes closed, for example, or reach and scratch an itch on your back precisely. Here we consider examples of proprioceptors found in various animals.

Statocysts in Invertebrates. Many aquatic invertebrates, including jellyfishes, some gastropods, and some arthropods, have organs of equilibrium called **statocysts** (*statos* = standing; *kystis* = bag). Most statocysts are fluid-filled chambers with walls that contain **sensory hair cells** enclosing one or more movable stonelike bodies called **statoliths (Figure 39.3).** For example, lobsters have statoliths consisting of sand grains stuck together by mucus. When the animal moves, the statoliths lag behind the movement, bending the sensory hairs and triggering action potentials in afferent neurons. In this way, the statocysts signal the brain about the body's position and orientation with respect to gravity.

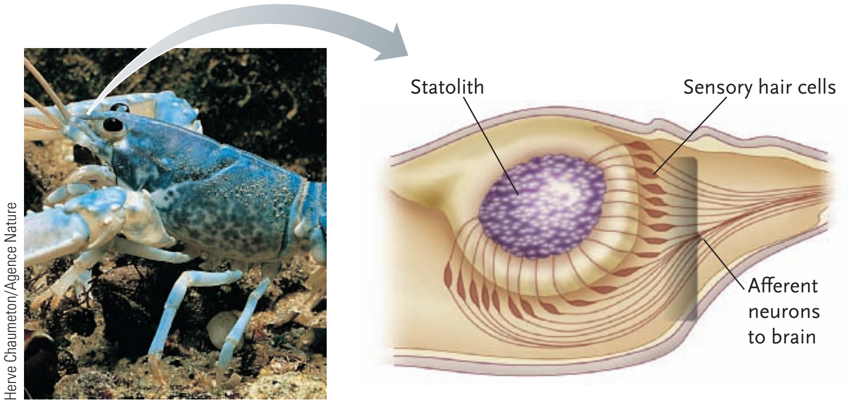
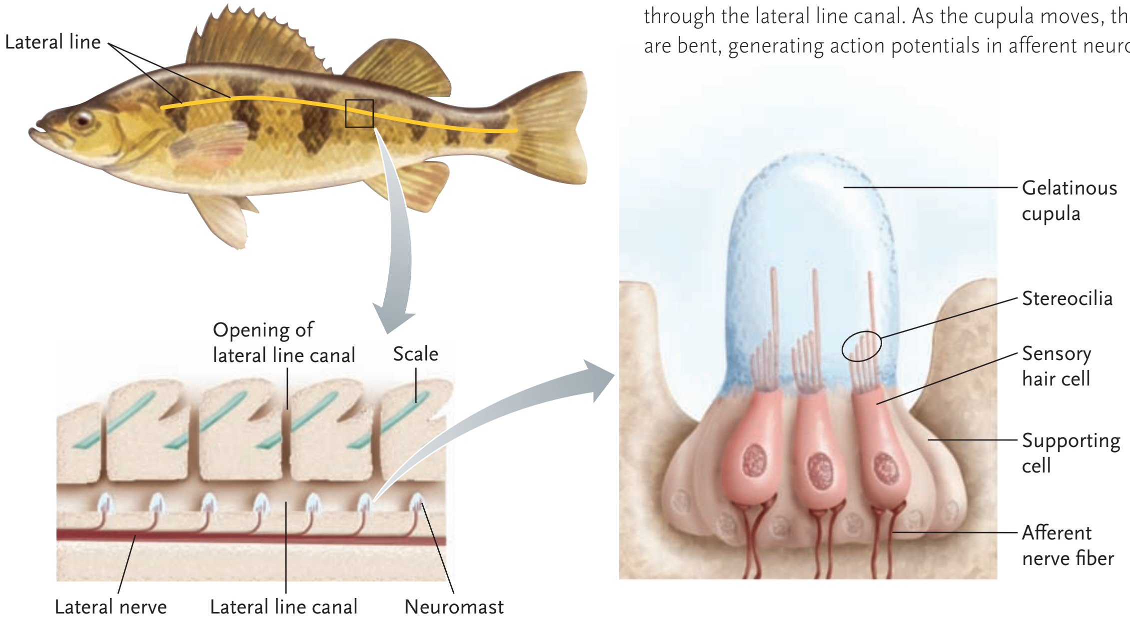

Herve Chaumeton/Agence Nature

Figure 39.3
A statocyst, an invertebrate organ of equilibrium, and its location at the base of an antenna in a lobster. The statoliths inside are usually formed from fused grains of sand, as they are in the lobster, or from calcium carbonate.

The Lateral Line System in Amphibians and Fish. Fishes and some aquatic amphibians detect vibrations and currents in the water through mechanoreceptors along the length of the body called the **lateral line system (Figure 39.4).** In fish, the mechanoreceptors, known as *neuromasts,* also provide information about the fish's orientation with respect to gravity and its swimming velocity. In some fishes, neuromasts are exposed on the body surface; in others, they are recessed in water-filled canals with porelike openings to the outside (as in Figure 39.4). Each dome-shaped neuromast has sensory hair cells clustered in its base. One surface of the hair cell is covered with **stereocilia,** which are actually microvilli (cell processes reinforced by bundles of microfilaments). The stereocilia extend into a gelatinous structure, the **cupula** (*cupule* = little cup), which moves with pressure changes in the surrounding water. Movement of the cupula bends the stereocilia, which causes the hair cell's plasma membrane to become depolarized and release neurotransmitter molecules; the neurotransmitters then generate action potentials in associated afferent neurons.

Vibrations detected by the lateral line enable fishes to avoid obstacles, orient in a current, and monitor the presence of other moving objects in the water. The system is also responsible for the ability of schools of fish to move in unison, turning and diving in what appears to be a perfectly synchronized aquatic ballet. In actual-

Figure 39.4
The lateral line system of fishes. The sensory receptor of the lateral line, the neuromast, has a gelatinous cupula that is pushed and pulled by vibrations and currents transmitted through the lateral line canal. As the cupula moves, the stereocilia of the sensory hair cells are bent, generating action potentials in afferent neurons that lead to the brain.



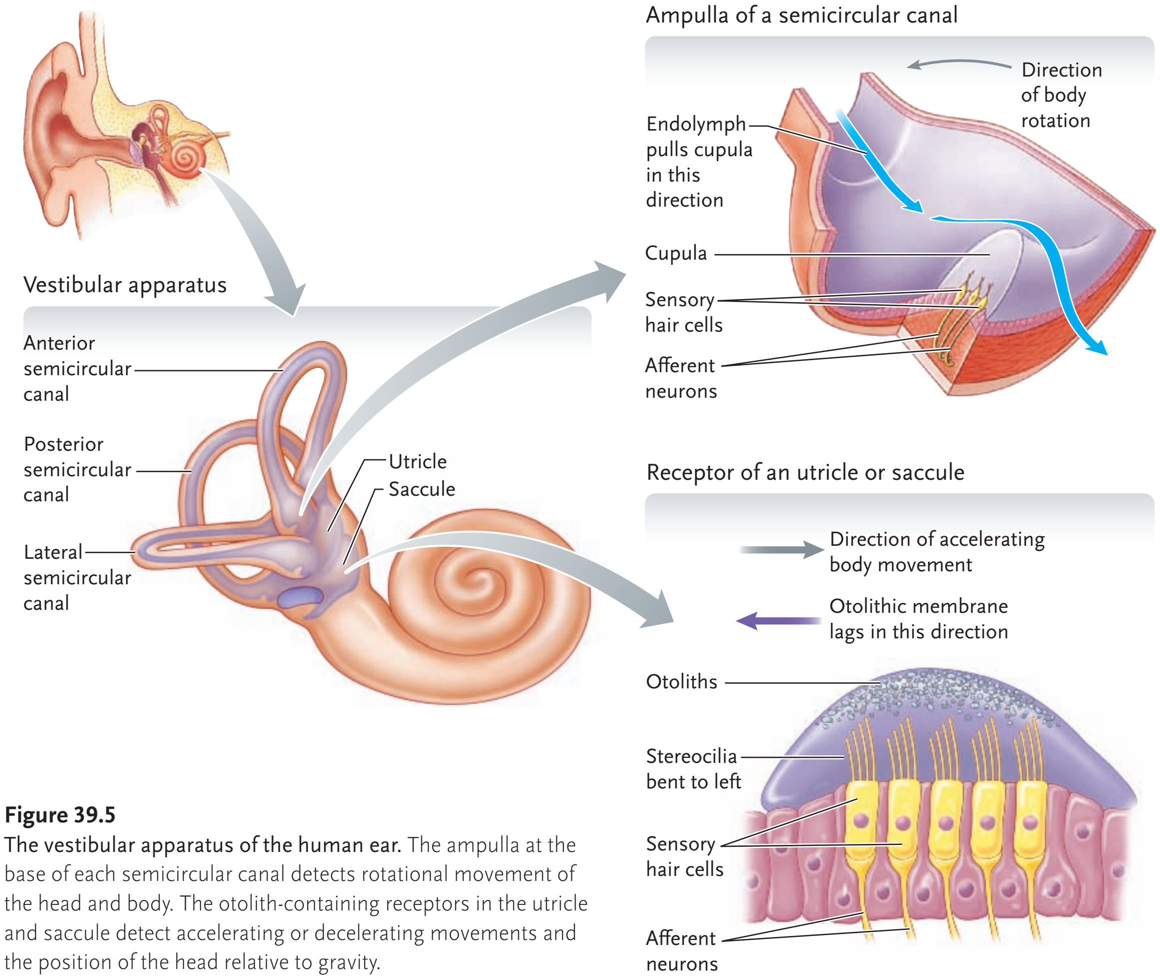


Figure 39.5
The vestibular apparatus of the human ear. The ampulla at the base of each semicircular canal detects rotational movement of the head and body. The otolith-containing receptors in the utricle and saccule detect accelerating or decelerating movements and the position of the head relative to gravity.

ity, the movement of each fish creates a pressure wave in the water that is detected by the lateral line systems of other fishes in the school. Schooling fish can still swim in unison even if blinded, but if the nerves leading from the lateral line system to the brain are severed, the ability to school is lost.

The Vestibular Apparatus in Vertebrates. The inner ear of most terrestrial vertebrates has two specialized sensory structures, the *vestibular apparatus* and the *cochlea*. The **vestibular apparatus** is responsible for perceiving the position and motion of the head and, therefore, is essential for maintaining equilibrium and for coordinating head and body movements. The cochlea is used in hearing, which we discuss later in this chapter.

The vestibular apparatus **(Figure 39.5)** consists of three **semicircular canals** and two chambers, the **utricle** and the **saccule,** filled with a fluid called *endolymph.* The semicircular canals, which are positioned at angles corresponding to the three planes of space, detect rotational (spinning) motions. Each canal has a swelling at its base called an *ampulla,* which is topped with sensory hair cells embedded in a cupula similar to that found in lateral line systems. The cupula protrudes into the endolymph of the canals. When the body or head rotates horizontally, vertically, or diagonally, the endolymph in the semicircular canal corresponding to that direction lags behind, pulling the cupula with it. The displacement of the cupula bends the sensory hair cells and generates action potentials in afferent neurons making synapses with the hair cells.

The utricle and saccule provide information about the position of the head with respect to gravity (up versus down), as well as changes in the rate of linear movement of the body. The ultricle and saccule, which are oriented approximately 30° to each other, each contain sensory hair cells with stereocilia. The hair cells are covered with a gelatinous *otolithic membrane* (which is similar to a cupula) in which **otoliths** (*oto* = ear; *lithos* = stone), small crystals of calcium carbonate, are embedded (see Figure 39.5); otoliths are similar to invertebrate statoliths.

When an animal is upright, the sensory hairs in the utricle are oriented vertically, and those in the saccule are oriented horizontally. When the head is tilted in any direction other than straight up and down, or when there is a change in linear motion of the body, the otolithic membrane of the utricle moves and bends the sensory hairs. Depending on the direction of movement, the hair cells release more or less neurotransmitter, and the brain integrates the signals it receives and generates a perception of the movement. The saccule responds to the tilting of the head away from the horizontal (such as in diving) and to a change in movement up and down (such as jumping up to dunk a basketball). The ultricle and saccule adapt quickly to the body's motion, decreasing their response when there is no change in the rate and direction of movement. In other words, the body adapts to the new position. For instance, when you move your head to the left, that new position becomes the "norm." Then, if you move your head again in any direction, signals from the utricle and saccule tell your brain that your head is moving to a new position.

Stretch Receptors in Vertebrates. In the muscles and tendons of vertebrates, proprioceptors called **stretch receptors** detect the position and movement of the limbs. The stretch receptors in muscles are **muscle spindles**, bundles of small, specialized muscle cells wrapped with the dendrites of afferent neurons and enclosed in connective tissue **(Figure 39.6).** When the muscle stretches, the spindle stretches also, stimulating the dendrites and triggering the production of action potentials. The strength of the response of stretch receptors to stimulation depends on how much and how fast the muscle is stretched. The proprioceptors of tendons, called **Golgi tendon organs,** are dendrites that branch within the fibrous connective tissue of the tendon (see Figure 39.6). These nerve endings measure stretch and compression of the tendon as the muscles move the limbs.

Proprioceptors allow the CNS to monitor the body's position and help keep the body in balance. They also allow muscles to apply constant force under a constant load, and to adjust almost instantly if the load changes. When you hold a cup while someone fills it with coffee, for example, the muscle spindles in your biceps muscle detect the additional stretch as the cup becomes heavier. Signals from the spindles allow you to compensate for the additional weight by increasing the contraction of the muscle, keeping your arm level with no conscious effort on your part. Proprioceptors are typically slow to adapt, so that the body's position and balance are constantly monitored.

STUDY BREAK

1. What is the function of proprioceptors?
2. What properties qualify proprioceptors as mechanoreceptors?

39.3 Mechanoreceptors and Hearing

In most animals, the receptors that detect sound are closely related to the receptors that detect body movement.

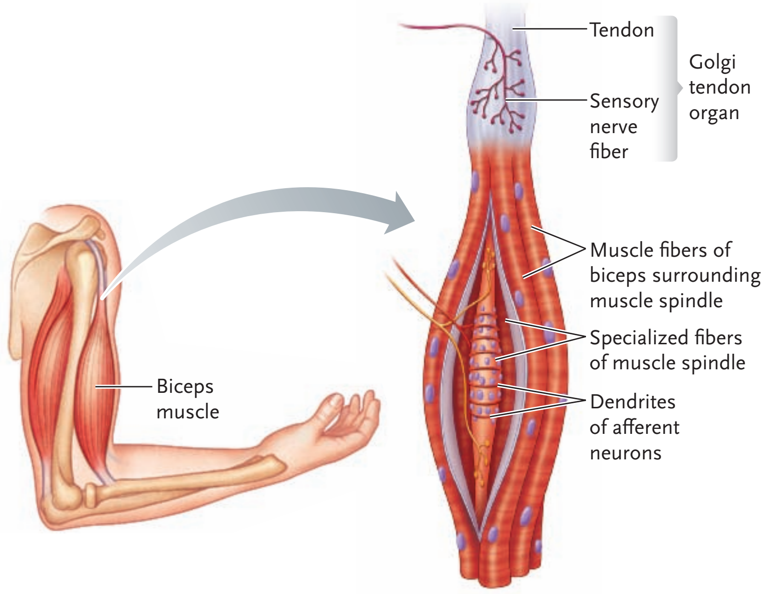


Figure 39.6
Muscle spindles, which detect the stretch and tension of muscles, and Golgi tendon organs, which detect the stretch of tendons.

Sounds are vibrations that travel as waves produced by the alternating compression and decompression of the air. Although sound waves travel through air rapidly—at speeds of about 340 meters per second (700 miles per hour) at sea level—the individual air molecules transmitting the waves move back and forth over only a short distance as the wave passes. The vibrations of sound waves travel through water and solids by a similar mechanism.

The loudness, or *intensity,* of a sound depends on the amplitude (height) of the wave. The *pitch* of a sound—whether a musical tone, for example, is a high note or a low note—depends on the frequency of the waves, measured in cycles per second. The more cycles per second, the higher the pitch. Some animals, such as the bat in the introduction to this chapter, can hear sounds well above 100,000 cycles per second. Humans can hear sounds between about 20 and 20,000 cycles per second, which is why we cannot hear the bat's sonar clicks.

Invertebrates Have Varied Vibration-Detecting Systems

Most invertebrates detect sound and other vibrations through mechanoreceptors in their skin or other surface structures. An earthworm, for example, quickly retracts into its burrow at the smallest vibration of the surrounding earth, even though it has no specialized structures serving as ears. Cephalopods such as squids and octopuses have a system of mechanoreceptors on their head and tentacles, similar to the lateral line of fishes, which detects vibrations in the surrounding water. Many insects have sensory receptors in the form

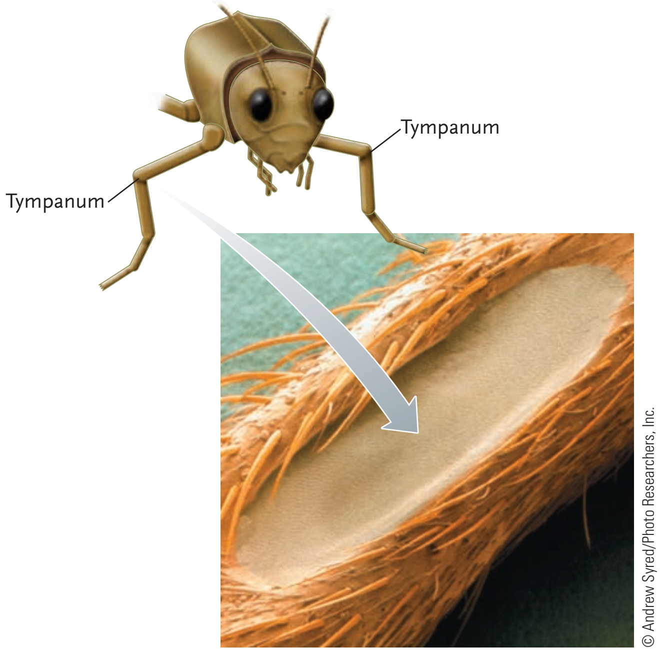


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Figure 39.7 The tympanum or eardrum of a cricket, located on the front walking legs.

of hairs or bristles that vibrate in response to sound waves, often at particular frequencies.

Some insects, such as moths, grasshoppers, and crickets, have complex auditory organs on either side of the abdomen or on the first pair of walking legs **(Figure 39.7).** These "ears" consist of a thinned region of the insect's exoskeleton that forms a tympanum (*tympanum* = drum) over a hollow chamber. Sounds reaching the tympanum cause it to vibrate; mechanoreceptors connected to the tympanum translate the vibrations into nerve impulses. Some insect ears respond to sounds only at certain frequencies, such as to the pitch of a cricket's song or, in certain moths, to the frequencies of the echolocation sounds emitted by foraging bats.

Human Ears Are Representative of the Auditory Structures of Mammals

The auditory structures of terrestrial vertebrates transmit the vibrations of sound waves to sensory hair cells, which respond by triggering action potentials. Here, we describe the human ear, which is representative of mammalian auditory structures **(Figure 39.8).**

The **outer ear** has an external structure, the **pinna** (*pinna* = wing or leaf), which concentrates and focuses sound waves. Most mammals can turn the pinnae to help focus sounds, but human pinnae are inefficient compared with the ears of dogs, rabbits, or horses. The sound waves enter the auditory canal, which leads from the exterior, and strike a thin sheet of tissue, the **tympanic membrane,** or eardrum, which vibrates back and forth in response.

Behind the eardrum is the **middle ear,** an air-filled cavity containing three small, interconnected bones: the **malleus** (hammer), the **incus** (anvil), and the **stapes** (stirrup). The stapes is attached to a thin, elastic membrane, the **oval window.** The vibrations of the eardrum, transmitted by the malleus and incus, push the stapes back and forth against the oval window. The levering action of the bones, combined with the much larger size of the eardrum as compared with the oval window, amplifies the vibrations transmitted to the oval window by more than 20 times.

Inside the oval window is the **inner ear.** It contains several fluid-filled compartments, including the semicircular canals, utricle, saccule, and a spiraled tube, the **cochlea** (*kochlias* = snail). The cochlea twists through about two and a half turns; if stretched out flat, it would be about 3.5 cm long. Thin membranes divide the cochlea into three longitudinal chambers, the *vestibular canal* at the top, the *cochlear duct* in the middle, and the *tympanic canal* at the bottom (see Figure 39.8). The vestibular canal and the tympanic canal join at the outer tip of the cochlea, so that the fluid within them is continuous. Within the cochlear duct is the **organ of Corti;** it contains the sensory hair cells that detect sound vibrations transmitted to the inner ear (see Figure 39.8).

The vibrations of the oval window pass through the fluid in the vestibular canal, make the turn at the end, and travel back through the fluid in the tympanic canal. At the end of the tympanic canal, they are transmitted to the **round window,** a thin membrane that faces the middle ear.

The vibrations traveling through the inner ear cause the *basilar membrane* to vibrate in response. The basilar membrane, which forms part of the floor of the cochlear duct, anchors the sensory hair cells in the organ of Corti. The stereocilia of these cells are embedded in the *tectorial membrane,* which extends the length of the cochlear canal. Vibrations of the basilar membrane cause the hair cells to bend, stimulating them to release a neurotransmitter that triggers action potentials in afferent neurons leading from the inner ear.

The basilar membrane is narrowest near the oval window and gradually widens toward the outer end of the cochlear duct. The high-frequency vibrations produced by high-pitched sounds vibrate the basilar membrane most strongly near its narrow end while vibrations of lower frequency vibrate the membrane nearer the outer end. Thus each frequency of sound waves causes hair cells in a different segment of the basilar membrane to initiate action potentials.

More than 15,000 hair cells are distributed in small groups along the basilar membrane. Each group of hairs is connected by synapses to afferent neurons, which in turn are bundled together in the *auditory nerve,* a cranial nerve that leads to the thalamus. From there, the signals are routed to specific regions in the auditory center of the temporal lobe. As sound waves of a particular frequency and intensity stimulate a specific segment of the basilar membrane, the region of

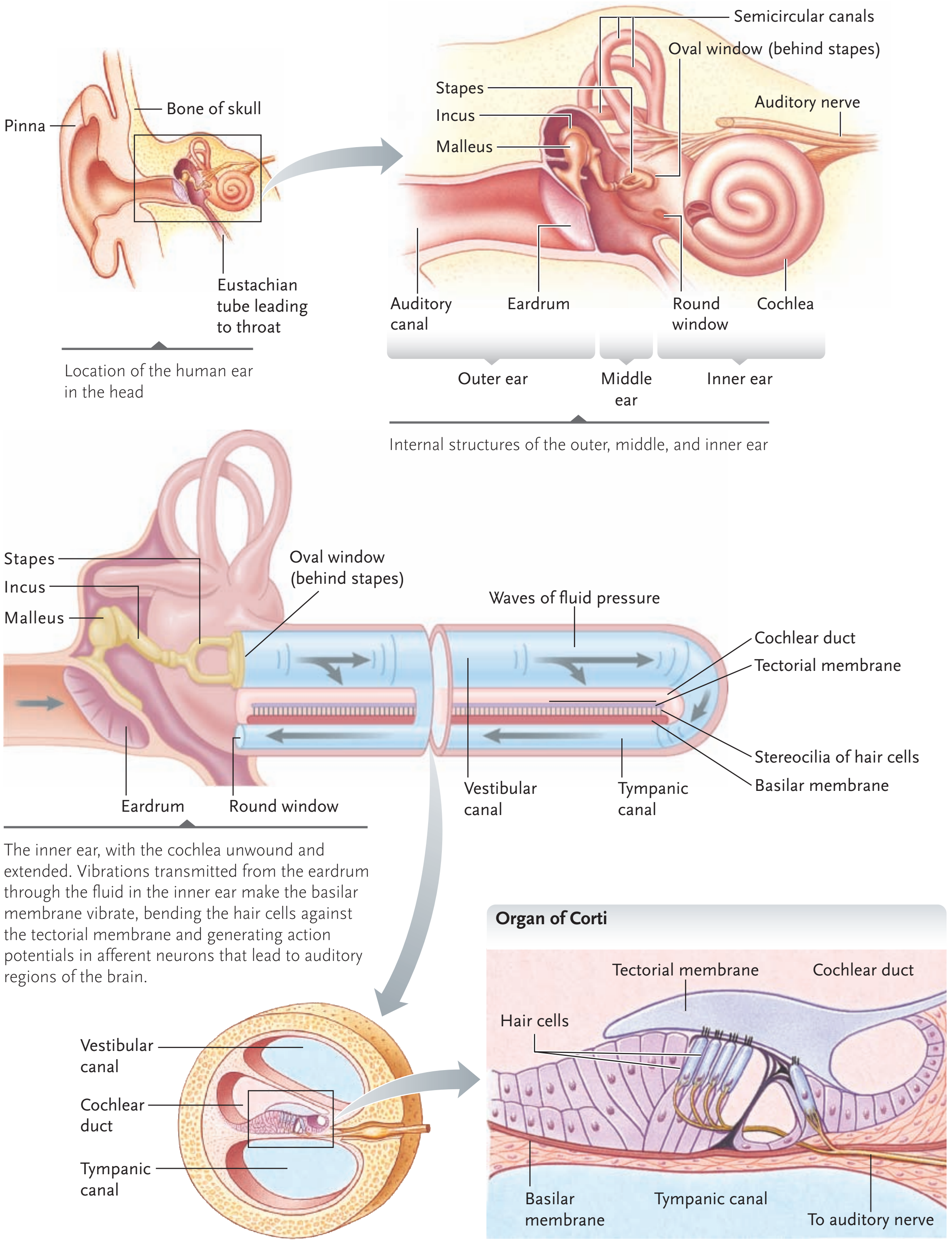

Figure 39.8
Structures of the human ear.

Location of the human ear in the head

Internal structures of the outer, middle, and inner ear

The inner ear, with the cochlea unwound and extended. Vibrations transmitted from the eardrum through the fluid in the inner ear make the basilar membrane vibrate, bending the hair cells against the tectorial membrane and generating action potentials in afferent neurons that lead to auditory regions of the brain.

the auditory center to which the signals are sent integrates the information into the perception of sound at a corresponding pitch and loudness.

The sounds we hear are usually a rich combination of vibrations at different frequencies and intensities, which result in hundreds to thousands of different keys being struck simultaneously, with different degrees of force, in the cochlear keyboard. The combination of signals transmitted from the cochlea to the auditory centers is integrated into the perception of a human voice, the song of a sparrow, the roar of a jet plane, or a Mozart symphony.

Another system protects the eardrum from damage by changes in environmental atmospheric pressure. The system depends on the *Eustachian tube,* a duct that leads from the air-filled middle ear to the throat (see Figure 39.8). As we swallow or yawn, the tube opens, allowing air to flow into or out of the middle ear to equalize the pressure on both sides of the eardrum. When swelling or congestion due to infections prevents the tube from admitting air, we complain of having stopped-up ears—we can sense that a pressure difference between the outer and middle ear is bulging the eardrum inward or outward and interfering with the transmission of sounds.

Many Vertebrates Keep Track of Obstacles and Prey by Echolocation

Many vertebrates, like the bat in the introduction to this chapter, locate prey or avoid obstacles by **echolocation**—by making squeaking or clicking noises, and then listening for the echoes that bounce back from objects in their environment. By sensing the direction of the echoes and the time between the squeak or click and the returning echo, the animal can pinpoint the locations of barriers or prey animals.

Porpoises and dolphins locate food fishes in murky water by echolocation, and whales also use echolocation to keep track of the sea bottom and rocky obstacles. Two bird species, the oilbird and the cave swiftlet, use echolocation to avoid obstacles and find their nests in the dark of caves. Even humans can learn to use echolocation—a blind person, for example, listens for the echoes from a tapping cane to avoid posts, walls, and other barriers.

Study Break

1. What vibration-detecting systems are found in cephalopods and insects?
2. How are sounds of particular frequencies distinguished and "heard" by humans?

39.4 Photoreceptors and Vision

Virtually all animals have receptors that can detect and respond to light. As animals evolved and became more complex, the complexity of their visual sensory receptors increased, leading to the highly developed eyes of vertebrates.

We begin our discussion of these remarkable receptors by examining the basic visual structures and their functions in animals. We then compare vision in representative invertebrates and vertebrates.

Vision Involves Detection and Perception of Radiant Energy

Photoreceptors detect light at particular wavelengths, while centers in a brain or central ganglion integrate signals arriving from the receptors into a perception of light. All animals use different forms of a single lipid-like pigment, *retinal* (synthesized from vitamin A), in the photoreceptors to absorb light energy. The absorbed energy generates action potentials in afferent neurons leading to visual centers in the CNS. The organ of vision that detects light is the *eye*. The simplest eyes are capable only of distinguishing light from dark, while the most complex eyes distinguish shapes and colors and focus an accurate image of objects being viewed onto a layer of photoreceptors. Signals originating from the photoreceptors are integrated in the brain into an accurate, point-by-point perception of the object being viewed.

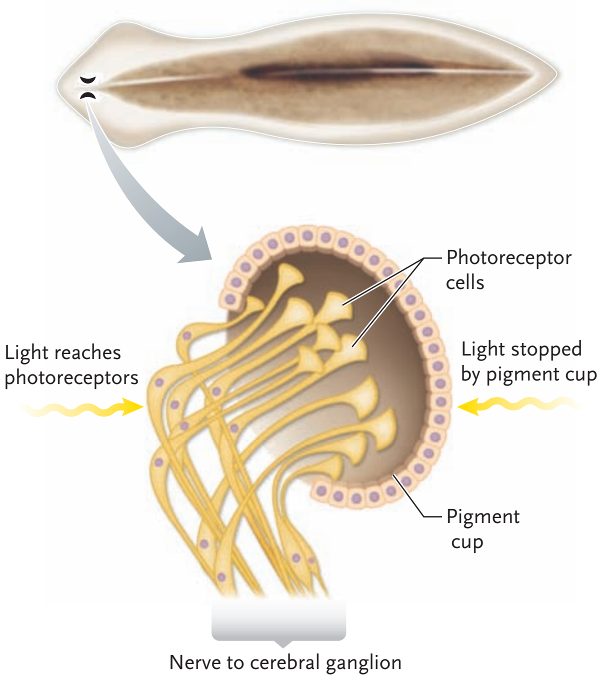

Figure 39.9
The ocellus of *Planaria*, a flatworm, and the arrangement of pigment cells on which its orientation response is based.

Invertebrate Eyes Take Many Forms

Some invertebrates, such as earthworms, do not have visual organs; instead, photoreceptors in their skin allow them to sense and respond to light. Earthworms respond negatively to light, as you can easily discover by shining a flashlight on an earthworm outside its burrow at night.

The eyes of other invertebrates are diverse, ranging from collections of photoreceptors with no lens and no image-forming capability to eyes remarkably like those of vertebrates. The photoreceptors of invertebrates are depolarized when they absorb light, and generate action potentials or increase their release of neurotransmitter molecules when they are stimulated. Vertebrate photoreceptors function differently, as we will see.

The simplest eye is the **ocellus** (plural, *ocelli;* also called an *eyespot* or *eyecup*). An ocellus, which detects light but does not form an image, consists of fewer than 100 photoreceptor cells lining a cup or pit. In planarians, for example, photoreceptor cells in a cuplike depression below the epidermis are connected to the dendrites of afferent neurons, which are bundled into nerves that travel from the ocelli to the cerebral ganglion **(Figure 39.9).** Each ocellus is covered on one side by a layer of pigment cells that blocks most of the light rays arriving from the opposite side of the animal. As a result, most of the light received by the pigment cells enters the ocellus from the side that it faces. Through integration of information transmitted to the cerebral ganglion from the eyecups, planarians orient themselves so that the amount of light falling on the two ocelli is equal and diminishes as they swim. This reaction carries them directly away from the source of the light and towards darker areas where the chance of a predator catching them is smaller. Similar ocelli are found in a variety of animals, including a number of insects, arthropods, and mollusks.

Two main types of image-forming eyes have evolved in invertebrates: compound eyes and single-lens eyes. The **compound eye** of insects, crustaceans, and a few annelids and mollusks contains hundreds to thousands of faceted visual units called **ommatidia** (*omma* = eye) fitted closely together **(Figure 39.10).** In insects, light entering an ommatidium is focused by a transparent **cornea** and a *crystalline cone* (just below the cornea) onto a bundle of photoreceptor cells. Microvilli of these cells interdigitate like the fingers of clasped hands, forming a central axis that contains rhodopsin, a **photopigment** (light-absorbing pigment) also found in the rods of vertebrate eyes. Absorption of light by rhodopsin causes action potentials to be generated in afferent neurons connected to the base of the ommatidium. Each ommatidium of a compound eye samples a small part of the visual field. From these signals, the brain receives a mosaic image of the world. Because even the slightest motion is detected simultaneously by many ommatidia, compound eyes are extraordinarily adept at detecting movement—a lesson soon learned by fly-swatting humans.

The **single-lens eye** of cephalopods **(Figure 39.11)** resembles a vertebrate eye in that both types operate like a camera. In the cephalopod eye, light enters through the transparent cornea, a **lens** concentrates the light, and a layer of photoreceptors at the back of the eye, the **retina,** records the image. Behind the cornea is the **iris,** which surrounds the **pupil,** the opening through which light enters the eye. Muscles in the iris adjust the size of the pupil to vary the amount of light entering the eye. When the light is bright, circular muscles in the iris contract, shrinking the size of the pupil and reducing the amount of light that enters the eye. In dim light, radial muscles contract and enlarge the pupil, increasing the amount of light that enters the eye. Muscles move the lens forward and back with respect to the retina to focus the image. This is an example of **accommodation,** a process by which the lens changes to enable the eye to focus on objects at different distances.

A neural network lies under the retina, meaning that light rays do not have to pass through the neurons to reach the photoreceptors. The vertebrate eye has the opposite arrangement. This and other differences in structure and function indicate that cephalopod and vertebrate eyes evolved independently.

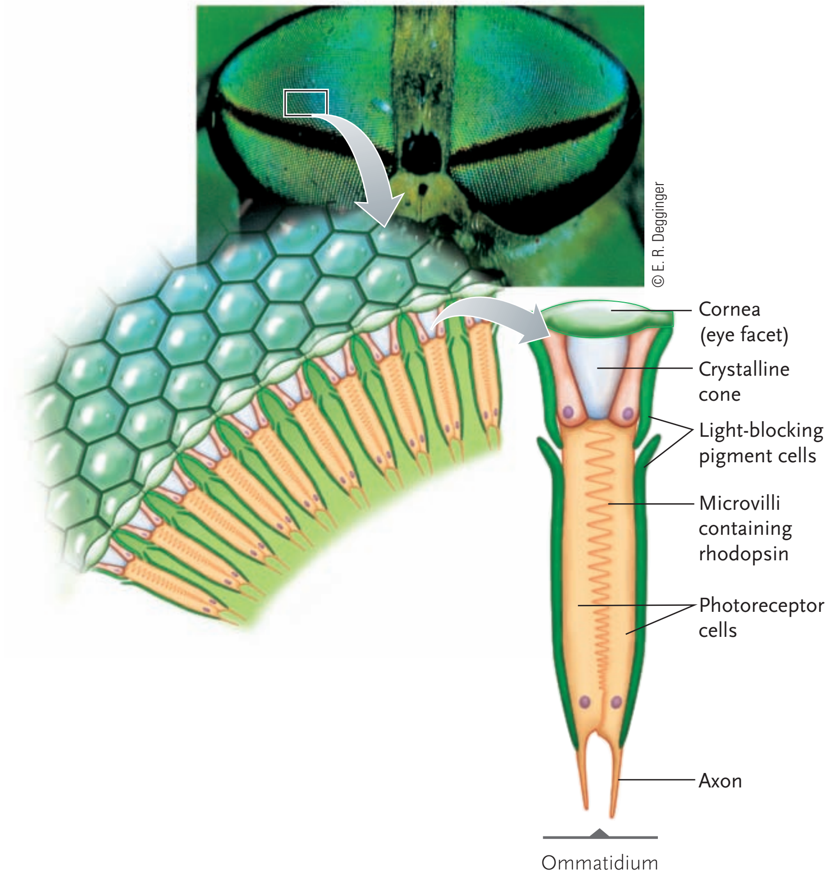

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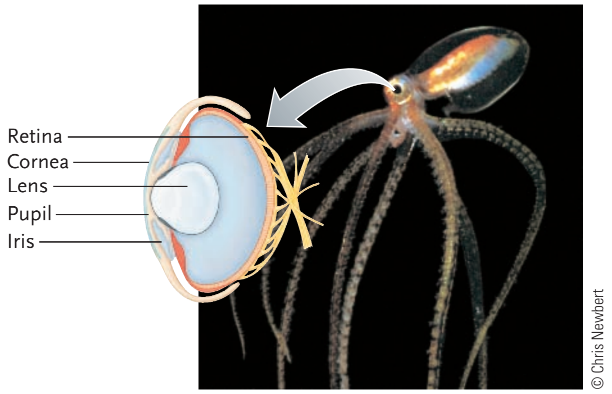
Figure 39.10
The compound eye of a deer fly. Each ommatidium has a cornea that directs light into the crystalline cone; in turn, the cone focuses light on the photoreceptor cells. A light-blocking pigment layer at the sides of the ommatidium prevents light from scattering laterally in the compound eye.

Figure 39.11
The eye of an octopus, a cephalopod mollusk.



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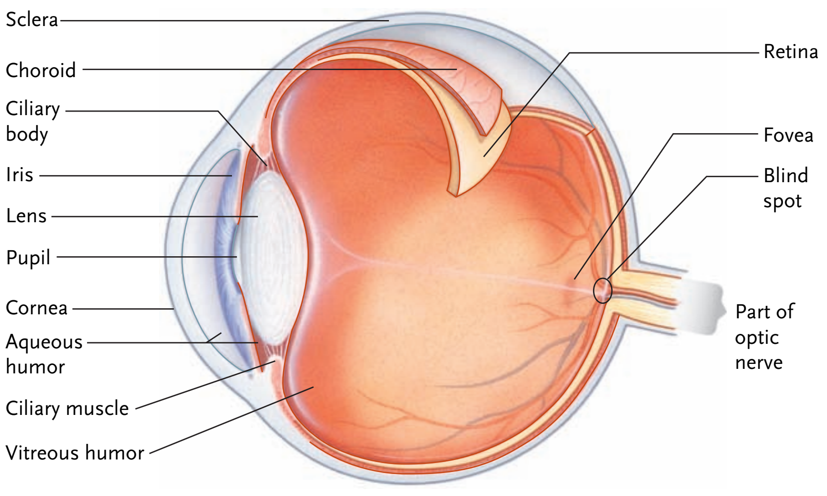


Figure 39.12 Structures of the human eye.

Vertebrate Eyes Have a Complex Structure

The human eye **(Figure 39.12)** has similar structures—cornea, iris, pupil, lens, and retina—to those of the cephalopod eye just described. Light entering the eye through the cornea passes through the iris and then the lens. The lens focuses an image on the retina, and the axons of afferent neurons originating in the retina converge to form the optic nerve leading from the eye to the brain.

A clear fluid called the **aqueous humor** fills the space between the cornea and lens. This fluid carries nutrients to the lens and cornea, which do not contain any blood vessels. The main chamber of the eye, located between the lens and the retina, is filled with the jellylike **vitreous humor** (*vitrum* = glass). The outer wall of the eye contains a tough layer of connective tissue (the *sclera*). Inside it is a darkly pigmented layer (the *choroid*) that prevents light from entering except through the pupil. It also contains the blood vessels nourishing the retina.

Two types of photoreceptors, rods and cones, occur in the retina along with layers of neurons that carry out an initial integration of visual information before it is sent to the brain. The **rods** are specialized for detection of light at low intensities; the **cones** are specialized for detection of different wavelengths (colors).

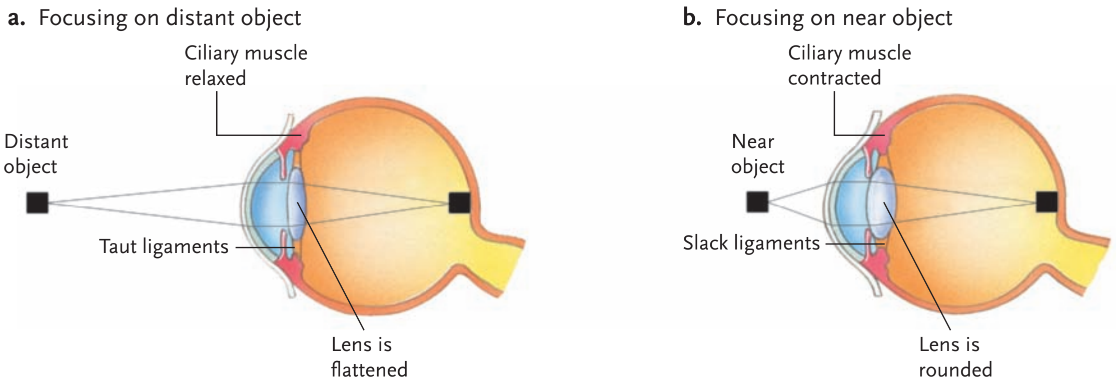
Accommodation does not occur by forward and back movement of the lens, as described for cephalopods. Rather, the lens of most terrestrial vertebrates is focused by changing its shape. The lens is held in place by fine ligaments that anchor it to a surrounding layer of connective tissue and muscle, the **ciliary body.** These ligaments keep the lens under tension when the ciliary muscle is relaxed. The tension flattens the lens, which is soft and flexible, and focuses light from distant objects on the retina **(Figure 39.13a).** When the ciliary muscles contract, they relieve the tension of the ligaments, allowing the lens to assume a more spherical shape and focusing light from nearby objects on the retina **(Figure 39.13b).**

The Retina of Mammals and Birds Contains Rods and Cones and a Complex Network of Neurons

The retina of a human eye contains about 120 million rods and 6 million cones organized into a densely packed, single layer. Neural networks of the retina are layered on top of the photoreceptor cells, so that light rays focused by the lens on the retina must pass through the neurons before reaching the photoreceptors. The light must also pass through a layer of fine blood vessels that covers the surface of the retina.

In mammals and birds with eyes specialized for daytime vision, cones are concentrated in and around a small region of the retina, the **fovea** (see Figure 39.12). The image focused by the lens is centered on

Figure 39.13 Accommodation in terrestrial vertebrates: the lens changes shape rather than moving forward and back to focus on **(a)** distant and **(b)** near objects.



When the eye focuses on a distant object, the ciliary muscles relax, allowing the ligaments that support the lens to tighten. The tightened ligaments flatten the lens, bringing the distant object into focus on the retina.

When the eye focuses on a near object, the ciliary muscles contract, loosening the ligaments and allowing the lens to become rounder. The rounded lens focuses a near object on the retina.

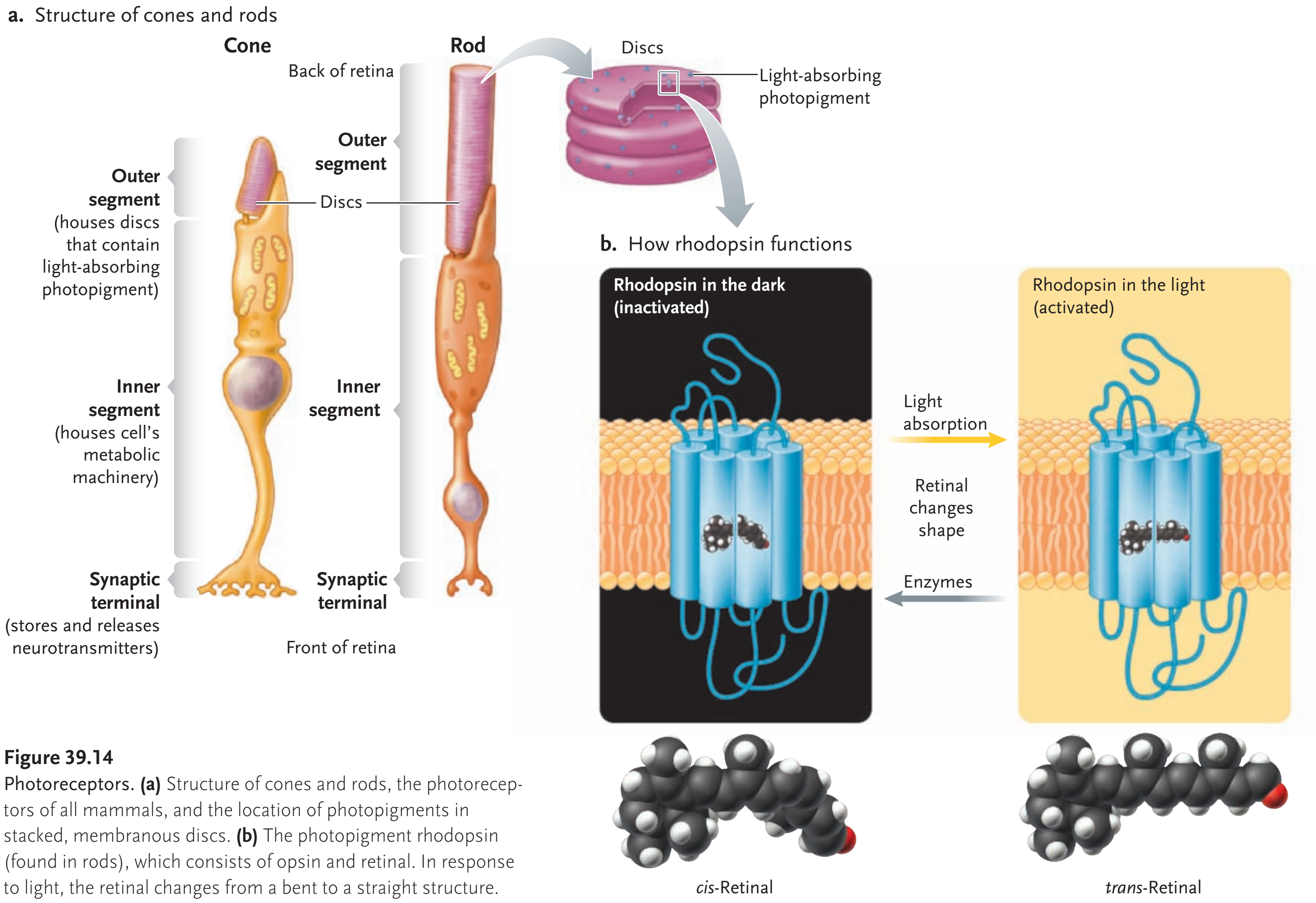


Figure 39.14

Photoreceptors. **(a)** Structure of cones and rods, the photoreceptors of all mammals, and the location of photopigments in stacked, membranous discs. **(b)** The photopigment rhodopsin (found in rods), which consists of opsin and retinal. In response to light, the retinal changes from a bent to a straight structure.

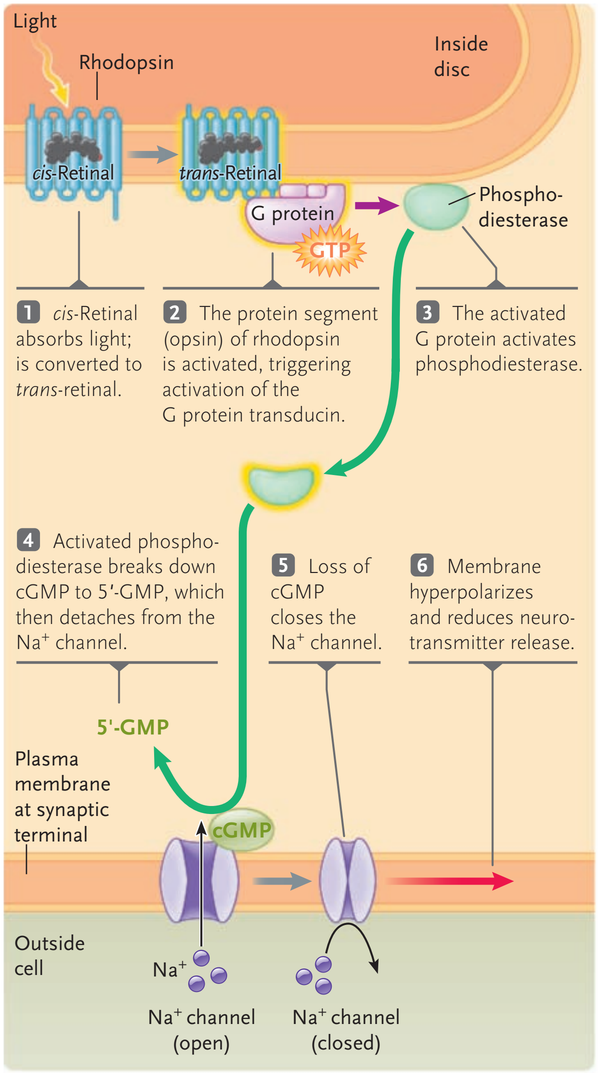
the fovea, which is circular and less than a millimeter in diameter in humans. The rods are spread over the remainder of the retina. We can see distinctly only the image focused on the fovea; the surrounding image is what we term *peripheral vision*. Mammals and birds with eyes specialized for night vision have retinas containing mostly rods, without a clearly defined fovea. Some fishes and many reptiles have cones generally distributed throughout their retina and very few rods.

The rods of mammals are much more sensitive than the cones to light of low intensity; in fact, they can respond to a single photon of light. This is why, in dim light, we can see objects better by looking slightly to the side of the object. This action directs the image away from the cones in the fovea to the highly light-sensitive rods in surrounding regions of the retina.

Sensory Transduction by Rods and Cones. Photoreceptors have three parts: an outer segment consisting of stacked, flattened, membranous discs; an inner segment where the cell's metabolic activities occur; and the synaptic terminal, where neurotransmitter molecules are stored and released **(Figure 39.14a).** The light-absorbing pigment of rods and cones, retinal, is bonded covalently in the photoreceptors with one of several different proteins called **opsins** to produce **photopigments.** The photopigments are embedded in the membranous discs of the photoreceptors' outer segments **(Figure 39.14b).** The retinal-opsin photopigment in rods is called **rhodopsin.** Let us see how light stimulating a rod photoreceptor is transduced; the mechanism is essentially the same in the cone photoreceptors.

In the dark, the retinal segment of the unstimulated rhodopsin is in an inactive form known as *cis*-retinal (see Figure 39.14b), and the rods steadily release the neurotransmitter glutamate. When rhodopsin absorbs a photon of light, retinal converts to its active form, *trans*-retinal (see Figure 39.14b), and the rods *decrease* the amount of glutamate they release. This will be discussed in the next section.

Rhodopsin is a membrane-embedded G-protein-coupled receptor (see Section 7.4). Recall that an extracellular signal received by a G-protein-coupled receptor activates the receptor, which triggers a signal transduction pathway within the cell, leading to a cellular response. Here, activated rhodopsin triggers a signal transduction pathway that leads to the closure of Na^+ channels in the plasma membrane **(Figure 39.15).** Closure of the channels hyperpolarizes the photoreceptor's membrane, thereby decreasing neuro-



1 *cis*-Retinal absorbs light; is converted to *trans*-retinal.

2 The protein segment (opsin) of rhodopsin is activated, triggering activation of the G protein transducin.

3 The activated G protein activates phosphodiesterase.

4 Activated phosphodiesterase breaks down cGMP to 5'-GMP, which then detaches from the Na$^+$ channel.

5 Loss of cGMP closes the Na$^+$ channel.

6 Membrane hyperpolarizes and reduces neurotransmitter release.

Figure 39.15 The signal transduction pathway that closes Na$^+$ channels in photoreceptor plasma membranes when rhodopsin absorbs light.

transmitter release. The response is graded in the sense that as light absorption by photopigment molecules increases, the amount of neurotransmitter released is reduced proportionately; if light absorption decreases, neurotransmitter release by the photoreceptor increases proportionately. Note that transduction in rods works in the opposite way from most sensory receptors, in which a stimulus increases neurotransmitter release.

Visual Processing in the Retina. In the retina of all vertebrates, the two types of photoreceptors are linked to a network of neurons that carries out initial integration and processing of visual information. The retina of mammals contains four types of neurons **(Figure 39.16).** Just over the rods and cones is a layer of **bipolar cells.** These neurons make synapses with the rods or cones at one end and with a layer of neurons called **ganglion cells** at the other end. The axons of ganglion cells extend over the retina and collect at the back of the eyeball to form the optic nerve, which transmits action potentials to the brain. The point where the optic nerve exits the eye lacks photoreceptors, resulting in a *blind spot* several millimeters in diameter. Two other types of neurons form lateral connections in the retina: **horizontal cells** connect photoreceptor cells, and **amacrine cells** connect bipolar cells and ganglion cells.

In the dark, the steady release of glutamate from rods and cones depolarizes some of the postsynaptic bipolar cells and hyperpolarizes others, depending on the type of receptor those cells have. In the light, the decrease in neurotransmitter release from rods and cones results in the polarized bipolar cells becoming hyperpolarized, and hyperpolarized bipolar cells becoming polarized. These membrane potential changes in response to light are transmitted to the brain for processing.

Signals from the rods and cones may move vertically or laterally in the retina. Signals move vertically from the photoreceptors to bipolar cells and then to ganglion cells. However, while the human retina has over 120 million photoreceptors, it has only about 1 million ganglion cells. This disparity is explained by the fact that each ganglion cell receives signals from a clearly defined set of photoreceptors that constitute the *receptive field* for that cell. Therefore, stimulating numerous photoreceptors in a ganglion cell's receptive field results in only a single message to the brain from that cell. Receptive fields are typically circular and are of different sizes. Smaller receptive fields result in sharper images because they send more precise information to the brain regarding the location in the retina where the light was received.

Signals that move laterally from a rod or cone proceed to a horizontal cell and continue to bipolar cells with which the horizontal cell makes inhibitory connections. To understand this, consider a spot of light falling on the retina. Photoreceptors detect the light and send a signal to bipolar cells and horizontal cells. The horizontal cells inhibit more distant bipolar cells that are outside the spot of light, causing the light spot to appear lighter and its surrounding dark area to appear darker. This type of visual processing is called **lateral inhibition** and serves both to sharpen the edges of objects and enhance contrast in an image.

Three Kinds of Opsin Pigments Underlie Color Vision

Many invertebrates and some species in each class of vertebrates have color vision. Color vision depends on the cones in the retina. Most mammals have only two types of cones, making their color vision limited, while humans and other primates have three types. Each human or primate cone cell contains one of three different photopigments, collectively called **photopsins**, in which retinal is combined with different opsins. The three photopsins absorb light over different, but overlapping, wavelength ranges, with peak absorptions at 445 nm (blue light), 535 nm (green light), and 570 nm

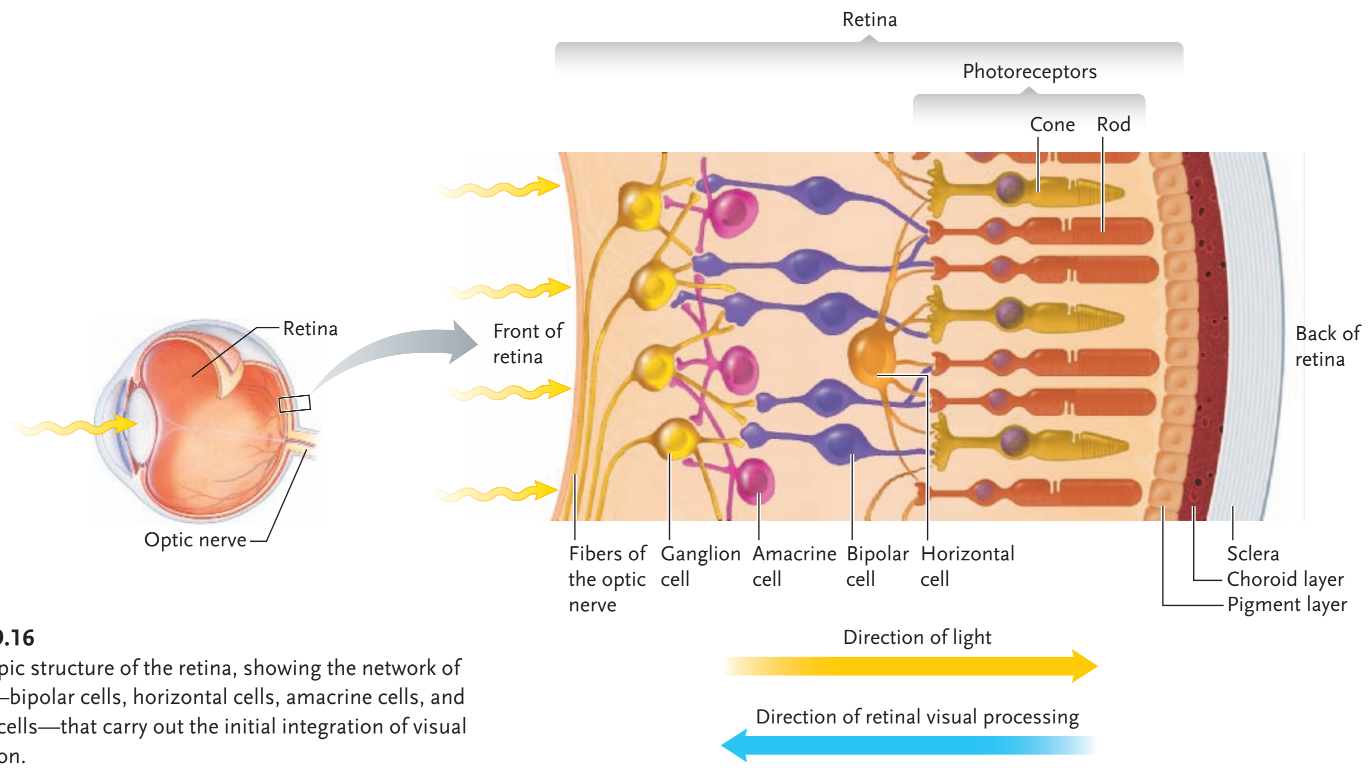


Figure 39.16
Microscopic structure of the retina, showing the network of neurons—bipolar cells, horizontal cells, amacrine cells, and ganglion cells—that carry out the initial integration of visual information.

(red light). The farther a wavelength is from the peak color absorbed, the less strongly the cone responds.

Having overlapping wavelength ranges for the three photoreceptors means that light at any visible wavelength will stimulate at least two of the three types of cones. However, because the maximal absorption of each type of cone is a different wavelength, it is stimulated to a different extent by light at a given wavelength. The differences, relayed to the visual centers of the brain, are integrated into the perception of a color corresponding to the particular wavelength absorbed. Light stimulating all three receptor types equally is seen as white.

The Visual Cortex Processes Visual Information

Just behind the eyes, the optic nerves converge before entering the base of the brain. A portion of each optic nerve crosses over to the opposite side, forming the **optic chiasm** (*chiasma* = crossing place). Most of the axons enter the **lateral geniculate nuclei** in the thalamus, where they make synapses with interneurons leading to the visual cortex **(Figure 39.17).**

Because of the optic chiasm, the left half of the image seen by both eyes is transmitted to the visual cortex in the right cerebral hemisphere, and the right half of the image is transmitted to the left cerebral hemisphere. The right hemisphere thus sees objects to the left of the center of vision, and the left hemisphere sees objects to the right of the center of vision. Communication between the right and left hemispheres integrates this information into a perception of the entire visual field seen by the two eyes.

If you look at a nearby object with one eye and then the other, you will notice that the point of view is slightly different. Integration of the visual field by the brain creates a single picture with a sense of distance and depth. The greater the difference between the images seen by the two eyes, the closer the object appears to the viewer.

The two optic nerves together contain more than a million axons, more than all other afferent neurons of the body put together. Almost one-third of the cerebral cortex is devoted to visual information. These numbers give some idea of the complexity of the information integrated into the visual image formed by the brain.

STUDY BREAK

For vertebrate photoreception, define: (a) photopigment; (b) cone; (c) receptive field.

39.5 Chemoreceptors

Chemoreceptors form the basis of taste (gustation) and smell (olfaction), and measure the levels of internal body molecules such as oxygen, carbon dioxide, and hydrogen ions. All chemoreceptors probably work through membrane receptor proteins that are stimulated when they bind with specific molecules in the

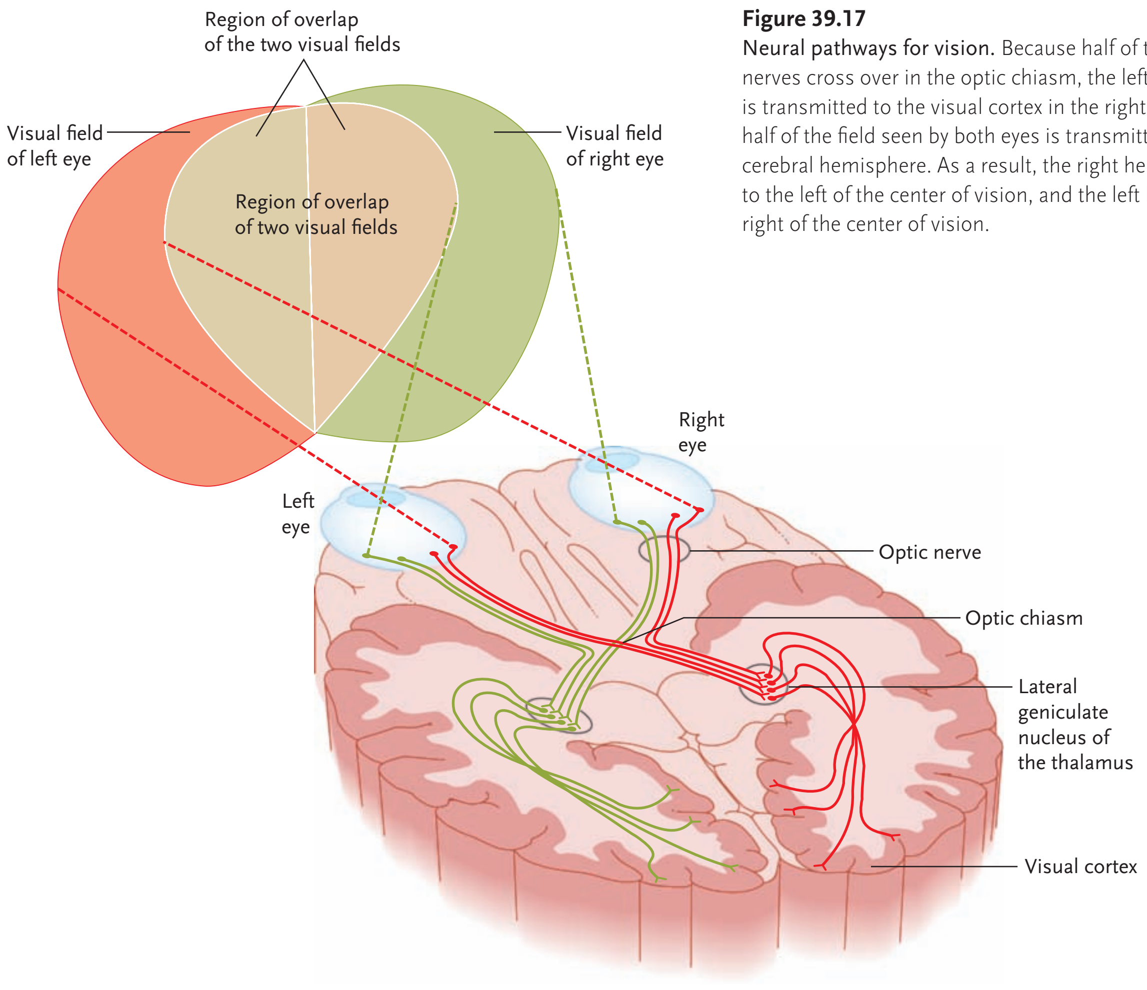


Figure 39.17

Neural pathways for vision. Because half of the axons carried by the optic nerves cross over in the optic chiasm, the left half of the field seen by both eyes is transmitted to the visual cortex in the right cerebral hemisphere. The right half of the field seen by both eyes is transmitted to the visual cortex in the left cerebral hemisphere. As a result, the right hemisphere of the brain sees objects to the left of the center of vision, and the left hemisphere sees objects to the right of the center of vision.

environment, generating action potentials in afferent nerves leading to the CNS.

Invertebrates Have Either the Same or Different Receptors for Taste and Smell

In many invertebrates the same receptors serve for the senses of smell and taste. These receptors may be confined to certain locations or distributed over the body surface. For example, the cnidarian *Hydra* has chemoreceptor cells around its mouth that respond to glutathione, a chemical released from prey organisms ensnared in the cnidarian's tentacles. Stimulation of the chemoreceptors by glutathione causes the tentacles to retract, resulting in ingestion of the prey. By contrast, earthworms have taste/smell receptors distributed over the entire body surface.

Some terrestrial invertebrates, particularly insects, have clearly differentiated taste and smell receptors. In insects, taste receptors occur inside hollow sensory bristles called *sensilla* (singular, *sensillum*), which may be located on the antennae, mouthparts, or feet **(Figure 39.18).** Pores in the sensilla admit molecules from potential food to the chemoreceptors, which are specialized to detect sugars, salts, amino acids, or other chemicals. Many female insects have chemoreceptors on their ovipositors, which allow them to lay their eggs on food appropriate for the hatching larvae.

Insect olfactory receptors detect airborne molecules. Some insects use odor as a means of communication, as with the pheromones released into the air as sexual attractants by female moths. Olfactory receptors in the bristles of male silkworm moth antennae **(Figure 39.19)** have been shown experimentally to be able to detect pheromones released by a female of the same species in concentrations as low as one attractant molecule per 10^{17} air molecules; when as few as 40 of the 20,000 receptor cells on its antennae have been stimulated by pheromone molecules, the male moth responds by fluttering its wings rapidly to attract the female's attention. Ants, bees, and wasps may identify members of the same hive or nest or communicate by means of odor molecules.

Taste and Smell Receptors Are Differentiated in Terrestrial Animals

In terrestrial animals, taste involves the detection of potential food molecules in objects that are touched by a receptor, while smell involves the detection of airborne molecules. Although both taste and smell receptors have hairlike extensions containing the proteins that bind environmental molecules, the hairs of taste receptors are derived from microvilli and contain microfilaments, while the hairs of smell receptors are derived from cilia and contain microtubules. Another significant difference between taste and smell is that information from taste receptors is typically processed in the parietal lobes, while information from smell receptors is processed in the olfactory bulbs and the temporal lobes.

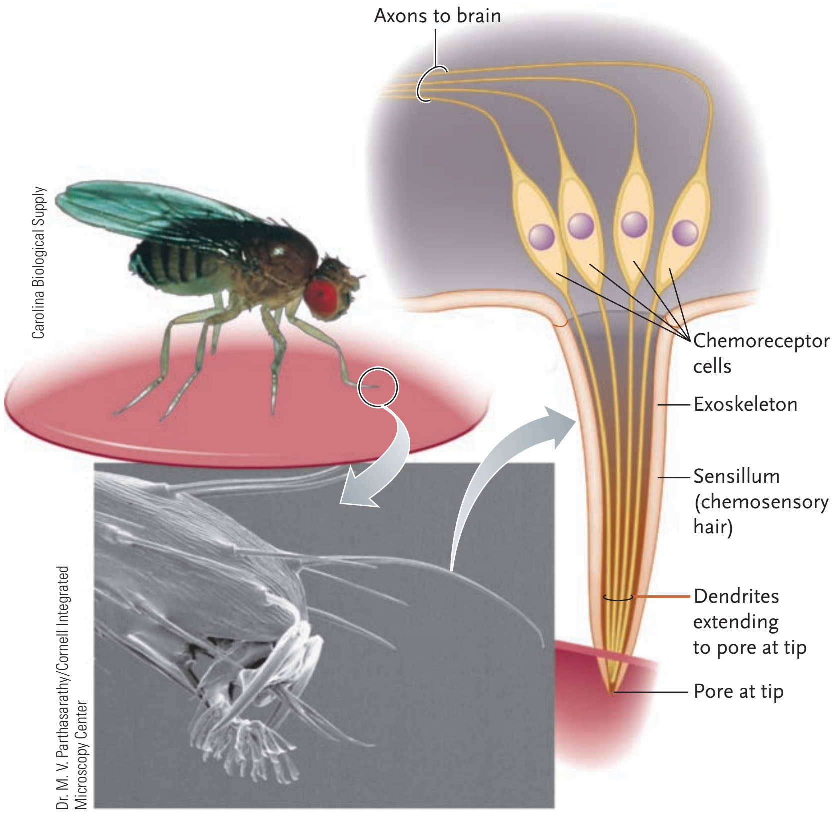
In Vertebrates, Taste Receptors Are Located in Taste Buds

The taste receptors of most vertebrates form part of a structure called a taste bud, a small, pear-shaped capsule with a pore at the top that opens to the exterior **(Figure 39.20).** The sensory hairs of the taste receptors pass through the pore of a taste bud and project to the exterior. The opposite end of the receptor cells forms synapses with dendrites of an afferent neuron.

The taste receptors of terrestrial vertebrates are concentrated in the mouth. Humans have about 10,000 taste buds, each 30 to 40 μm in diameter, scattered over the tongue, roof of the mouth, and throat. Those on the tongue are embedded in outgrowths called *papillae* (*papula* = pimple), which give the surface of the tongue its rough or furry texture.

Taste receptors on the human tongue are thought to respond to five basic tastes: sweet, sour, salty, bitter, and umami (savory). Some of the receptors for umami respond to the amino acid glutamate (familiar as monosodium glutamate or MSG). Recent research indicates that the classes of receptors may all have many subtypes, each binding a specific molecule within that class.

Signals from the taste receptors are relayed to the thalamus. From there, some signals lead to gustatory centers in the cerebral cortex, which integrate them into the perception of taste, while others lead to the brain stem and limbic system, which links tastes to involuntary visceral and emotional responses. Through these connections, a pleasant taste may lead to salivation, secretion of digestive juices, sensations of pleasure, and even sexual arousal, while an unpleasant taste may produce revulsion, nausea, and even vomiting.



Carolina Biological Supply

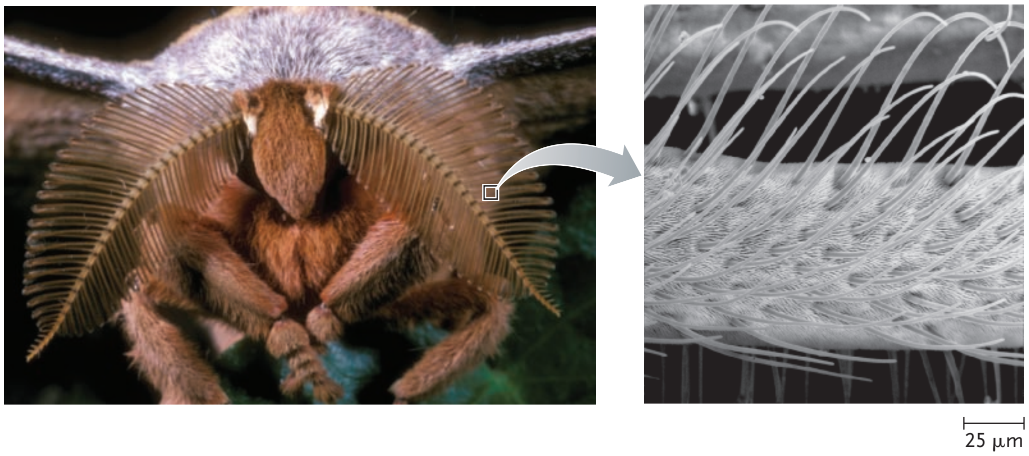
Dr. M. V. Parthasarathy/Cornell Integrated Microscopy Center

Figure 39.18
Taste receptors on the foot of a fruit fly, *Drosophila.*

Olfactory Receptors Are Concentrated in the Nasal Cavities in Terrestrial Vertebrates

Receptors that detect odors are located in the nasal cavities in terrestrial vertebrates. Bloodhounds have more than 200 million olfactory receptors in patches of olfactory epithelium in the upper nasal passages; humans have about 5 million olfactory receptors.

On one end, each olfactory receptor cell has 10 to 20 sensory hairs that project into a layer of mucus covering the olfactory area in the nose **(Figure 39.21).** To be



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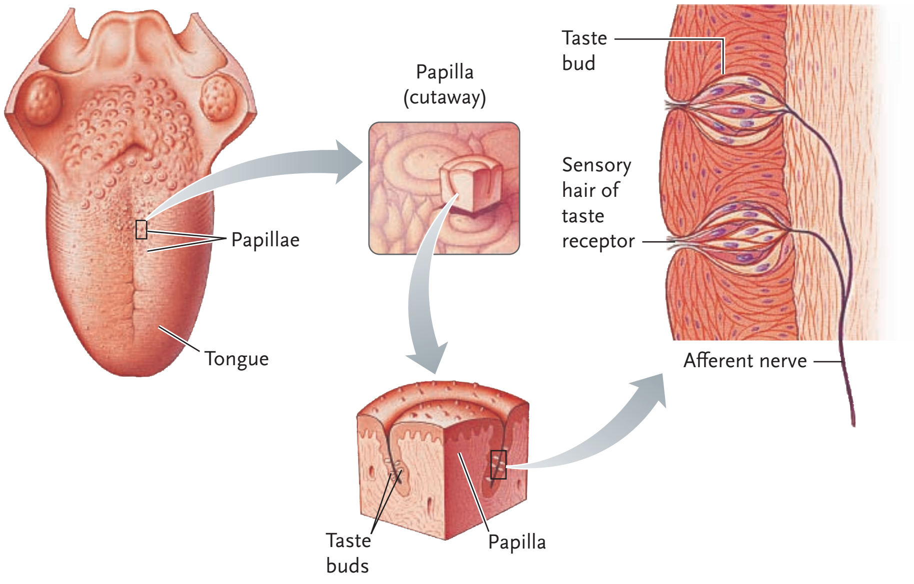
Louisa Howard, Dartmouth College EM Facility

Figure 39.19
The brushlike antennae of a male silkworm moth. Fine sensory bristles containing olfactory receptor cells cover the filaments of the antennae.

Figure 39.20
Taste receptors in the human tongue. The receptors occur in microscopic taste buds that line the sides of the furry papillae.



detected, airborne molecules must dissolve in the watery mucus solution. On the other end, the olfactory receptors make synapses with interneurons in the olfactory bulbs. Olfactory receptors are the only receptor cells that make direct connections with brain interneurons, rather than via afferent neurons.

From the olfactory bulbs, nerves conduct signals to the olfactory centers of the cerebral cortex, where they are integrated into the perception of tantalizing or unpleasant odors from a rose to a rotten egg. Most odor perceptions arise from a combination of different olfactory receptors. In the early 1990s, Richard Axel and Linda Buck discovered that about 1000 different human genes give rise to an equivalent number of olfactory receptor types, each of which responds to a different class of chemicals. Axel and Buck received the Nobel Prize in 2004 in recognition of their research.

Other connections from the olfactory bulbs lead to the limbic system and brain stem where the signals elicit emotional and visceral responses similar to those caused by pleasant and unpleasant tastes (see Section 38.3). As a result, different odors, like tastes, may give rise to a host of involuntary responses, from salivation to vomiting, as well as conscious responses.

Olfaction contributes to the sense of taste because vaporized molecules from foods are conducted from the throat to the olfactory receptors in the nasal cavities. Olfactory input is the reason why anything that dulls your sense of smell—such as a head cold, or holding your nose—diminishes the apparent flavor of food.

Many mammals use odors as a means of communication. Individuals of the same family or colony are identified by their odor; odors are also used to attract mates and to mark territories and trails. Dogs, for example, use their urine to mark home territories with identifying odors. Humans use the fragrances of perfumes and colognes as artificial sex attractants.

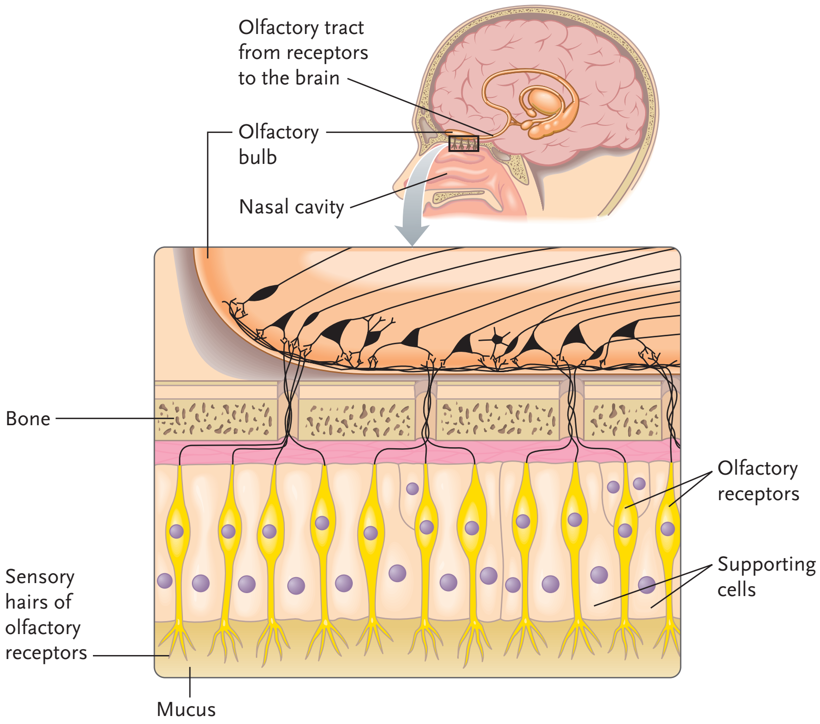


Figure 39.21
Olfactory receptors in the roof of the nasal passages in humans. Axons from these receptors pass through holes in the bone separating the nasal passages from the brain, where they make synapses with interneurons in the olfactory bulbs.

STUDY BREAK

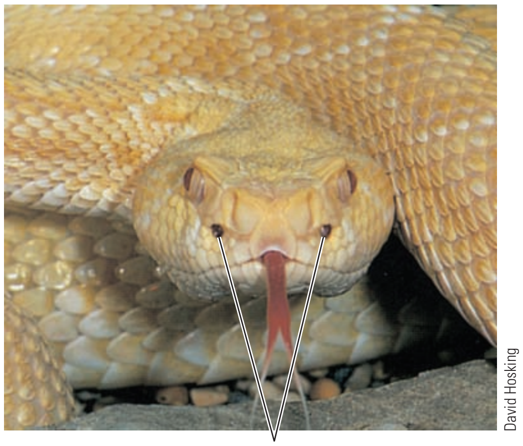
1. How do we distinguish different kinds of smells?
2. For terrestrial vertebrates, describe the pathway by which a signal generated by taste receptors leads to a response.

39.6 Thermoreceptors and Nociceptors

Thermoreceptors detect changes in the surrounding temperature. Nociceptors respond to stimuli that may potentially damage their tissues. Both types of receptors consist of free nerve endings formed by the dendrites of afferent neurons, with no specialized receptor structures surrounding them.

Thermoreceptors Can Detect Warm and Cold Temperatures and Temperature Changes

Most animals have thermoreceptors. Some invertebrates such as mosquitoes and ticks use thermoreceptors to locate their warm-blooded prey. Some snakes, including rattlesnakes and pythons, use thermoreceptors called *pit organs* to detect the body heat of warm-blooded prey animals **(Figure 39.22).**



David Hosking

Figure 39.22
The pit organs of an albino Western diamondback rattlesnake *(Crotalus atrox)*, located in depressions on both sides of the head below the eyes. These thermoreceptors detect infrared radiation emitted by warm-bodied prey animals such as mice.

In mammals, distinct thermoreceptors respond to heat and cold. Researchers have shown that three members of the *transient receptor potential* (TRP) gated Ca^{2+} channel family act as heat receptors. One responds when the temperature reaches 33°C and another responds above 43°C, where heat starts to be painful; these two receptors are believed to be involved in thermoregulation. The third receptor responds at 52°C and above, in this case producing a pain response rather than being involved in thermoregulation.

Two cold receptors are known in mammals. One responds between 8 and 28°C, and is thought to be involved in thermoregulation. The second responds to temperatures below 8°C and appears to be associated with pain rather than thermoregulation. The molecular mechanisms that control the opening and closing of heat and cold receptor channels are not currently known.

Some neurons in the hypothalamus of mammals also function as thermoreceptors, an ability that has only recently been investigated. Not only do these neurons sense changes in brain temperature, but they also receive afferent thermal information. These neurons are highly sensitive to shifts from the normal body temperature, and trigger involuntary responses such as sweating, panting, or shivering, which restore normal body temperature.

Nociceptors Protect Animals from Potentially Damaging Stimuli

The signals from nociceptors—receptors in mammals, and possibly other vertebrates, that detect damaging stimuli—are interpreted by the brain as pain. Pain is a protective mechanism; in humans, it prompts us to do something immediately to remove or decrease the damaging stimulus. Often pain elicits a reflex response—such as withdrawing the hand from a hot stove—that proceeds before we are even consciously aware of the sensation.

Various types of stimuli cause pain, including mechanical damage such as a cut, pinprick, or blow to the body, and temperature extremes. Some nociceptors are specific for a particular type of damaging stimulus, while others respond to all kinds.

The axons that transmit pain are part of the somatic system of the PNS (see Section 38.2). They synapse with interneurons in the gray matter of the spinal cord, and activate neural pathways to the CNS by releasing the neurotransmitters glutamate or substance P (see Section 37.3). Glutamate-releasing axons produce sharp, prickling sensations that can be localized to a specific body part—the pain of stepping on a tack, for example. Substance P–releasing axons produce dull, burning, or aching sensations, the location of which may not be easily identified—the pain of tissue damage such as stubbing your toe.

As part of their protective function, pain receptors adapt very little, if at all. Some pain receptors, in fact, gradually intensify the rate at which they send out action potentials if the stimulus continues at a constant level.

The CNS also has a pain-suppressing system. In response to stimuli such as exercise, hypnosis, and stress, the brain releases *endorphins,* natural painkillers that bind to membrane receptors on substance P neurons, reducing the amount of neurotransmitter released.

Nociceptors contribute to the taste of some spicy foods, particularly those that contain hot peppers. In fact, researchers who study pain often use *capsaicin,* the organic compound that gives jalapeños and other peppers their hot taste, to identify nociceptors. To some, the burning sensation from capsaicin is addictive. Here is the reason. Nociceptors in the mouth, nose, and throat immediately transmit pain messages to the brain when they detect capsaicin. The brain re-

Insights from the Molecular Revolution

Hot News in Taste Research

Biting into a jalapeño pepper (a variety of *Capsicum annuum*) can produce a burning pain in your mouth strong enough to bring tears to your eyes. This painfully hot sensation is due primarily to *capsaicin*, a chemical that probably evolved in pepper plants as a defense against foraging animals. The defense is obviously ineffective against the humans who relish peppers and foods containing capsaicin (such as buffalo wings).

Research by David Julius and his coworkers at the University of California, San Francisco, revealed the molecular basis for detection of capsaicin by nociceptors. They designed their experiments to test the hypothesis that the responding nociceptors have a cell surface receptor that binds capsaicin. Binding the chemical opens a membrane channel in the receptor that admits calcium ions and initiates action potentials interpreted as pain.

The Julius team isolated the total complement of messenger RNAs from nociceptors able to respond to capsaicin and made complementary DNA (cDNA) clones of the mRNAs. The cDNAs, which represented sequences encoding proteins made in the nociceptors, contained thousands of different sequences. The cDNAs were transformed individually into embryonic kidney cells (which do not normally respond to capsaicin), and the transformed cells were screened with capsaicin to identify which took in calcium ions; presumably, these cells had received a cDNA encoding a capsaicin receptor. Messenger RNA transcribed from the identified cDNA clone was injected into both frog oocytes and cultured mammalian cells. Tests showed that both the oocytes and the cultured cells responded to capsaicin by admitting calcium ions, which confirmed that the researchers had found the capsaicin receptor cDNA.

Among the effects noted when the receptor was introduced into oocytes was a response to heat. Increasing the temperature of the solution surrounding the oocytes from 22°C to about 48°C produced a strong calcium inflow. In short, capsaicin and heat produce the same response in cells containing the receptor. Therefore the feeling that your mouth is on fire when you eat a hot pepper probably results from the fact that, as far as your nociceptors and CNS are concerned, it *is* on fire.

sponds by releasing endorphins, which act as a painkiller and create temporary euphoria—a natural high, if you will. *Insights from the Molecular Revolution* describes a series of experiments investigating the molecular basis of the pain caused by capsaicin.

Study Break

What distinguishes thermoreceptors and nociceptors from the other types of sensory receptors discussed previously?

39.7 Magnetoreceptors and Electroreceptors

Some animals have poorly developed visual systems but can gain information about their environment by sensing magnetic or electrical fields. In so doing, they directly sense stimuli that humans can detect only with scientific instruments.

Magnetoreceptors Are Used for Navigation

Some animals that navigate long distances, including migrating butterflies, beluga whales, sea turtles, homing pigeons, and foraging honeybees, have **magnetoreceptors** that allow them to detect and use Earth's magnetic field as a source of directional information (experiments with sea turtles are described in **Figure 39.23**).

The pattern of Earth's magnetic field differs from region to region yet remains almost constant over time, largely unaffected by changing weather and day and night. As a result, animals with magnetic receptors are able to monitor their location reliably. Although little is known about the receptors that detect magnetic fields, they may depend on the fact that moving a conductor, such as an electroreceptor cell, through a magnetic field generates an electric current.

Some magnetoreceptors may depend on the effect of Earth's magnetic field on the mineral *magnetite*. Magnetite is found in the bones or teeth of many vertebrates, including humans, and also in insects—in the abdomen of honeybees and in the heads and abdomens of certain ants, for example.

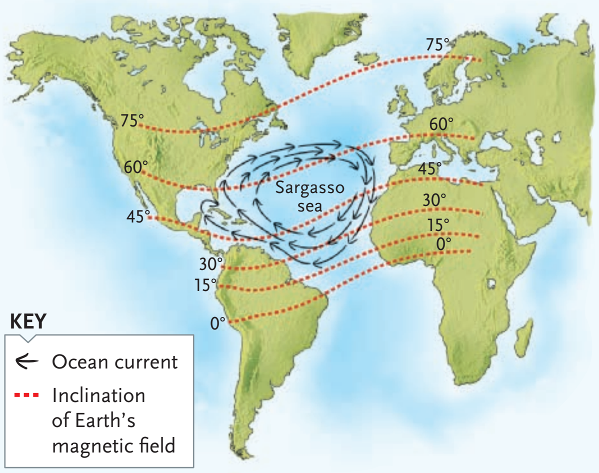
Other animals, including homing pigeons, which are famous for their ability to find their way back to their nests even when released far from home, navigate by detecting their position with reference to both Earth's magnetic field and the sun. Magnetite is located in the bills of these birds, which is where research indicates magnetoreception likely occurs.

Electroreceptors Are Used for Location of Prey or for Communication

Many sharks and bony fishes, some amphibians, and even some mammals (such as the star-nosed mole and duckbilled platypus) have specialized **electroreceptors**

Figure 39.23 Experimental Research

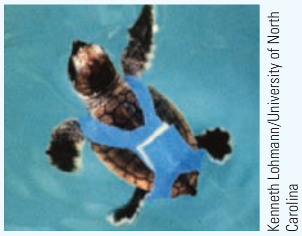
Demonstration That Magnetoreceptors Play a Key Role in Loggerhead Sea Turtle Migration



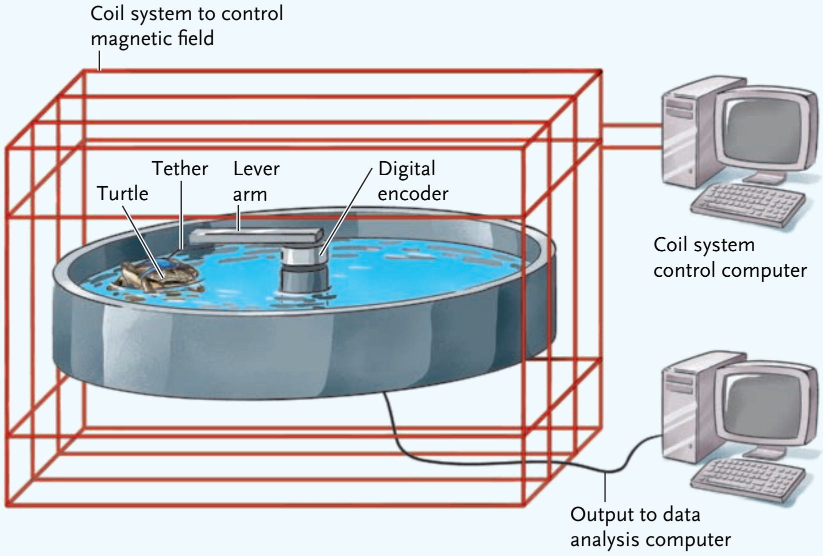
QUESTION: Do loggerhead sea turtles use a magnetoreceptor system for migration?

EXPERIMENT: Loggerhead sea turtles *(Caretta caretta)* that hatch along the east coast of Florida spend much of their lives traveling the North Atlantic current system around the Sargasso Sea, a pool of warm water with a unique seaweed ecosystem. Eventually and unerringly, the turtles return to their hatching beach for the mating season. Kenneth Lohmann of the University of North Carolina hypothesized that magnetoreception, likely involving magnetite, plays a central role in loggerhead migration. Lohmann tested his hypothesis using an experimental system in which the direction hatchling turtles swam was analyzed in different magnetic fields.

1. Lohmann placed each turtle hatchling he tested in a harness and tethered it to a swiveling, electronic system in the center of a circular pool of water. The pool was surrounded by a large electromagnetic coil system that allowed the researchers to reverse the direction of the magnetic field. The direction the turtle swam was recorded by the tracking system and relayed to a computer.


Kenneth Lohmann/University of North Carolina

2. Lohmann allowed the turtles to swim under two experimental conditions: half of the turtles swam in Earth's magnetic field, and the other half swam in a reversed magnetic field.



RESULTS: The turtle hatchlings tested in Earth's magnetic field swam in an east-to-northeast direction on average, mimicking the direction they follow normally when migrating at sea. The turtle hatchlings tested in the reversed magnetic field on average swam in a direction 180° opposite that of the hatchlings swimming in Earth's magnetic field.

CONCLUSION: The results indicate that loggerhead sea turtle hatchlings have the ability to detect Earth's magnetic field and use it as a way to orient their migration. Their direction of migration, east to northeast, matches the inclination of Earth's magnetic field in the Atlantic Ocean where they migrate (see map figure). Lohmann believes that the magnetoreception system in the turtles involves magnetite.

that detect electrical fields. The plasma membrane of an electroreceptor cell is depolarized by an electrical field, leading to the generation of action potentials. The electrical stimuli detected by the receptors are used to locate prey or navigate around obstacles in muddy water, or, by some fishes, to communicate. Some electroreception systems are passive—they detect electric fields in the environment, not the animal's own electric currents. Passive systems are used mainly to find prey. For example, the electroreceptors of sharks and rays can locate fish buried under the sand from the electrical currents generated by their prey's heartbeat or by the muscle contractions that move water over their gills.

Other electroreception systems are active—the animal emits and receives low voltage electrical signals, either to locate prey or to communicate with members of the same species. The electrical signals

UNANSWERED QUESTIONS

What happens when the senses get scrambled—when listening to music causes you to "see" colors, or when you "taste" certain words? Synesthesia (joined senses) occurs when two senses, normally separate, are perceived together. For the most part, people with synesthesia are born with it, and it tends to run in families. A recent study by Michael Esterman and his colleagues at the University of California, Berkeley, showed that the posterior parietal cortex, a region of the brain thought to be involved in sensory integration, appears to be crucial to sensory commingling. Some researchers think that this commingling is how the senses function early in development, when the nervous system is still immature. They believe that the senses normally separate from one another around four months after birth. In synesthetes, however, this separation is incomplete and two of their senses remain mingled.

London's Science Museum collaborated with Jamie Ward of University College London in an experiment that paired sounds and music. They wanted to determine if volunteers visiting the museum would prefer combinations of sound and vision as described by synesthetes over combinations randomly generated by a computer. Interestingly, people found the synesthetic combinations more pleasing than the computer-generated ones. Thus, it is possible that everyone may have a built-in understanding of what sounds and colors go together.

In an evolutionary context, which "sense" developed first? The descriptions of the senses in this chapter focus primarily on vertebrate sensory systems, but the nervous systems of many invertebrates can be quite complex. Indeed, squids, sea hares, leeches, horseshoe crabs, lobsters, and cockroaches have been quite instrumental in helping scientists understand the nervous system. As for senses, squids have sensitive eyes and accentuated smell and taste, and they respond to touch and vibration. Clearly, vertebrates aren't the only multicellular organisms to develop senses.

However, is a nervous system necessary for organisms to have senses? Can single-celled organisms (which, of course, do not have nervous systems) respond to stimuli? Clearly, the answer is yes. Consider *Paramecium tetraurelia,* a single-celled organism covered with cilia that lives in water. It can detect substances in its environment and swim toward certain chemicals while avoiding others. It also responds to solid objects by turning when it runs into one. Thus, it has a "chemical sense" similar to taste or smell, and it responds to a type of "touch." We will probably never know which sense developed first, but some type of touch or chemical sense seems the most likely.

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are generated by special electric organs. A few species, such as the electric eel and the electric catfish, produce discharges on the order of several hundred volts. These discharges are used to stun or kill prey. The voltage is high enough to stun, but not kill, a human.

STUDY BREAK

What are three ways electroreceptors are used in aquatic vertebrates?

Review

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39.1 Overview of Sensory Receptors and Pathways

- Sensory receptors are formed by the endings of afferent neurons or specialized cells adjacent to the neurons. They detect stimuli such as mechanical pressure, sound waves, light, or specific chemicals. Action potentials generated by the receptors are carried by the axons of afferent neurons to pathways leading to specific parts of the brain, where signals are processed into sensory sensations (Figure 39.1).
- Receptors are specialized as mechanoreceptors, photoreceptors, chemoreceptors, thermoreceptors, and nociceptors. Some animals have receptors that detect electrical or magnetic fields.
- The routing of information from sensory receptors to particular regions of the brain identifies a specific stimulus as a sensation. The intensity of a stimulus is determined by the frequency of action potentials traveling along the neural pathways and the number of afferent neurons carrying action potentials.
- Many sensory systems show sensory adaptation, in which the frequency of action potentials decreases while a stimulus remains constant. Some sensory receptors, such as those related to pain, show little or no sensory adaptation.

Animation: Action potentials

39.2 Mechanoreceptors and the Tactile and Spatial Senses

- Mechanoreceptors detect touch, pressure, acceleration, or vibration. Touch and pressure receptors are free nerve endings or encapsulated nerve endings of sensory neurons (Figure 39.2).
- Mechanoreceptors called proprioceptors detect stimuli used by the CNS to monitor and maintain body and limb positions.
- Proprioceptors based on sensory hair cells generate action potentials when the hairs are moved (Figures 39.3–39.5).
- Receptors in muscles, tendons, and joints of vertebrates detect changes in stretch and tension of body parts (Figure 39.6).

Animation: Dynamic equilibrium

39.3 Mechanoreceptors and Hearing

- Many invertebrates have mechanoreceptors in their skin or other surface structures that detect sound and other vibrations.
- Hearing relies on sensory hair cells in organs that respond to the vibrations of sound waves.
- In terrestrial vertebrates, the ear consists of three parts. The outer ear directs sound to the eardrum. Vibrations of the eardrum are transmitted through one or more bones in the middle ear to the fluid-filled inner ear. In the inner ear, the vibrations are transmitted through membranes that bend the stereocilia of the hair cells, leading to bursts of action potentials that are reflected in the frequency of the sound waves (Figure 39.8).

Animation: Ear structure and function

Animation: Properties of sound

39.4 Photoreceptors and Vision

- Invertebrates possess many forms of eyes, from the simplest, an ocellus, to single-lens eyes that are similar to vertebrate eyes (Figures 39.9–39.11).
- The photoreceptors of all animal eyes contain the pigment retinal, which absorbs the energy of light and uses it to generate changes in membrane potential.
- The transparent cornea admits light into the vertebrate eye. Behind the cornea, the iris controls the diameter of the pupil, regulating the amount of light that strikes the lens. The lens focuses an image on the retina lining the back of the eye, where photoreceptors and neurons carry out the initial integration of information detected by the photoreceptors (Figure 39.12).
- In terrestrial vertebrates, the lens is focused by adjusting its shape (Figure 39.13). The retina contains two types of photoreceptors, rods and cones. Rods are specialized for detecting light of low intensity; cones are specialized for detecting light of different wavelengths, which are perceived as colors.
- The light-absorbing pigment in photoreceptor cells consists of retinal combined with an opsin protein. When it absorbs light, retinal changes form, initiating reactions that alter the amount of neurotransmitter released by the photoreceptor cells (Figures 39.14 and 39.15).
- Rods and cones are linked to neurons in the retina that perform the initial processing of visual information. The processed signal is sent via the optic nerve through the lateral geniculate nuclei to the visual cortex (Figures 39.16 and 39.17).

Animation: Eye structure

Animation: Visual accommodation

Animation: Organization of cells in the retina

Animation: Receptive fields

Animation: Pathway to visual cortex

Animation: Focusing problems

39.5 Chemoreceptors

- Chemoreceptors respond to the presence of specific molecules in the environment. In vertebrates, they form parts of receptor organs for taste (gustation) and smell (olfaction).
- Taste receptors detect molecules from food or other objects that come into direct contact with the receptor and are used primarily to identify foods (Figures 39.18 and 39.20).
- Olfactory receptors detect molecules from distant sources; besides identifying food, they are used to detect predators and prey, identify family and group members, locate trails and territories, and communicate (Figures 39.19 and 39.21).

Animation: Olfactory pathway

Animation: Taste receptors

39.6 Thermoreceptors and Nociceptors

- Thermoreceptors, which consist of free nerve endings located at the body surface and in limited numbers in the body interior, detect changes in body temperature.
- Nociceptors, located on both the body surface and interior, detect stimuli that can damage body tissues. Information from these receptors is integrated in the brain into the sensation of pain.

Animation: Sensory receptors in the human skin

Animation: Referred pain

39.7 Electroreceptors and Magnetoreceptors

- Some vertebrates have electroreceptors that detect electrical currents and fields, or magnetoreceptors that detect magnetic fields (Figure 39.23).

Questions

Self-Test Questions

1. The frequency of a blast from a nearby ambulance siren can cause a dog to howl in pain. Activated under this circumstance are:
   a. thermoreceptors and chemoreceptors.
   b. photoreceptors and nociceptors.
   c. mechanoreceptors and nociceptors.
   d. chemoreceptors and mechanoreceptors.
   e. photoreceptors and chemoreceptors.
2. Two common side effects of Hansen's disease (leprosy) are a permanent numbness in the hands, feet, and buttocks of affected people and a loss of perception of their spatial position. Affected are:
   a. mechanoreceptors.
   b. adapting receptors.
   c. pH change receptors.
   d. the vestibular apparatus.
   e. vibration detecting systems.
3. Neuromasts are best described as:
   a. nonadapting pain receptors.
   b. components of the fish lateral line system.
   c. statoliths that detect motion.
   d. motor axons that activate motion.
   e. cupulas that detect vibrations.
4. Structures are activated by sound waves in the vertebrate ear in the following order:
   a. oval window, tympanum, semicircular canals, Golgi tendon organ, incus, malleus, stapes.
   b. organ of Corti, malleus, incus, stapes, auditory nerve, eardrum.
   c. eustachian tube, round window, vestibular canal, tympanic canal, cochlear canal, oval window, pinna.
   d. basilar membrane, tectorial membrane, otoliths, utricle, saccule, malleus, cochlea.
   e. pinna, tympanic membrane, malleus, incus, stapes, oval window, cochlear duct.

5. The following situation is associated with movement and position in the human body:
   a. Statoliths in statocysts bend sensory hairs and trigger action potentials.
   b. If sensory hairs in the utricle are oriented horizontally and those in the saccule are oriented vertically, the person is lying down.
   c. When the head rotates, the endolymph in the semicircular canal pulls the cupula with it to activate sensory hair cells.
   d. Displacement of the utricle and saccule generates action potentials.
   e. If the body is spinning at a constant rate and direction, the cupula is displaced and action potentials are initiated.
6. The difference between the vertebrate eye and the cephalopod eye is that the vertebrate eye has:
   a. an iris surrounding the pupil, whereas in cephalopods the pupil surrounds the iris.
   b. a lens that changes shape when focusing, whereas in cephalopods the lens moves back and forth to focus.
   c. a retina that moves in the socket when recording the image, whereas in cephalopods the retina changes shape when stimulated.
   d. a pupil that shrinks in size in bright light, whereas cephalopods have a pupil that enlarges in bright light.
   e. retinal synthesized from vitamin A, whereas cephalopods lack retinal.
7. Which of the following events does not occur during light absorption in the vertebrate eye?
   a. The retinal component of rhodopsin changes from *cis* to *trans* form.
   b. Rhodopsin, a G membrane-embedded protein, triggers a signal transduction pathway to close Na^+ channels in the plasma membrane.
   c. The light stimulus passes from rods and cones to bipolar cells and horizontal cells and then to ganglion cells, whose axons compose the optic nerve.
   d. As light absorption increases, the rhodopsin response causes an increase in the release of neurotransmitters.
   e. When integrating information across the retina, horizontal cells connect the rods and cones, and amacrine cells join with the bipolar cells and ganglion cells.
8. The variety of color seen by humans is directly dependent upon the:
   a. activation of three different photopsins in cones.
   b. transmission of an image to separate brain hemispheres by the optic chiasm.
   c. transmission of impulses from rods across the lateral geniculate nuclei.
   d. lateral inhibition by amacrine cells.
   e. light stimulation of all photoreceptor types equally.
9. In terrestrial animals:
   a. the hairs of taste receptors are derived from cilia and contain microtubules.
   b. the hairs of smell receptors are derived from microvilli and contain microfilaments.
   c. signals from taste receptors are relayed to the temporal lobes.
   d. information from olfactory receptors is processed in the parietal lobes.
   e. connections from the olfactory bulbs lead to the limbic system.
10. In the human response to temperature or pain:
   a. all three transient receptor potential (TRP) gated Ca^{2+} channels act as pain receptors.
   b. cold receptors are activated between 27°C and 37°C.
   c. pain receptors decrease the rate at which they send out action potentials if the pain is constant.
   d. nociceptors, activated by capsaicin in the mouth and nose, can sense pain.
   e. the CNS releases glutamate or substance P to dull the pain sensation.

Questions for Discussion

1. Humans have about 200 million photoreceptors in two eyes, and about 32,000 sensory hair cells in two ears. About 3% of the somatosensory cortex is devoted to hearing, whereas roughly 30% of it is devoted to visual processing. Suggest an explanation for these differences from the perspective of natural selection and adaptation.
2. In owls and many other birds of prey, the fovea is located toward the top of the retina rather than at the center as in humans. This arrangement correlates with the birds' hunting behavior, in which they look down when they fly, scanning the ground for a meal. With this arrangement in mind, why do you think the standing owl in the picture is turning its head upside down?


Chase Smith

3. A patient made an appointment with her doctor because she was experiencing recurrent episodes of dizziness. Her doctor asked questions to distinguish whether she had sensations of lightheadedness, as if she were going to faint, or vertigo, as if she or objects near her were spinning around. Why was this clarification important in the evaluation of her condition?

Experimental Analysis

The fruit fly *Drosophila melanogaster* can distinguish a large repertoire of odors in the environment. Their response may be to move toward food or away from danger. Moreover, particular odors play an important role in their mating behavior. The olfactory organs of a fruit fly are the antennae and an elongated bulge on the head called the maxillary pulp. Because of the ease with which fruit fly genes can be manipulated, identifying and studying their olfactory receptors likely would contribute significantly to our understanding of neural pathways of odor recognition more generally. How could you identify candidate fruit fly genes that encode components of olfactory receptors?

Evolution Link

In 2005, researchers took saliva and blood samples from six cats, including domestic cats, a tiger, and a cheetah, and found that all have a defective gene for one of the two chemoreceptor proteins needed to identify food as sweet. (The scientists conjecture that the lack of a sweet tooth may explain why cats are finicky eaters.) What are the evolutionary implications of the finding?

How Would You Vote?

Noise pollution from commercial shipping and other human activities generates low-frequency sounds that are believed to interfere with the acoustical signals that whales use for navigation, location of food, and communication. To what extent should we limit these activities to protect whales against potential harm? Would you support banning activities that exceeded a certain noise level from U.S. territorial waters? If so, how would you get other nations to do the same? Go to www.thomsonedu.com/login to investigate both sides of the issue and then vote.