35 SENSORY PERCEPTION

A Whale of a Dilemma

Imagine yourself in the sensory world of a whale. You are 200 meters below the ocean surface, where little sunlight penetrates, so you cannot see well as you move through the water. Many fishes detect the wavelike motion of your body with their lateral line system, which responds to differences in water pressure. Like other fishes, they also use chemicals dissolved in the water as navigational cues. However, a whale has no lateral line, it has few chemical receptors, and its olfactory lobes are greatly reduced.

So how does a whale sense where it is going? It uses sounds—acoustical cues. Water is an ideal medium for transmitting sound waves, which move five times faster in water than in air. Also, compared to mammals on land, whales have far more neurons that collect and integrate auditory information.

Unlike humans, whales do not have external ear flaps that collect sound waves. Some species do not even have a canal that leads from the body surface to each middle ear. Other species have ear canals packed with wax. How, then, do whales hear? Their jaws pick up vibrations traveling through water. The vibrations are transmitted from the jaws, through a layer of fat, to a pair of middle ears.

Whales use sound to communicate, locate food, and map out the contours of their surroundings. A killer whale or some other species of toothed whale uses *echolocation*. It emits high-pitched sounds and listens as echoes bounce off objects, including prey. Its ears are especially sensitive to high-frequency sounds. Baleen whales, including the humpback whale, make very low-pitched sounds that can travel across an entire ocean basin. Their ears are attuned to sounds in this range.

The ocean is becoming a lot noisier, and the superb acoustical adaptations of whales put them at risk. In 2001, for instance, a number of whales beached themselves near an area where the United States Navy was testing a sonar system (Figure 35.1). This sonar system uses echoes of low-frequency sounds to detect a new generation of missile-launching submarines that can run in near-silence. Humans cannot hear the intense sounds. Whales can.

Autopsies showed that the beached whales had blood in their ears and in acoustic fat. Apparently the intense sounds—as high as 235 decibels—made the whales race to the surface in fear. As they fled, the rapid change in pressure damaged their internal tissues.

Figure 35.1 A few children drawn to one of the whales that beached itself during military testing of a new sonar system. Of sixteen stranded whales, six died on the beach. Volunteers pushed the others out to sea, and their fate is unknown.

IMPACTS, ISSUES

Public outcry halted the deployment of the new sonar system. Testing continues, however, because the threat of stealth attacks against the United States is real.

Besides, noise pollution from commercial shipping may be a more pervasive problem for whales. Each day, huge tankers generate low-frequency sounds that frighten whales or drown out acoustical cues. Realistically, the global shipping of oil and other resources that nations require is not going to stop. If research shows that whales are at risk, will those same nations be willing to design and deploy new tankers that minimize the damage?

With this chapter we turn to sensory systems. With these organ systems, animals receive signals from inside and outside the body, then decode them in ways that give rise to awareness of sounds, sights, odors, and other sensations. Most systems contain sensory neurons, nerve pathways, and specialized brain regions. Depending on the type and the numbers of sensory receptors, animals sample the environment in different ways, and they differ in their perception of it. How to meet pressing human needs while respecting sensory diversity can be something of a dilemma.

Watch the video online!

How Would You Vote?

Shipping and other human activities generate an underwater ruckus. 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 United States territorial waters? If so, how would you get other nations to do the same? See BiologyNow for details, then vote online.

Key Concepts

HOW SENSORY PATHWAYS WORK

Sensory systems are front doors of the nervous system. Each has sensory receptors, nerve pathways to the brain, and brain regions that receive and process sensory input. A stimulus is a form of energy that activates a specific type of sensory receptor. Information becomes encoded in the number and frequency of action potentials sent to the brain along particular nerve pathways. Section 35.1

SOMATIC SENSES

Touch, pressure, pain, temperature, and muscle sense are somatic sensations, which start at mechanoreceptors in skin, muscles, and the wall of internal organs. Section 35.2

CHEMICAL SENSES

Olfaction (smell) and taste require chemoreceptors, which bind molecules of specific substances that have become dissolved in the fluid bathing them. Section 35.3

BALANCE AND HEARING

The sense of balance starts at mechanoreceptors, which detect gravity, velocity, acceleration, and other forces that affect the position and motion of the body or its parts.

In vertebrates, the sense of hearing involves structures that collect, amplify, and sort out pressure variations caused by sound waves. The variations trigger action potentials in mechanoreceptors called hair cells. Sections 35.4, 35.5

VISION

All organisms have light-sensitive pigments, but vision requires eyes with a dense array of photoreceptors and image formation in the brain. Cephalopod and vertebrate eyes are like cameras. They collect and process data on the distance, shape, position, brightness, and movement of visual stimuli. A sensory pathway starts at the retina and ends in the visual cortex. Sections 35.6–35.9

Links to Earlier Concepts

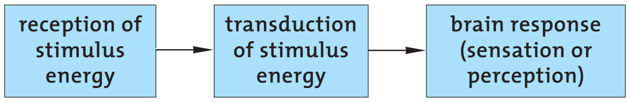
We did not expect you to memorize Chapter 34, but you will find yourself drawing repeatedly upon its content. We provide ample cross-references to specific sections. You may wish to reflect on the properties of light (7.1) and how lenses bend light (4.2). You will come across specific cases of signal transduction pathways (28.5). You will reflect again on the evolution of fast-moving cephalopods (25.9) and on the challenges facing the first vertebrates on land (26.1, 26.2).

35.1 Overview of Sensory Pathways

LINKS TO SECTIONS 34.2, 34.7

Sensory systems are portions of a nervous system. Each typically consists of cell communication pathways from sensory neurons and nerves to specific brain regions.

Reflect on Section 28.5. In all *sensory* communication pathways, energy from a stimulus activates receptors, which transduce it to a form that travels to the brain and may trigger a sensation or perception in response:



A **stimulus** (plural, stimuli) is a form of energy that activates receptor endings of a sensory neuron (Section 34.2). That energy is transduced to the electrochemical energy of action potentials—the messages by which brain cells continually monitor and respond to the presence or absence of stimuli. The brain's responses are *sensations*, or conscious awareness of a stimulus. A sensation is not the same as *perception*, which is an understanding of what a sensation means.

The **mechanoreceptors** detect forms of mechanical energy: changes in pressure, position, or acceleration. Figure 35.2 shows an example. **Pain receptors** detect damage to tissues. **Thermoreceptors** are sensitive to heat or cold. **Chemoreceptors** detect chemical energy of substances dissolved in the fluid bathing them. **Osmoreceptors** detect changes in the solute levels of some body fluid. **Photoreceptors** detect differences in the energy of visible and ultraviolet light (Table 35.1).

Regardless of the differences, all sensory receptors transduce stimulus energy into action potentials. But action potentials are not like an ambulance siren; they do not vary in amplitude. How, then, does the brain assess each stimulus? It assesses *which* nerve pathways are carrying action potentials, the *frequency* of action potentials traveling on each axon in the pathway, and the *number* of axons recruited by the stimulus.

First, an animal's brain is prewired, or genetically programmed, to interpret action potentials in certain

Table 35.1 Major Categories of Sensory Receptors

Category	Examples	Stimulus
Mechanoreceptors		
Touch, pressure	Certain free nerve endings and Pacinian corpuscles in skin	Mechanical pressure against body surface
Baroreceptor	Arterial baroreceptors (Figure 38.11)	Pressure changes in the fluid that bathes them
Stretch	Muscle spindle in skeletal muscle	Stretching
Auditory	Hair cells in organ inside ear	Vibrations (sound or ultrasound waves)
Balance	Hair cells in organ inside ear	Movement of some body fluid in confined space
Pain Receptors (Nociceptors)*	Certain free nerve endings	Tissue damage (e.g., distortions, burns)
Thermoreceptors	Certain free nerve endings	Change in temperature (heating, cooling)
Chemoreceptors		
Internal chemical sense	Carotid bodies in blood vessel wall	Substances (O_2, CO_2, etc.) dissolved in extracellular fluid
Taste	Taste receptors of tongue	Substances dissolved in saliva, etc.
Smell	Olfactory receptors of nose	Odors in air, water
Osmoreceptors	Hypothalamic osmoreceptors (Section 42.4)	Change in solute concentration (water volume) of the fluid that bathes them
Photoreceptors		
Visual	Rods, cones of eye	Wavelengths of light

* Extremely intense stimulation of any sensory receptor also may be perceived as pain.

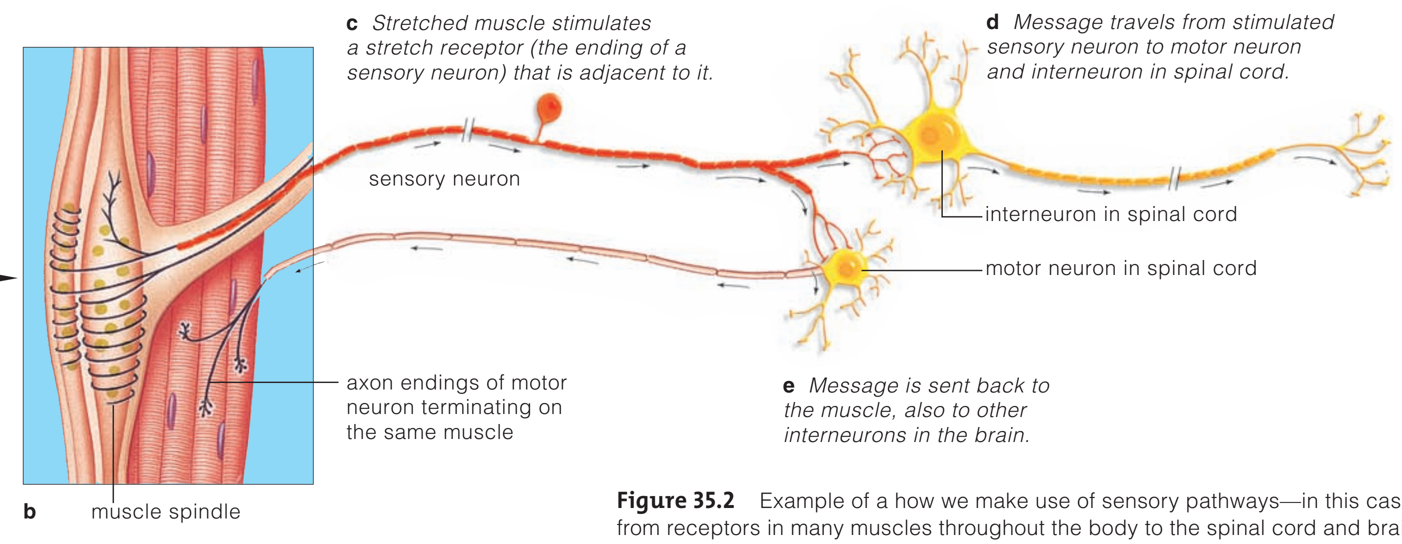


Figure 35.2 Example of a how we make use of sensory pathways—in this case, from receptors in many muscles throughout the body to the spinal cord and brain.

ways. That is why you can "see stars" after an eye gets poked, even in a dark room. Many photoreceptors in the eye were mechanically disturbed and sent signals down one of two optic nerves to the brain, which will interpret any signals from an optic nerve as "light."

Second, a strong signal makes receptors fire action potentials more often and longer. The same receptor might detect the sound of a throaty whisper or a wild screech. The brain interprets such differences through variations in the frequency of signals (Figure 35.3).

Third, a strong stimulus recruits far more sensory receptors, compared to a weak stimulus. Gently tap a spot of skin on one of your arms and you will activate a few receptors. Press harder on the same spot and you will activate more receptors in a larger area. A big disturbance translates into action potentials in many sensory axons, and the brain interprets the combined activity as an increase in stimulus intensity.

In certain cases, the frequency of action potentials declines or ends even when the stimulus continues at constant strength. For instance, after you put on a sock, your awareness of the pressure the sock is exerting on your skin ceases. Such a diminishing response to an ongoing stimulus is called **sensory adaptation**.

Some mechanoreceptors adapt fast to a sustained stimulus and only signal its onset and removal. Other receptors adapt more slowly to a stimulus or not at all; they continue to keep the brain informed about it.

The gymnast in Figure 35.2 is holding his position in response to signals from his skin, skeletal muscles, joints, tendons, and ligaments. For example, how fast and how far a muscle stretches depends on activation of stretch receptors in muscle spindles (Section 34.7). By responding to changes in the length of muscles, the brain helps him maintain his balance and posture.

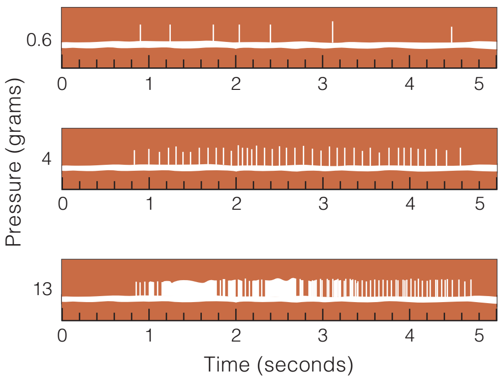


Figure 35.3 ***Animated!*** Recordings of action potentials from a pressure receptor with endings in a human hand. They correspond to variations in stimulus strength. A thin rod was pressed against skin with the amount of pressure indicated to the left of each diagram. Vertical bars above each thick horizontal line record individual action potentials. Increases in their frequency correspond to increases in the stimulus strength.

In sections to follow, you will consider the *somatic* sensations that arise from sensory receptors located in tissues throughout the body. You also will consider *special senses*, such as taste, smell, balance, hearing, and vision. These senses depend on receptors that are restricted to certain body parts, such as ears and eyes.

A sensory system has sensory receptors for specific stimuli, nerve pathways that conduct information from receptors to the brain, and brain regions that receive the information.

The brain assesses a stimulus according to which nerve pathway is signaling it, the frequency of action potentials from the pathway, and the number of axons that the stimulus recruited.

35.2 Somatic Sensations

LINKS TO SECTIONS 34.5, 34.7, 34.8, 34.10

Somatic sensations are responses to receptors near the body surface, in skeletal muscles, and in the wall of internal organs. These receptors are most highly developed in birds and mammals. Fishes and amphibians have only a few.

Somatic sensations arise in the cerebrum's outer layer of gray matter, the cerebral cortex. In its sensory areas, interneurons are organized like a map corresponding to the body surface (Figure 35.4). The largest regions of the map correspond to body parts having the most sensory acuity, such as fingers, thumbs, and lips. Less sensitive regions are represented by fewer neurons.

RECEPTORS NEAR THE BODY SURFACE

Mammals discern sensations of touch, pressure, cold, warmth, and pain near the body surface. Regions with the greatest number of sensory receptors, such as the fingertips and tip of the tongue, are most sensitive to stimulation. Less sensitive regions, such as the back of the hand, do not have nearly as many.

Free nerve endings are the unmyelinated or thinly myelinated, branched endings of sensory neurons in skin and internal tissues. These nerve endings are the simplest kinds of mechanoreceptors, thermoreceptors, and pain receptors. All adapt slowly to stimulation. One subpopulation gives rise to a sense of prickling pain, as when you jab a finger with a pin. Another contributes to itching or warming sensations that are responses to chemicals, such as histamine. Two kinds are most sensitive to temperatures that are higher and lower than the body's normal core temperature. One mechanoreceptive type coils around hair follicles and detects the motion of hair (Figure 35.5).

Encapsulated receptors near the body surface also detect somatic sensations. Four types are called the Meissner's corpuscle, bulb of Krause, Ruffini endings, and Pacinian corpuscle (Figure 35.5). The Meissner's corpuscle is notably abundant in the fingertips, lips, eyelids, nipples, and genitals. It can adapt very slowly to low-frequency vibrations. The bulb of Krause, one of the thermoreceptors, is activated at 20°C (68°F) or lower. Below about 10°C, it contributes to painful freezing sensations. Slowly adapting Ruffini endings detect steady touch and pressure, and temperatures above 45°C (113°F). The Pacinian corpuscle is sensitive to fine textures. It occurs in the dermis, near freely movable joints, and in some internal organs. Its outer capsule is an onionlike layering of plasma membrane with fluid-filled spaces in between (Figure 35.5). The layering is most sensitive to rapid pressure changes brought on by touch and vibrations.

MUSCLE SENSE

You read about stretch receptors in muscle spindle fibers in Section 34.7. These receptors increase their firing rate as a muscle stretches. Along with receptors in the skin and near joints, they signal the brain about the positions of the body's limbs.

PAIN

Pain is the perception of a tissue injury. *Somatic* pain is a response to signals from pain receptors in skin, skeletal muscles, joints, and tendons. *Visceral* pain is associated with internal organs. It a response to high chemical stimulation, muscle spasms, muscle fatigue, excessive distension of the gut, inadequate blood flow to organs, and other abnormal conditions.

Superficial somatic pain arises at or near the skin surface. It is sharp or prickling and often does not last long. Deep somatic pain arises deeper in the skin or in

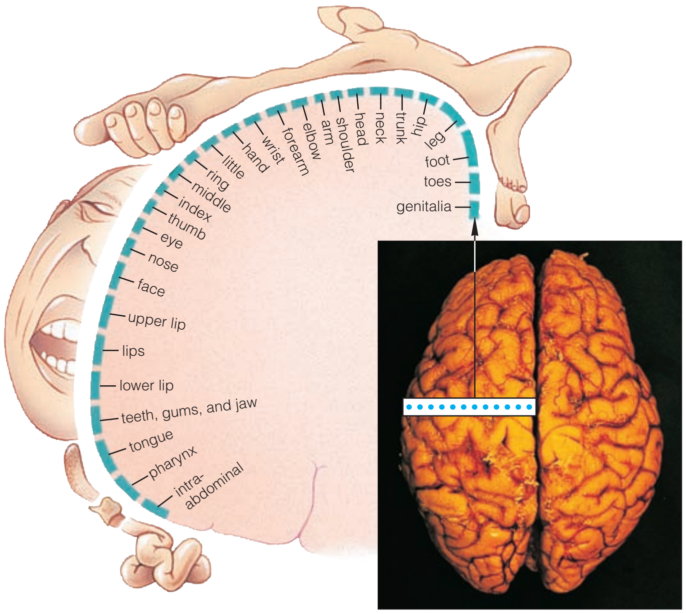
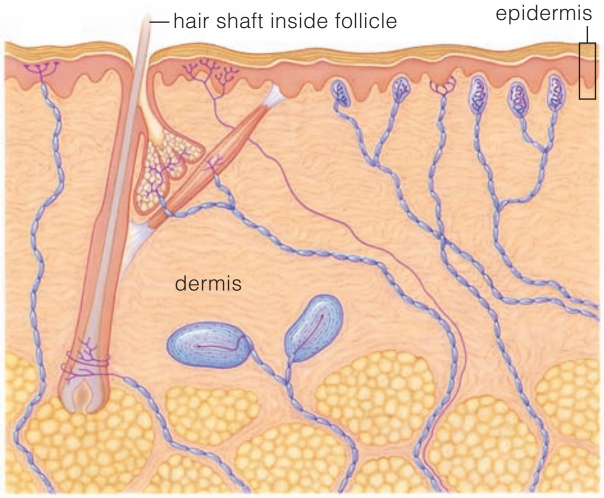


Figure 35.4 Differences in representation of different body parts in the primary somatosensory cortex of a human. This region is a strip of cerebral cortex, about an inch wide, from the top of the head to above the ear. Compare Section 34.10.



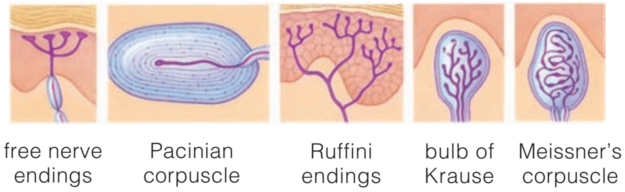


Figure 35.5 ***Animated!*** A sampling of receptors in human skin.

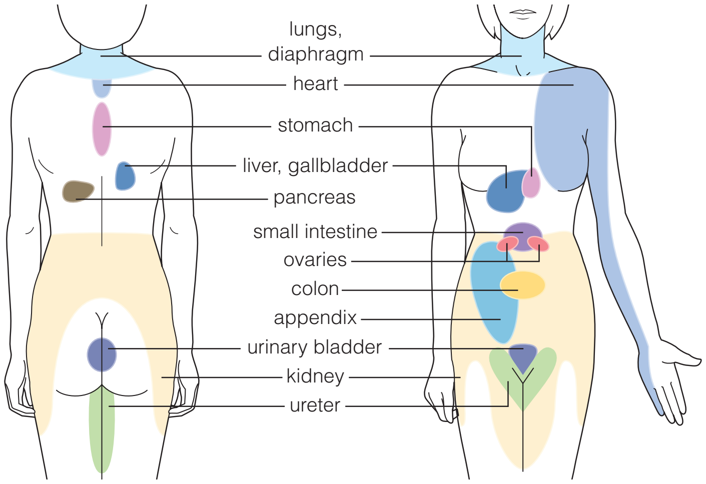


Figure 35.6 Referred pain. Receptors in some internal organs detect painful stimuli. Instead of localizing the pain at the organs, the brain projects the sensation to the skin areas indicated.

muscles or joints. It is more diffuse and lasts longer. This is also the case for visceral pain. We characterize both as burning or gnawing pain, or a dull ache.

When cells are injured, they release chemicals that activate neighboring pain receptors. The most potent, bradykinins, open the floodgates for an outpouring of histamine, prostaglandins, and other participants in inflammatory responses (Section 39.3). They also may bind with and activate pain receptor endings.

Signals from pain receptors enter the spinal cord and cause the release of a neuromodulator, substance P, which activates neurons that can signal the sensory cortex. There, neurons assess the intensity and type of pain. Different signals rouse the body and mediate emotional responses. They bring about the release of natural opiates—endorphins and enkephalins—that lower pain perception (Section 34.5).

Emotional states, cultural factors, and possibly age influence pain tolerance (older people tend to handle it better). Intense or long-lasting pain also may lead to *hyperalgesia*, a condition in which pain is amplified. For example, pain gets worse when someone with a bad sunburn steps into a hot shower.

REFERRED PAIN

Pain perception depends on the brain's capacity to identify the affected tissue and project a sensation back to it. Get smacked in the face with a snowball and you "feel" the contact on facial skin. But sometimes the brain projects pain from internal organs to skin. Such *referred pain* is the perception of visceral sensations as somatic sensations. For instance, a heart attack often is wrongly perceived as pain radiating from the chest wall, from the neck, and along the left shoulder and arm (Figure 35.6). How can the brain make such a bad mistake? We find the answer in the construction of the nervous system. Sensory inputs from skin and certain internal organs enter the same segments of the spinal cord (Section 34.8). The skin encounters more painful stimuli than internal organs do, so its signals travel more often along the somatic pathway to the brain. The brain may interpret most sensory input as arriving from skin—the more frequent source.

Referred pain is not the same as the *phantom pain* reported by amputees. They often sense the presence of a missing body part as if it were still there. In some undetermined way, severed sensory nerves continue to respond to the amputation. The brain projects the pain back to the missing part, past the healed region.

Sensory receptors near the body surface and in internal organs detect touch, pressure, temperature, pain, motion, and positional changes of body parts.

35.3 Sampling the Chemical World

LINKS TO SECTIONS 2.6, 34.10

In the remainder of this chapter, we will sample the special senses, which have receptors in specific organs. They include smell, taste, balance, hearing, and vision.

The sensory pathways of olfaction (smell) and taste start at chemoreceptors, which become activated by binding molecules of a substance that is dissolved in the fluid bathing them. In both sensory pathways, a stimulus can trigger signals that travel along nerve expressways through the thalamus. The signals end up in the cerebral cortex. There, perceptions of certain stimuli take shape and undergo fine-tuning. Sensory information also reaches the limbic system, which acts to integrate it with emotional states and with stored memories (Section 34.10).

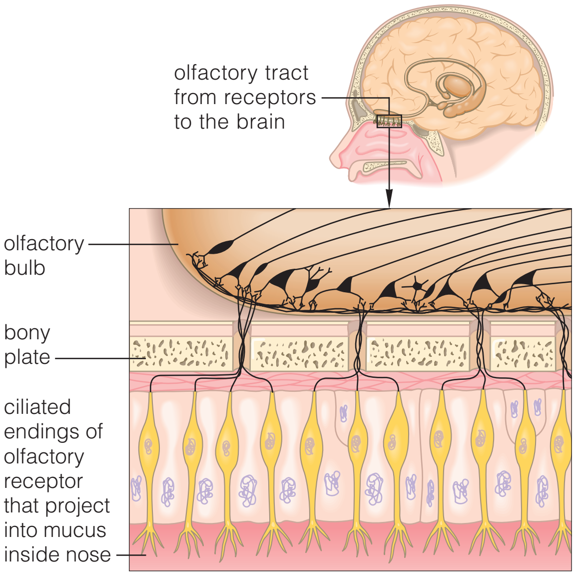


Figure 35.7 Pathway from sensory endings of olfactory receptors in the human nose to the cerebral cortex and the limbic system. Receptor axons pass through holes in a bony plate between the lining of the nasal cavities and the brain.

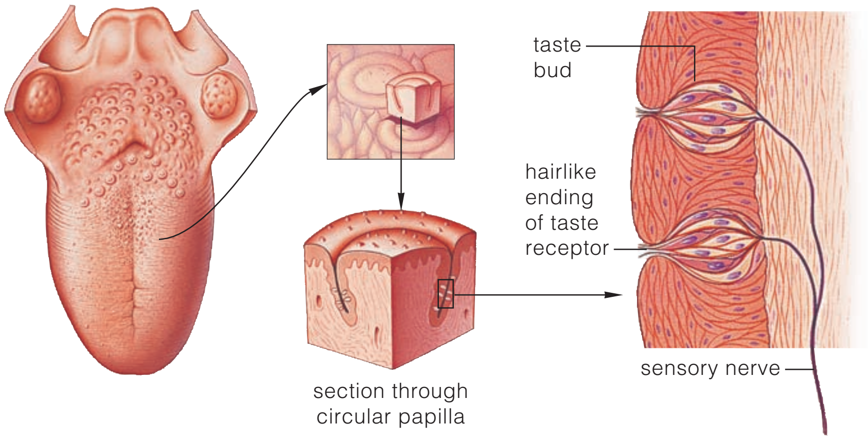


Figure 35.8 Taste receptors in the human tongue. The structures called circular papillae ring epithelial tissue that contains taste buds. A human tongue has approximately 10,000 of these sensory organs, each of which has as many as 150 chemoreceptors.

Olfactory receptors fire off signals when they are exposed to water-soluble or volatile (easily vaporized) chemicals. The lining of your nose has about 5 million olfactory receptors. That of a bloodhound nose has more than 200 million. Receptor axons lead into one of two olfactory bulbs. In these small brain structures, axons synapse with clusters of cells that sort out the components of a scent. From there, information flows along an olfactory tract to the cerebrum, where it is further processed (Figure 35.7).

Many animals use olfactory cues to navigate, find food, and communicate socially, as with pheromones. As later chapters explain, **pheromones** are signaling molecules secreted by one individual that change the social behavior of other individuals of its species. As one example, olfactory receptors on the antennae of a male silk moth help him find a pheromone-secreting female that may be more than a kilometer upwind.

In reptiles and most mammals (but not primates), a cluster of sensory cells forms a *vomeronasal organ* that detects pheromones. Humans have a reduced version of this organ about 12.7 millimeters (1/2 inch) inside the nose. It may or may not be functional, but recent studies show that human females and males manage to respond to certain pheromones (Chapter 49).

Different animals have **taste receptors** on antennae, legs, or tentacles, or inside the mouth. On the surface of your mouth, throat, and upper part of the tongue especially, chemoreceptors are located in about 10,000 sensory organs called taste buds (Figure 35.8). Fluids in the mouth reach the receptors by entering a pore in each taste bud.

You perceive many tastes, but all are a combination of five main sensations: sweet (elicited by glucose and the other simple sugars), sour (acids), salty (NaCl or other salts), bitter (plant toxins, including alkaloids), and *umami* (elicited by amino acids such as glutamate, which has a savory taste typical of aged cheese and meat). With its strong savory taste and no texture or odor of its own, MSG (monosodium glutamate) has become a common flavor enhancer.

The senses of smell and taste start at chemoreceptors. Both involve sensory pathways that lead to processing regions in the cerebral cortex and in the limbic system.

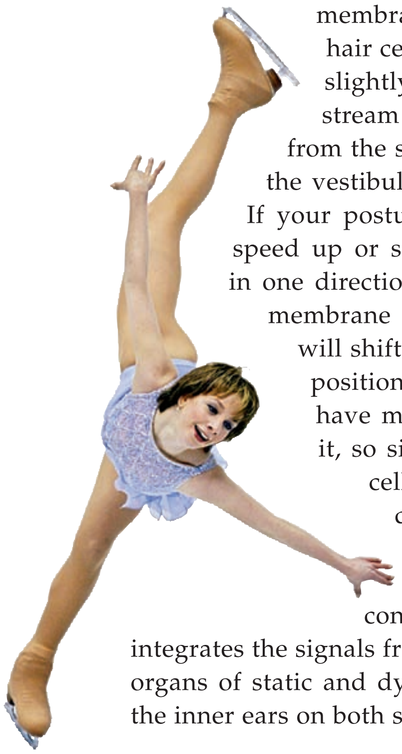
35.4 Keeping the Body Balanced

All animals assess and respond to displacements from equilibrium, when the body is balanced in relation to gravity, acceleration, and other forces that may affect its position and movement. Even brainless jellyfishes right themselves when turned upside down.

The first organs of equilibrium evolved in fishes. You have a pair of them, one inside each ear. A **vestibular apparatus** in each ear consists of two sacs—the utricle and the saccule—along with three semicircular canals (Figure 35.9). The sacs and canals interconnect into a continuous, fluid-filled system. In this system, many mechanoreceptors are stimulated whenever you move about or rotate your head.

Inside the bulging base of a semicircular canal is an organ of *dynamic* equilibrium. It has a gelatinous mass into which hair cells, a type of mechanoreceptor, project. Any rotation of the head displaces fluid in the canals. Hydrostatic pressure exerted by the moving fluid shifts the gelatinous mass, which in turn bends the hair cells. The bending causes signals to flow from sensory neurons to the vestibular nerve, which carries signals about motion to the brain.

Inside each utricle and saccule is an organ of *static* equilibrium. These organs send messages to the brain about how the head is oriented relative to the ground. In each organ, a thick membrane rests on hair cells that project upward from the floor of the sac. That membrane contains a mass of crystals, which weigh it down. When your head is held upright, the weighted membrane presses down on hair cells, which bends them slightly. This sends a steady stream of action potentials from the sensory neurons along the vestibular nerve to the brain. If your posture changes or if you speed up or slow down movement in one direction, the position of the membrane above these hair cells will shift. Depending upon the position, a hair cell will now have more or less weight on it, so signaling from sensory cells will step up or slow down. To interpret the body's posture and movement, the brain constantly compares and integrates the signals from sensory cells in all organs of static and dynamic equilibrium in the inner ears on both sides of the head.



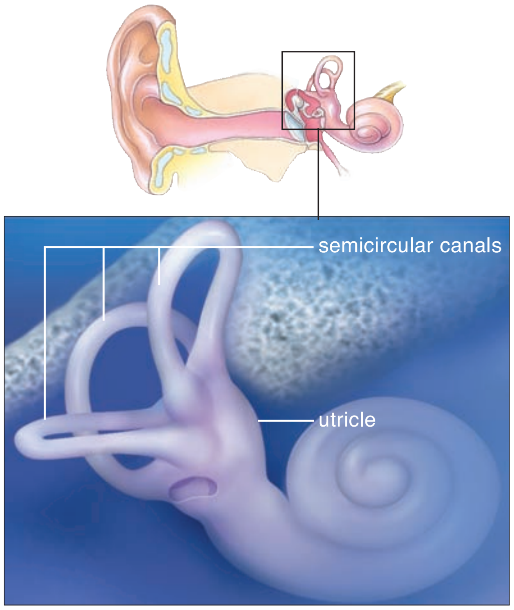


Figure 35.9 The vestibular apparatus inside the human ear. Organs of dynamic and static equilibrium inside this fluid-filled organ contribute to the sense of balance.

At the same time, the brain evaluates input from receptors in the skin, joints, and tendons. Integration of all the information allows your brain to control eye muscles and keep the visual field in focus, even as your position shifts or your head rotates. Integration also helps maintain awareness of the body's position and motion in space, as demonstrated by champion figure skater Sarah Hughes.

A stroke, an inner ear infection, or loose particles in the semicircular canals cause *vertigo*, a sensation that the world is moving or spinning around. Vertigo also arises from conflicting sensory inputs, as when you stand on the top viewing deck of a skyscraper and look down. The vestibular apparatus reports that you are motionless even as your eyes report that your body is floating in space far above the ground.

Mismatched signals also give rise to the dizziness and nausea of *motion sickness*. Passengers in a vehicle moving fast on a hilly, curvy road experience changes in acceleration and direction that scream "motion" to each vestibular apparatus. At the same time, signals from the eyes about objects inside of the vehicle tell the brain that the body is standing still. Being the driver minimizes motion sickness because a driver is forced to focus on the scenery rushing past, so visual signals are consistent with vestibular signals.

Organs of equilibrium help keep the body balanced in relation to gravity, velocity, acceleration, and other forces that influence its position and movement.

35.5 Collecting, Amplifying, and Sorting Out Sounds

LINKS TO SECTIONS
26.1, 26.4, 28.5

Many arthropods and most vertebrates perceive sounds; they have a sense of ***hearing****. Land vertebrates have ears that capture and sort out sound waves traveling in air.*

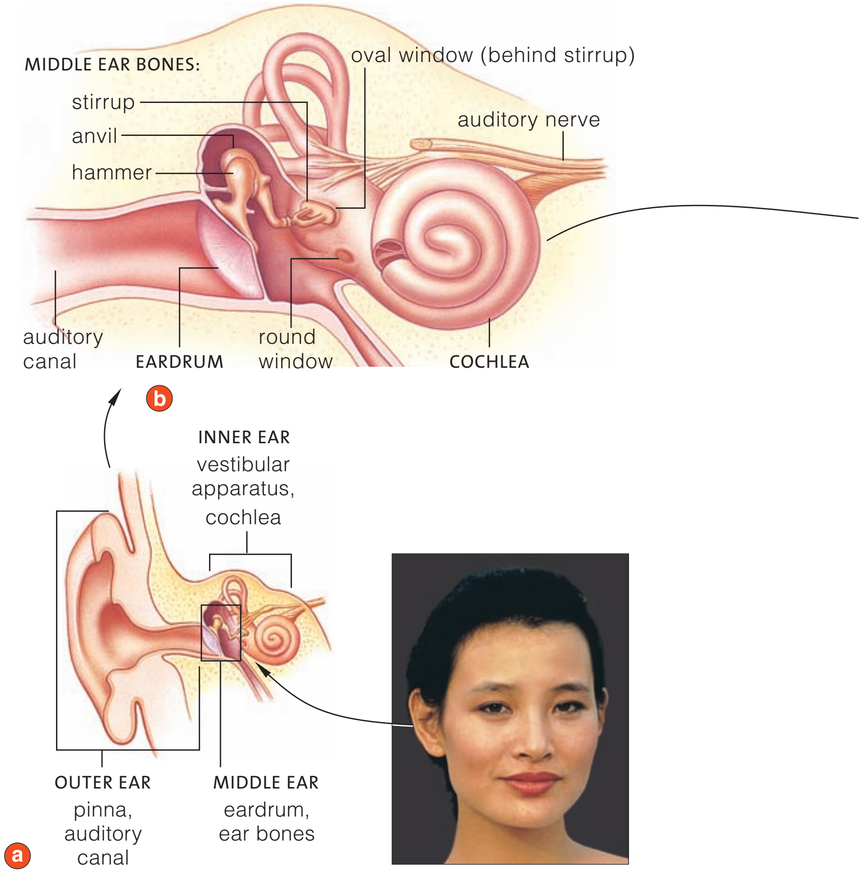


Figure 35.11 ***Animated!*** Components of the human ear.

PROPERTIES OF SOUND

All sounds are forms of mechanical energy. They arise when a vibrating object causes pressure variations in air, water, or some other medium. We can represent pressure variations as wave forms. The *amplitude* of a sound corresponds to loudness (intensity), which we measure in decibels. Every ten decibels is a tenfold increase above the faintest sounds that humans hear. A sound's *frequency* is the number of wave cycles per second. Each cycle extends from the peak (or trough) of one wave to the peak (or trough) of the next in line. The more cycles per second, the higher the frequency and the perceived pitch (Figure 35.10).

Unlike a tuning fork's pure tone, most sounds are combinations of waves of different frequencies. Their timbre, or quality, varies. Differences in timbre make your voice nasal or deep.

THE VERTEBRATE EAR

Water readily transfers vibrations to body tissues. As you might expect, fishes do not require elaborate ears to detect them. However, sounds spread out in air. When some vertebrates invaded land, the capacity to collect and then amplify vibrations became important (Sections 26.1, 26.2). Some structures evolved in ways that trap sound waves moving through air and that also amplify and make sense of them.

Focus on the structures of the paired human ears (Figure 35.11*a*). The *outer* ear is adapted for gathering sounds from air, as it is for most mammals. Its pinna is a much-folded flap of cartilage, sheathed in skin, that projects from the side of the head. An auditory canal leads from the pinna into the middle ear.

The *middle* ear amplifies and transmits air waves to the inner ear. It has an eardrum, which originated in early reptiles as a shallow depression on each side of the head. The "drum," a thin membrane, vibrates fast in response to pressure waves. Behind the drum is an air-filled cavity and small bones: the hammer, anvil, and stirrup (Figure 35.11*b*). By interacting, the bones transmit the force of sound waves from the eardrum to a smaller surface: the oval window. The "window" is an elastic membrane in front of the inner ear.

The *inner* ear, remember, has a vestibular apparatus (Section 35.4). It also has a **cochlea**, which in humans is a pea-sized, fluid-filled structure that resembles a coiled snail shell (the Greek *koklias* means snail). The transduction of waves of sound into action potentials takes place inside the cochlea (Figure 35.11*c*).

When sound waves make the stirrup vibrate, this middle earbone pushes against the oval window. It transmits pressure waves to the fluid in two of three cochlear ducts (scala vestibuli and scala tympani). The waves end at another membrane, the round window, which bows inward and outward in response.

The third cochlear duct sorts out pressure waves. Its wall, a *basilar* membrane, is stiff and narrow near the oval window, then it broadens and becomes more

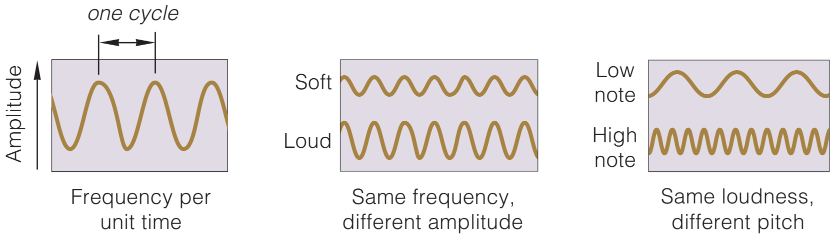
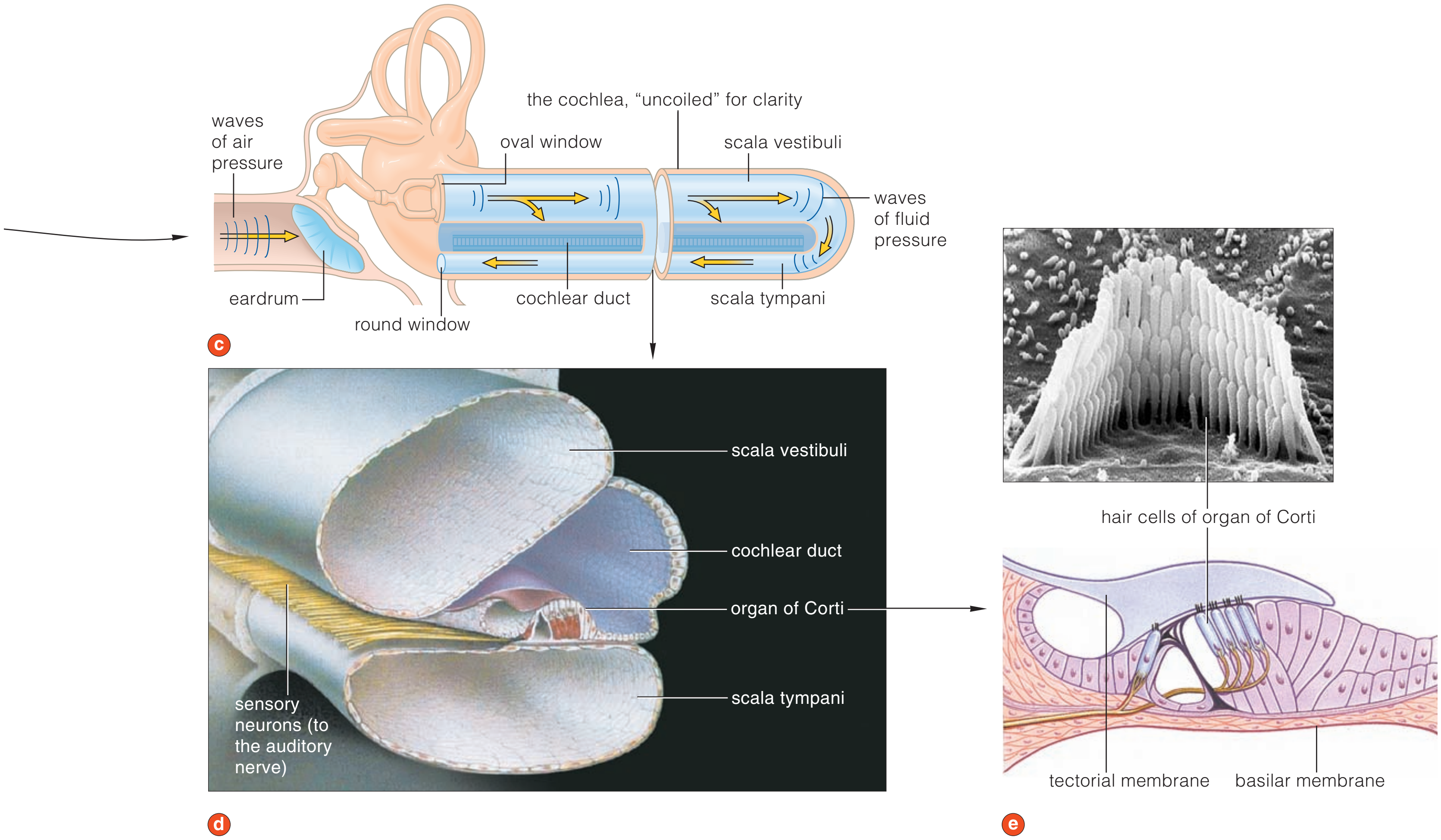


Figure 35.10 ***Animated!*** Wavelike properties of sound.



flexible deeper in the coil. Because of the differences, frequency variations have different effects along the length of the basilar membrane. High-pitched sounds make the stiff, narrow part of the cochlear duct vibrate; low-pitched sounds make the flexible part vibrate.

Attached to one surface of the basilar membrane is an acoustical organ. This organ of Corti has arrays of **hair cells**, a type of acoustical receptor having a tuft of modified cilia at one end. The cilia project into a wall extension—a *tectorial* membrane—draped over them (Figure 35.11*d*,*e*). The cilia bend when pressure moves the basilar membrane. The mechanical energy is transduced into action potentials that reach the brain by an auditory nerve. Hearing loss occurs when hair cells are damaged, as by chronic exposure to intense sounds. Figure 35.12 is an example of the damage.

Ears of land vertebrates collect, amplify, and sort out sound waves. In the inner ear, sound waves produce fluid pressure variations and trigger action potentials in hair cells.

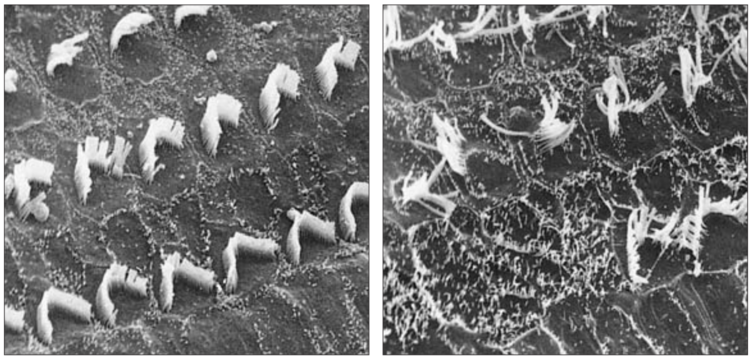


Figure 35.12 Results of an experiment on the effect of intense sound on the inner ear. *Left:* From a guinea pig ear, two rows of hair cells that normally project into the tectorial membrane in the organ of Corti. *Right:* Hair cells inside the same organ after twenty-four hours of exposure to noise levels comparable to extremely loud music.

To give you a sense of how sound intensity is measured, a ticking watch measures 10 decibels. Normal conversation is about 60 decibels, a food blender operating at high speed is about 90 decibels, and an amplified rock concert is about 120 decibels. The perceived loudness of a sound depends not only on its intensity but also on its frequency.

35.6 Do You See What I See?

LINKS TO SECTIONS 4.2, 7.2, 25.9, 34.10

Shine a light on a single-celled amoeba and it abruptly stops moving. Sunflowers track the sun as it arcs overhead. Most organisms are sensitive to light, but few "see" as you do.

REQUIREMENTS FOR VISION

At the minimum, a sense of **vision** requires eyes and image perception in brain centers that can interpret patterns of visual stimulation. Images are assembled from information on the shapes, brightness, positions, and movements of visual stimuli. **Eyes** are sensory organs that contain a tissue of many densely packed photoreceptors. Regardless of variation in the details, all **photoreceptors** have this in common: *They contain pigment molecules that can absorb photon energy, which can be converted to excitation energy in sensory neurons.*

There are two types of photoreceptors, but both are derived from epidermal cells that have one cilium. In *ciliary* photoreceptors, the plasma membrane around the cilium develops into the photosensitive surface. Cnidarians, some flatworms, and all vertebrates have this type. By contrast, in *rhabdomeric* photoreceptors, the photosensitive surface develops from microvilli around the cilium. This type occurs in most flatworms and mollusks, annelids, arthropods, and echinoderms.

A SAMPLING OF INVERTEBRATE EYES

In earthworms and some other eyeless invertebrates, photoreceptors are dispersed through the integument. The simplest kind of eye is an ocellus (plural, ocelli). Photoreceptors project into these pigmented spots or shallow cups of the integument (Figure 35.13*a*). The pigments partially shade the photoreceptors, which helps the animal determine the direction of the light source. Such animals use light as a cue to orient the body, detect a predator's shadow, or adjust biological clocks, but that is about it.

Vision arose among swift predatory fishes that had to discriminate among prey and other objects in their rapidly shifting visual field. A **visual field** is the part of the outside world that the eye sees (Section 34.11). At the least, photoreceptors must sample the intensity of light from different parts of the visual field, which the brain interprets as contrasting details of a visual stimulus. However, fine visual detail requires a lot of photoreceptors, and the eyes of most invertebrates are too small to have enough of them. The pigment cup of a planarian has about 200 photoreceptors, compared to 70,000 per square millimeter in an octopus eye.

Also, an eye **lens** helps image formation. This type of transparent structure bends all light rays from a given point in the visual field so that they converge onto photoreceptors (Sections 4.2 and 7.2). Abalones have a round lens, but it does not bend incoming rays to the same points, so blurred images form (Figure 35.13*b*). Images sharpen a bit when photoreceptors are some distance away from the lens, as in the snail eye (Figure 35.13*c*). They sharpen more with a **cornea**, a transparent cover that directs light rays onto the lens, as happens in a snail or conch eye (Figure 35.13*d*,*e*).

Invertebrates that evolved on land are far better at discriminating among objects in the visual field. For example, consider the simple and more complex eyes of arthropods. A *simple* arthropod eye has one lens for all photoreceptors. Spiders have these (Section 25.12). Crustaceans and insects have **compound eyes**, with many closely packed rhabdomeric units, as in Figure 35.14*a*. Some compound eyes have thousands of units, of a sort called ommatidia (singular, ommatidium). Inside each unit is a photoreceptor with rhabdomeric

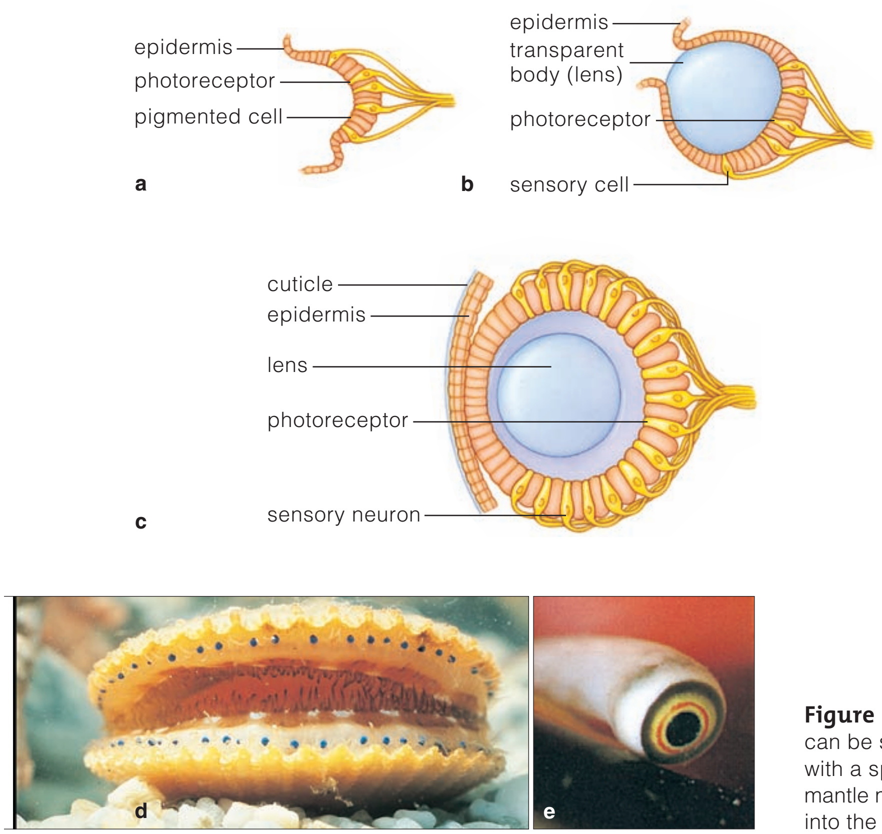


Figure 35.13 Invertebrate eyes. There are far more photoreceptors than can be shown in the simple diagrams. (**a**) Limpet ocellus. (**b**) Abalone eye, with a spherical, transparent lens. (**c**) Eye of a land snail. (**d**) Ocelli at the mantle margin of a scallop. (**e**) Well-developed eye of a conch, peering into the waters of the Great Barrier Reef along the east coast of Australia.

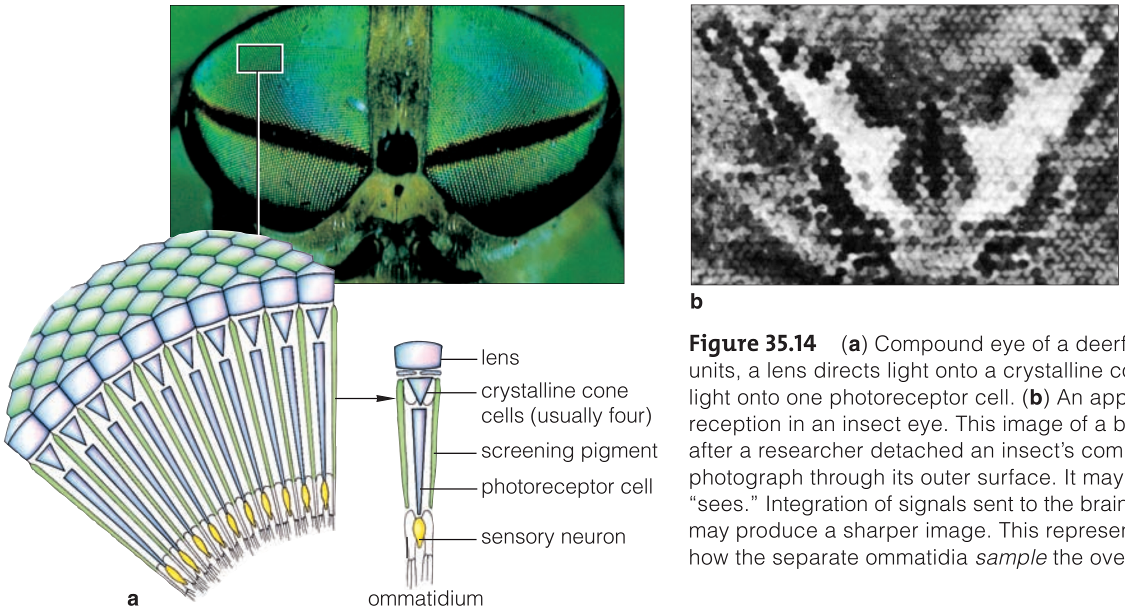


Figure 35.14 (**a**) Compound eye of a deerfly. In each of many units, a lens directs light onto a crystalline cone, which focuses light onto one photoreceptor cell. (**b**) An approximation of light reception in an insect eye. This image of a butterfly was formed after a researcher detached an insect's compound eye and took a photograph through its outer surface. It may not be what the insect "sees." Integration of signals sent to the brain from photoreceptors may produce a sharper image. This representation does suggest how the separate ommatidia *sample* the overall visual field.

microvilli. A visual pigment, rhodopsin, is embedded in the membrane of these photosensitive structures.

By the mosaic theory of image formation, each unit in an arthropod's compound eye samples a small part of the visual field. The brain then constructs images based on signals about differences in light intensities among units, with each unit contributing a small bit to the formation of a visual mosaic (Figure 35.14*b*).

The cephalopods called octopuses and squids have the most complex invertebrate eyes (Section 25.9). Like vertebrates, they have **camera eyes**, so named because the eyeball is structured like a camera. Light enters the interior, a dark chamber, through the pupil, an opening in a ring of contractile tissue called the iris (equivalent to the camera diaphragm). Behind the pupil, a lens focuses light on a **retina**, a tissue with many photoreceptors (equivalent to a light-sensitive film inside a camera). In this region, axons of sensory nerves converge to form an optic tract (Figure 35.15). One tract from each eye extends into the brain.

The structural similarities between cephalopod and vertebrate eyes might be an outcome of convergent evolution. Genes that affected the development of the nervous system in both groups were appropriated for the task of eye formation. This may have happened more than once in different animal lineages.

Vision requires eyes with a dense array of photoreceptors and image formation in the brain. Brain centers receive and process patterns of information about brightness, shapes, positions, and movement in the visual field.

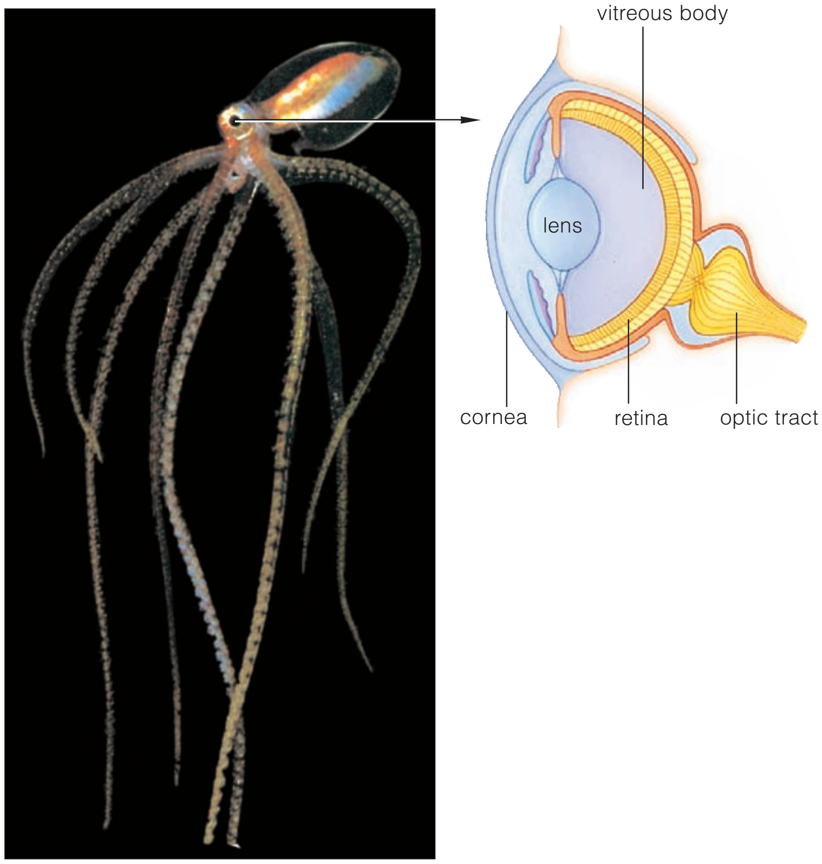


Figure 35.15 Octopus eye. The pupil constricts into slits and flares open in response to stimuli, changing light conditions, or the presence of a potential mate or enemy. Experiments show that cephalopods form distinct images. They sense the size, shape, and vertical and horizontal orientation and possibly the color of objects. They are nearsighted. Even so, they can snag tiny prey three meters away in the water.

35.7 Structure and Function of Vertebrate Eyes

LINKS TO SECTIONS 4.2, 7.1

Like cephalopods, vertebrates have a pair of camera eyes. In most species, the eye has a three-layered wall, and one layer has a tissue of densely packed photoreceptors. The wall forms a chamber. A jellylike substance fills the chamber, and a lens lets in light from the outside.

Figure 35.16 Here's looking at you! In owls and some other birds of prey, photoreceptors are concentrated more on top of the inner eyeball, not back. Such birds look down more than up when they fly and scan the ground for a meal. When they are on the ground, they cannot see something overhead very easily unless they turn their head almost upside-down.

COMPONENTS OF THE EYE

In a vertebrate eye, the transduction of light energy starts at the retina, a tissue that has densely packed photoreceptors. The retina usually is at the back of the eyeball, but in birds of prey, such as hawks and owls, it is closer to the roof of the eyeball (Figure 35.16). Remember, vision requires more than arrays of photoreceptors. It also requires image formation in brain centers that receive and interpret patterns of stimulation from different parts of the eye. Images are based on information about the shapes, brightness, positions, and movements of visual stimuli. Figure 35.17 has a cutaway view of the human eye and a list of its component parts. Like most vertebrate eyes, a human eye has a three-layer wall. The retina rests on the eyeball's inner layer.

The middle layer has a choroid, ciliary body, iris, and pupil. The choroid is a tissue rich in pigments and blood vessels. It absorbs light that photoreceptors do not and prevents it from scattering inside the eye. Suspended behind the cornea is a doughnut-shaped, pigmented iris (the Latin *iris* refers to the rings of a rainbow). The dark "hole" in the center of an iris is the pupil, the entrance for light. When bright light strikes an eye, circular muscles embedded in the iris contract, so the pupil diameter shrinks. In dim light, radial muscles in the iris contract, so the pupil dilates.

The eyeball's outermost layer consists of the sclera and cornea. The sclera, the dense, fibrous "white" of an eye, protects most of the eyeball. The cornea, made of transparent collagen fibers, covers the rest of it.

Wall of eyeball	(three layers)
Sensory Tunic (inner layer)	*Retina.* Absorbs, transduces light energy *Fovea.* Increases visual acuity
Vascular Tunic (middle layer)	*Choroid.* Blood vessels nutritionally support wall cells; pigments prevent light scattering *Ciliary body.* Its muscles control lens; shape; its fine fibers hold lens upright *Iris.* Adjusting iris controls incoming light *Pupil.* Serves as entrance for light *Start of optic nerve.* Carries signals to brain
Fibrous Tunic (outer layer)	*Sclera.* Protects eyeball *Cornea.* Focuses light

Interior of eyeball	
Lens	Focuses light on photoreceptors
Aqueous humor	Transmits light, maintains pressure
Vitreous body	Transmits light, supports lens and eyeball

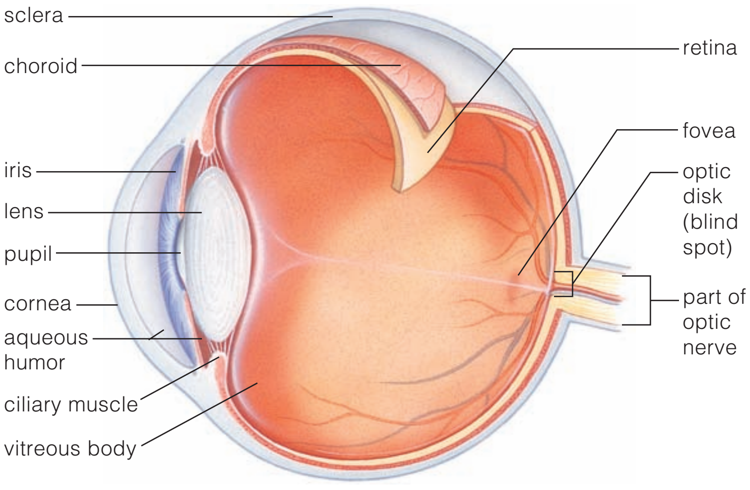
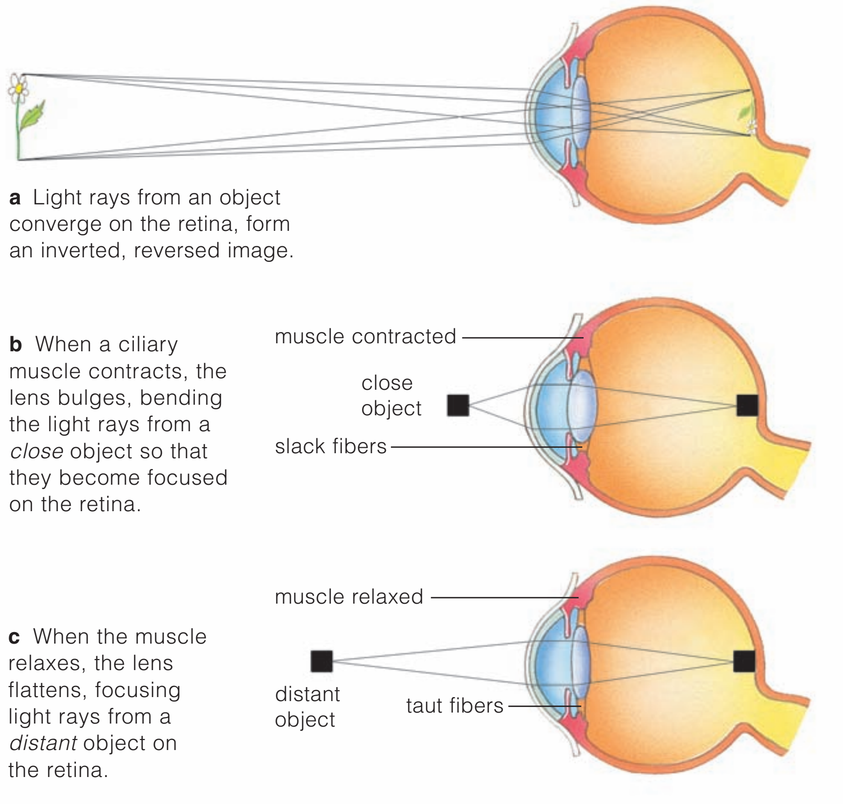


Figure 35.17 ***Animated!*** Structure and components of the human eye.

Light enters the eyeball's chamber only through a lens that is constructed of layers of transparent fibers of proteins. A clear fluid, the aqueous humor, bathes the lens. A jellylike substance called the vitreous body fills the eyeball chamber behind the lens.

Eyes that have a large pupil and iris are clues to animal life-styles. Species that move about actively at night or in dimly lit habitats are less likely to stumble, bump into objects, or fall off cliffs when they intercept as much of the available light as they can. The greater the amount of incoming light, the better is the visual discrimination. Large pupils let in more light. Large irises can be dilated more to let in far more light than small ones, which is a useful option for animals that are active at night as well as during the day.

When light rays converge at the back of the eye, they stimulate the retina in a distinct pattern. Because the cornea and lens both have a curved surface, all of the rays from some point in the visual field hit them at different angles, so their trajectories change. Rays of light bend at the boundaries between substances of different densities, and bending sends them off in new directions (Sections 4.2 and 7.1). Because of their newly angled trajectories, rays that converge at the back of the eye stimulate the retina in a pattern that is upside-down and reversed left to right, relative to the original light source. Figure 35.18*a* is a simple sketch of this outcome.


a Light rays from an object converge on the retina, form an inverted, reversed image.

b When a ciliary muscle contracts, the lens bulges, bending the light rays from a *close* object so that they become focused on the retina.

c When the muscle relaxes, the lens flattens, focusing light rays from a *distant* object on the retina.

Figure 35.18 (**a**) Pattern of retinal stimulation in a human eye. A curved, transparent cornea in front of the pupil changes the trajectories of light rays as they enter the eye. (**b**,**c**) Two focusing mechanisms use a ciliary muscle that encircles the lens and attaches to it.

VISUAL ACCOMMODATION

Light rays from sources at varying distances from the eye strike the cornea at different angles. They could become focused at different distances in back of it and impair image formation. However, by mechanisms of **visual accommodation**, the lens position or its shape are adjusted in ways that focus all incoming rays onto the retina. Without these normal adjustments, rays of light from distant objects would become improperly focused in front of the retina, and the rays from close objects would be focused behind it.

In fish and reptilian eyes, muscles move the lens forward or back, like a camera's focusing apparatus. Extending the distance between the lens and retina moves the focal point forward; shrinking it moves the focal point back. The lens shape is adjusted in birds and mammals. A ciliary muscle encircles the lens and is anchored to it by fiberlike ligaments (Figure 35.17). When this muscle contracts, the lens bulges and the focal point moves forward (Figure 35.18*b*). When this muscle relaxes, the lens flattens and moves the focal point back, as in Figure 35.18*c*.

In some cases, the lens position or shape cannot be adjusted enough to make the focal point match up precisely with the retina. For instance, in some people, the eyeball is not shaped quite right, and the position of the lens is either too close or too far away from the retina. When this is the case, accommodation alone cannot bring about an exact match. Eyeglasses often correct both visual disorders, which you may know as nearsightedness and farsightedness. Section 35.9 takes a look at both visual disorders as well as others.

For most vertebrate eyes, the eyeball has three layers, and its interior has a lens, aqueous humor, and vitreous body. Adjustments in the positioning or shape of the lens focus incoming visual stimuli onto the retina inside.

A protective sclera and a light-focusing cornea make up the outer layer. The middle layer has a vascularized, pigmented choroid and other parts that admit and control incoming light. Photoreception occurs at the retina of the inner layer.

35.8 A Closer Look at the Retina

LINKS TO SECTIONS 7.1, 28.5, 34.9–34.11

Each eye is an outpost of the brain, busily collecting and analyzing information about the distance, shape, position, brightness, and movement of visual stimuli. Its sensory pathway starts at the retina and ends in the brain.

THE RETINA'S RODS AND CONES

In between the retina and the choroid is a pigmented epithelium. Anchored to the epithelium are densely packed arrays of **rod cells** and **cone cells**, which are two categories of ciliary photoreceptors (Figure 35.19). Rod cells and cone cells transduce photon energy into action potentials, the messages by which brain cells monitor the visual field.

In most mammals, rod cells are the most abundant outside the fovea, a small circular area near the center of the retina. Rod cells detect very dim light and are the basis for coarse perception of movement across a visual field.

Part of the rod cell membrane is folded into several hundred disks. Each disk has about 10^8 molecules of the visual pigment rhodopsin. The membrane folding and the high density of pigments enormously increases the odds of intercepting photons, the packets of light energy you read about in Section 7.1. When photons of blue-to-green light stimulate it, rhodopsin changes shape, and that is the start of signal transduction. The change triggers a cascade of reactions that affect ion distributions across the rod cell's plasma membrane. The outcome is a reduction in the release of a certain neurotransmitter that suppresses activity in neurons that are adjacent to the rods.

Cone cells, which detect bright light, are the basis of sharp vision and color perception. Our sense of color and daytime vision starts when red, green, and blue cone cells, each with a different kind of visual pigment, absorb photons. Photon energy is transduced as it is in rod cells. The fovea has the greatest density of cone cells, and it is the basis of the greatest visual acuity—the most precise discrimination between any two points in the visual field.

A SIGNAL TRANSDUCTION PATHWAY

Layers of distinct types of sensory neurons lie above the rods and cones between the pigmented epithelium and lens on the opposite side of the eyeball (Figure 35.20). These neurons receive, process, and start to integrate signals that arise from the transduction of photon energy. Their activity is organized as receptive fields, or tiny circles where a signal may stimulate or inhibit neural activity.

At the first level of synaptic integration, input from about 125 million rods and cones converges on the retinal neurons known as bipolar cells (Figure 35.20). Humans have eleven types of these bipolar neurons—ten for cones and one for rods. They sort out objects that are lighter than darker ones in the visual field's background. Information also flows laterally among amacrine cells and horizontal cells.

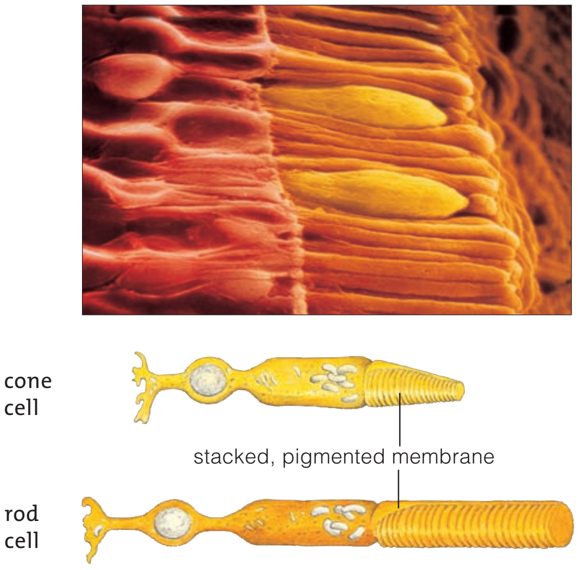


Figure 35.19 Scanning electron micrograph and sketches of rod cell and cone cell structure.

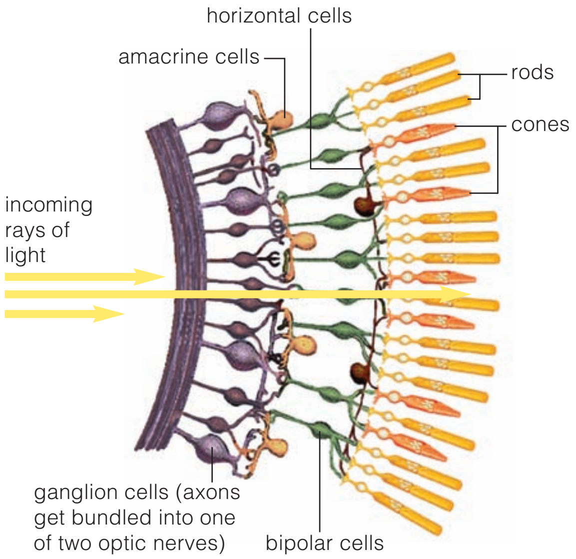


Figure 35.20 *Animated!* General organization of photoreceptors and sensory neurons in the retina. The array is about 0.5 millimeter thick.

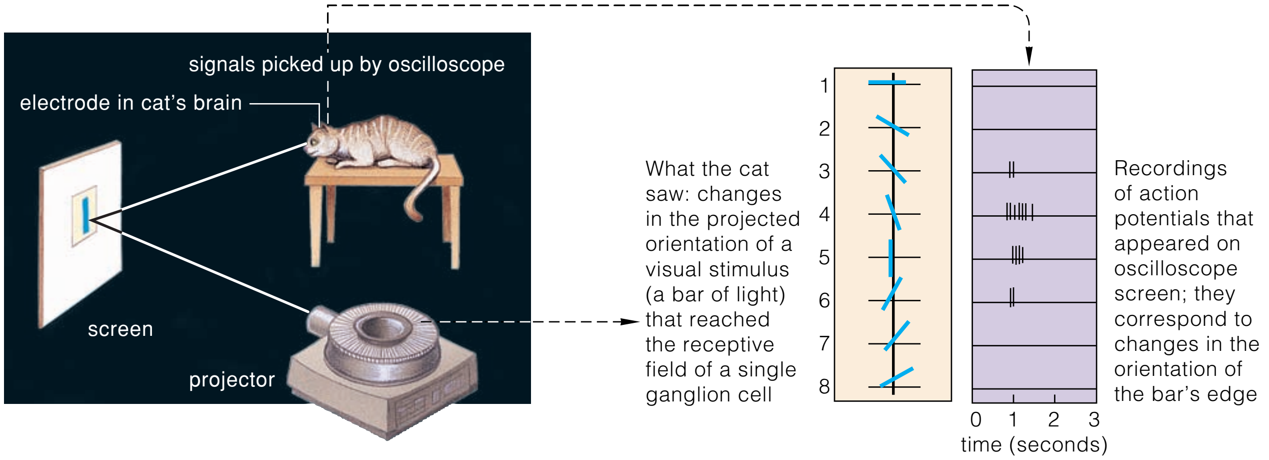


Figure 35.21 ***Animated!*** Example of experiments into the nature of receptive fields for visual stimuli. David Hubel and Torsten Wiesel implanted an electrode in an anesthetized cat's brain. They placed the cat in front of a small screen upon which different patterns of light were projected—here, a hard-edged bar. Light or shadow falling on part of the screen excited or inhibited signals sent to a single neuron in the visual cortex. Tilting the bar at different angles produced changes in the neuron's activity. A vertical bar image produced the strongest signal (*numbered 5 in the sketch*). When the bar image tilted slightly, signals were less frequent. When it tilted past a certain angle, signals stopped.

The messages converge on 1 million ganglion cells. These are the output neurons; their axons are the start of an optic nerve that carries action potentials to the brain. Different ganglion cells respond to rapid shifts in light intensity, a spot of one color, motion, and so on in their tiny receptive field. Figure 35.21 highlights one example. Thus, *before a transduced signal leaves the retina, neurons start integrating and processing it.*

Humans have two optic nerves, one from the retina in each eye (Figure 35.22). Each optic nerve delivers signals concerning a stimulus from the *left* visual field to the right cerebral hemisphere. Each optic nerve also delivers signals from the *right* visual field to the left hemisphere, as Section 34.11 explains.

Optic nerve axons end in a layered brain region named the lateral geniculate nucleus (Figure 35.23). Each layer has a map corresponding to the receptive fields and deals with one kind of visual stimulus, such as form, movement, depth, color, and texture. After early processing, signals rapidly and simultaneously reach different parts of the visual cortex. There, final integration organizes the incoming action potentials and produces visual sensations.

Organization of visual signals begins at receptive fields in the retina. Signals are further processed in a layered brain region and finally integrated in the visual cortex.

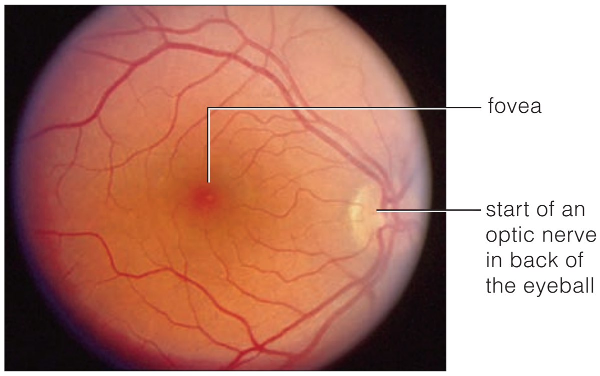


Figure 35.22 Location of the fovea and start of the optic nerve, which rings the entrance for blood vessels that service the eye.

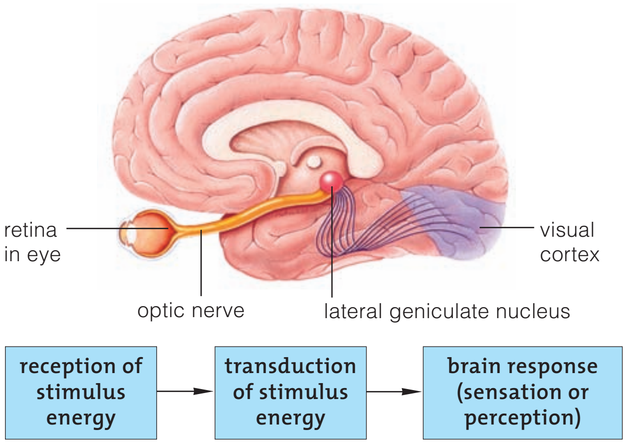


Figure 35.23 Sensory pathway from the retina into centers of the brain. Photon energy is transduced into the electrical energy of action potentials in the retina. Action potentials travel along an optic nerve from each eye into a layered brain region, the lateral geniculate nucleus. Each layer processes messages about one kind of visual signal, then relays information to the visual cortex. Synaptic integration in the cortex results in a sense of vision.

35.9 Visual Disorders and Diseases

LINK TO SECTION 12.7

Given their essential part in monitoring the outside world, a lot of attention is paid to eye problems that result from injuries, inherited abnormalities, diseases, and advancing age. Each year, many millions of people deal with these problems.

Color Blindness Occasionally, some or all of the cone cells that selectively respond to light of red, green, or blue wavelengths fail to develop. Rare individuals who have only one of three kinds of cones are completely color-blind. They perceive the world in shades of gray.

You read about *red–green color blindness* in Section 12.7. This X-linked recessive trait shows up most often in males. Some or all of the cone cells that respond to light of red or green wavelengths are missing from the retina. Individuals who are affected by this condition typically have trouble distinguishing red from green in dim light. Some cannot distinguish them even in bright light.

Focusing Problems Heritable alterations in the shape of the eyeball affect the focusing of light. *Astigmatism*, for example, results from unevenly curved corneas, which cannot properly bend all of the incoming light rays to the same focal point.

Nearsightedness, or *myopia*, often occurs when the horizontal axis of the eyeball is longer than the vertical axis. It also occurs when the ciliary muscle responsible for adjusting the lens contracts too strongly. The outcome is that images of distant objects get focused in front of the retina instead of on it (Figure 35.24*a*).

Farsightedness, or *hyperopia*, is the opposite of myopia. The eyeball's vertical axis is longer than the horizontal axis, or the lens is "lazy." Either way, light rays from close objects get focused behind the retina (Figure 35.24*b*).

Even a normal lens loses some of its natural flexibility as a person grows older. That is why people over forty years old often start wearing eyeglasses. Most focusing problems can be corrected with glasses or surgery. Today, lasers are used to reshape the cornea. In 2002, the most common procedure, LASIK, was performed on 1.8 million Americans. When all goes well, laser surgery eliminates the need for glasses during most activities, although the elderly may still need reading glasses. Results vary. Chronic eye irritation is common, and the rare complications can be serious.

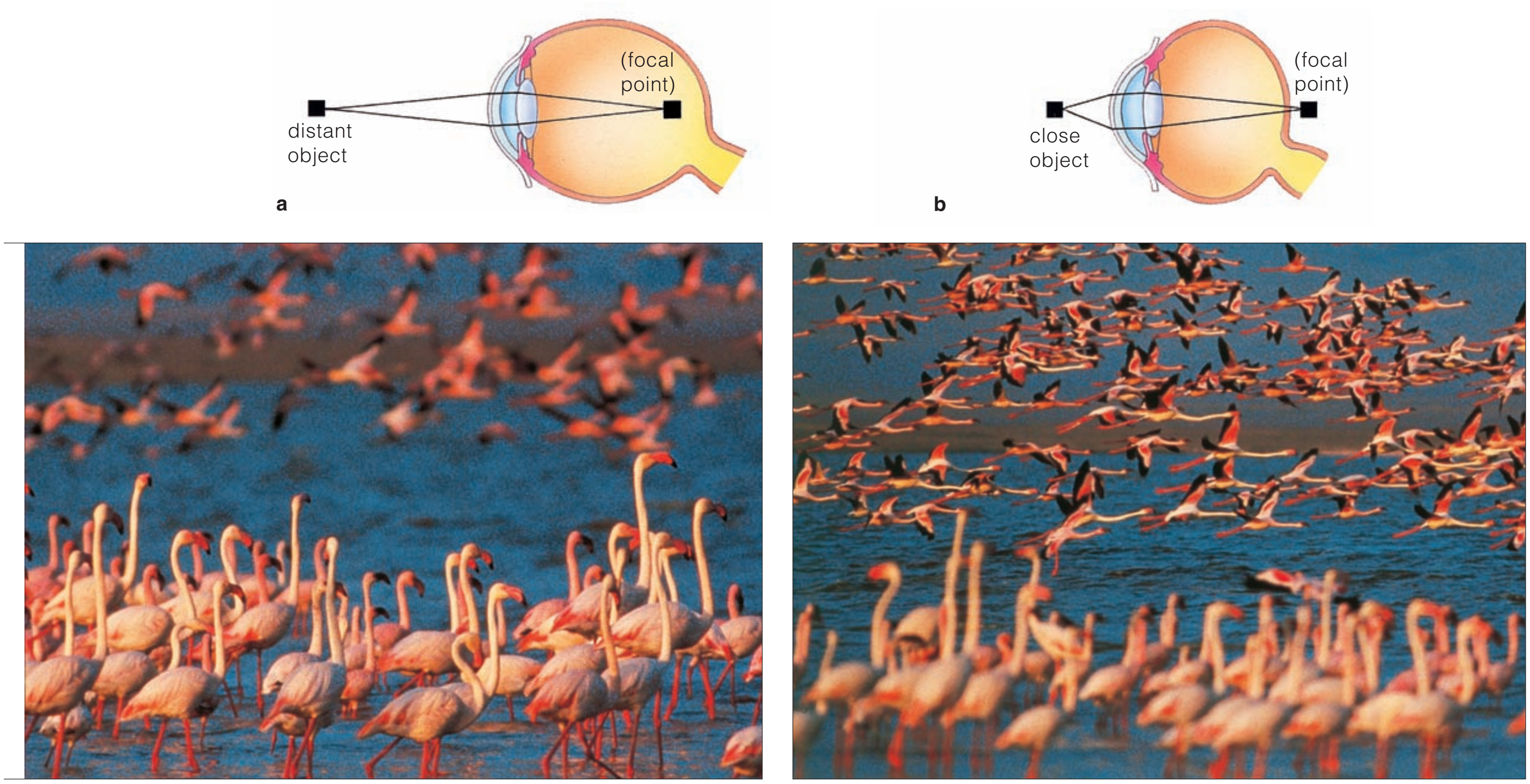


Figure 35.24 Focusing problems. In nearsightedness (**a**) light rays from distant objects converge in front of the retina. In farsightedness (**b**) light rays from close objects have not converged when they arrive at the retina.

Age-Related Disorders The macula is a retinal region with a high density of photoreceptors. It fully surrounds the fovea (Figure 35.22). Without it, we cannot see enough detail to read, drive, even to recognize faces. *Macular degeneration* is one of the most common causes of blindness among those who are age fifty-five or older. In the United States, about 13 million people have age-related macular degeneration (AMD). Destruction of photoreceptor cells in the macula and fovea clouds the center of the visual field more than the periphery. The causes of AMD are not fully known, although there is a genetic component. Smoking, obesity, and high blood pressure increase the risk.

AMD cannot be cured, but its progression can be slowed with eye drops, vitamins, and laser therapy. An experimental treatment filters cholesterol and certain proteins from an affected person's blood. So far, it has helped about 30 percent of those treated.

Glaucoma results when too much aqueous humor builds up inside the eyeball. The excess damages blood vessels and ganglion cells, and it can interfere with peripheral vision and visual processing. Glaucoma can be treated with medication and surgery. Although we often associate chronic glaucoma with advanced age, conditions that give rise to the disorder actually start to develop in middle age. When doctors detect the fluid pressure that tends to build up in the eye early enough, they can prescribe drugs or perform surgery before the damage becomes severe.

A *cataract*, a gradual clouding of the lens, alters the amount of light that reaches the retina and where light is focused. Possibly cataracts form when the transparent proteins that make up the eye's lens undergo structural changes. When the lens becomes fully opaque, vision is impossible. The clouded lens can be replaced with an artificial implant. Each year, millions of people undergo cataract surgery. It is a problem associated with aging, although an injury or diabetes also may cause it.

Eye Diseases The eyes are vulnerable to infectious diseases. For instance, a fungus that causes the lung disease *histoplasmosis* sometimes invades the eyes as well. Partial or total loss of vision may follow. *Herpes simplex*, a virus that causes skin sores, also can infect the cornea and result in its ulceration. You read about these diseases in Chapter 21.

Trachoma is an extremely contagious disease that has blinded millions, mostly in North Africa and the Middle East. The infectious agent is a bacterium that also is responsible for the sexually transmitted disease chlamydia (Section 44.8). The eyeball and the lining of the eyelids (the conjunctiva) become damaged.

These damaged tissues are entry points for other kinds of pathogenic bacteria that may cause secondary infections. In time, the cornea may become so scarred that blindness follows.

Summary

Section 35.1 Sensory pathways are examples of cell communication, from reception and transduction of a signal to a suitable response. In this case, different classes of sensory receptors transduce the energy of a specific stimulus, such as pressure, into electrochemical energy of action potentials. The main classes are called mechanoreceptors, pain receptors, thermoreceptors, chemoreceptors, osmoreceptors, and photoreceptors.

The brain evaluates action potentials from sensory receptors based on which nerve delivers them, their frequency, and the number of axons firing in a given interval. Continued stimulation of a receptor may lead to a diminished response (sensory adaptation).

Receptors for somatic sensations, such as touch and warmth, are not localized in a special organ or tissue. Receptors for special senses—taste, smell, hearing, balance, and vision—are in special sensory organs.

BiologyNow

See how the intensity of a stimulus affects action potential frequency with the animation on BiologyNow.

Section 35.2 Somatic sensations start at free nerve endings, encapsulated receptors, and stretch receptors near the body surface, in the wall of internal organs, and in skeletal muscles. Signals arrive in sensory areas of the cerebral cortex, where interneurons are organized like maps for individual parts of the body surface.

BiologyNow

Learn about the sensory receptors in human skin with the animation on BiologyNow.

Section 35.3 The senses of taste and smell involve pathways from chemoreceptors to processing regions in the cerebral cortex and limbic system. Taste receptors are concentrated in taste buds in the tongue and mouth. Olfactory receptors line the nasal passages. Pheromones are chemical signals secreted by many animals that also have specialized organs or structures to detect them.

Section 35.4 The vestibular apparatus is a fluid-filled organ of equilibrium in the vertebrate inner ear. It detects gravity, acceleration, and other forces that affect the body's position and movement.

Section 35.5 Sound is a form of mechanical energy. A vibrating object generates pressure waves, which can vary in amplitude and frequency. Humans have a pair of ears with three regions: the outer, middle, and inner ear. The outer ear collects sound waves. The middle ear amplifies sound waves and transmits them to the inner ear, which includes the vestibular apparatus and the cochlea: a coiled, fluid-filled structure with three ducts.

Pressure waves traveling through the fluid inside the cochlea bend mechanoreceptors called hair cells, which are embedded in one of the cochlear membranes. Sounds get sorted out according to their amplitude. In this case, mechanical energy is transduced to action potentials that are relayed along auditory nerves to the brain.

BiologyNow

Explore the structure and function of the human ear with the animation on BiologyNow.

Sections 35.6, 35.7 All organisms are sensitive to light, but vision requires eyes and brain centers that can process visual information. An eye is a sensory organ that contains a dense array of photoreceptors.

Like squids and octopuses, humans have camera eyes, each with an iris that adjusts incoming light and a lens that focuses light on the retina in the back of the eyeball chamber. The retina has densely packed photoreceptors.

Section 35.8 Rods detect dim light, and cones detect bright light and colors. These photoreceptors interact with other retinal cells to process visual information even before sending it on to the brain. Two optic nerves carry signals that eventually reach the cerebral cortex.

BiologyNow

Investigate the structure and function of the human eye with the animation on BiologyNow.

Section 35.9 Abnormalities in eye shape, in the lens, and with retinal cells often impair vision.

BiologyNow

Learn about the organization of the retina and how visual stimuli are processed with the animation on BiologyNow.

Self-Quiz

Answers in Appendix II

1. A stimulus is a specific form of energy in the outside environment that is detected by ______ .
   a. a sensory receptor c. the brain
   b. nerves d. all of the above

2. ______ is defined as a decrease in the response to an ongoing stimulus.
   a. Perception c. Sensory adaptation
   b. Visual accommodation d. Somatic sensation

3. Which is a somatic sensation?
   a. taste c. touch e. a through c
   b. smell d. hearing f. all of the above

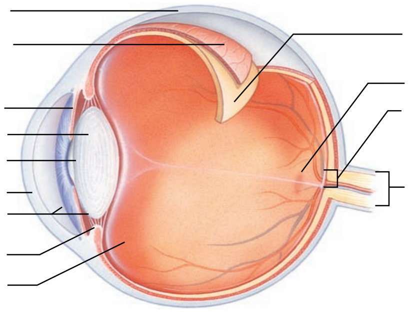
4. Chemoreceptors play a role in the sense of ______ .
   a. taste c. touch e. both a and b
   b. smell d. hearing f. all of the above

5. In the ______ neurons are arranged like maps that correspond to different parts of the body surface.
   a. cerebral cortex c. basilar membrane
   b. retina d. all of the above

6. Mechanoreceptors in the ______ send signals to the brain about the body's position relative to gravity.
   a. eye b. ear c. tongue d. nose

7. The middle ear functions in ______ .
   a. detecting shifts in body position
   b. amplifying and transmitting sound waves
   c. sorting sound waves out by frequency
   d. both b and c

8. Label the components of the human eye, as indicated in the following diagram:



9. Match each structure with its description.
   ____ rod cell
   ____ cochlea
   ____ lens
   ____ hair cell
   ____ cone cell
   ____ taste bud
   ____ vestibular apparatus
   ____ free nerve ending

   a. sensitive to vibrations
   b. function in balance
   c. detects color
   d. detects dim light
   e. contains chemoreceptors
   f. focuses rays of light
   g. sorts out sound waves
   h. helps brain assess heat, pressure, pain

Additional questions are available on **BiologyNow™**

Critical Thinking

1. Laura loves to eat broccoli and brussels sprouts. Lionel cannot stand them. Everyone has the same five kinds of taste receptors, so what is going on? Is Lionel just being difficult? Perhaps not. The number and distribution of receptors that respond to bitter substances vary among individuals of a population—and studies now indicate that some of this variation is heritable.

People who have the greatest number of receptors for bitter substances find many fruits and vegetables highly unpalatable. These *supertasters* make up about 25 percent of the general population. They tend to be slimmer than average but are more likely to develop colon polyps and colon cancer. How might Lionel's highly sensitive taste buds put him at increased risk for colon cancer?

2. Above and below a python's mouth are rows of pits that contain thermoreceptors (Figure 35.25*a*). They detect body heat, or infrared energy, of nearby prey. Name the type of prey organisms the receptors can detect. Which kinds of otherwise edible animals would they miss so that the snake would slither on by?

3. Think about the bats. Nearly all of these mammalian species sleep during the day and spread their webbed wings at dusk. Different kinds take to the air in search of nectar, fruit, frogs, or insects. Many sensory receptors in their eyes, nose, ears, mouth, and skin are not all that different from yours. Others are very different. They help even tiny-eyed, nearly blind species navigate and capture flying insects swiftly in the dark.

As one of these bats flies, it emits a steady stream of about ten clicking sounds per second. The bat shown in Figure 35.25*b* is emitting these clicks. You cannot hear a bat's clicks. They are ultrasounds, of an intensity beyond the

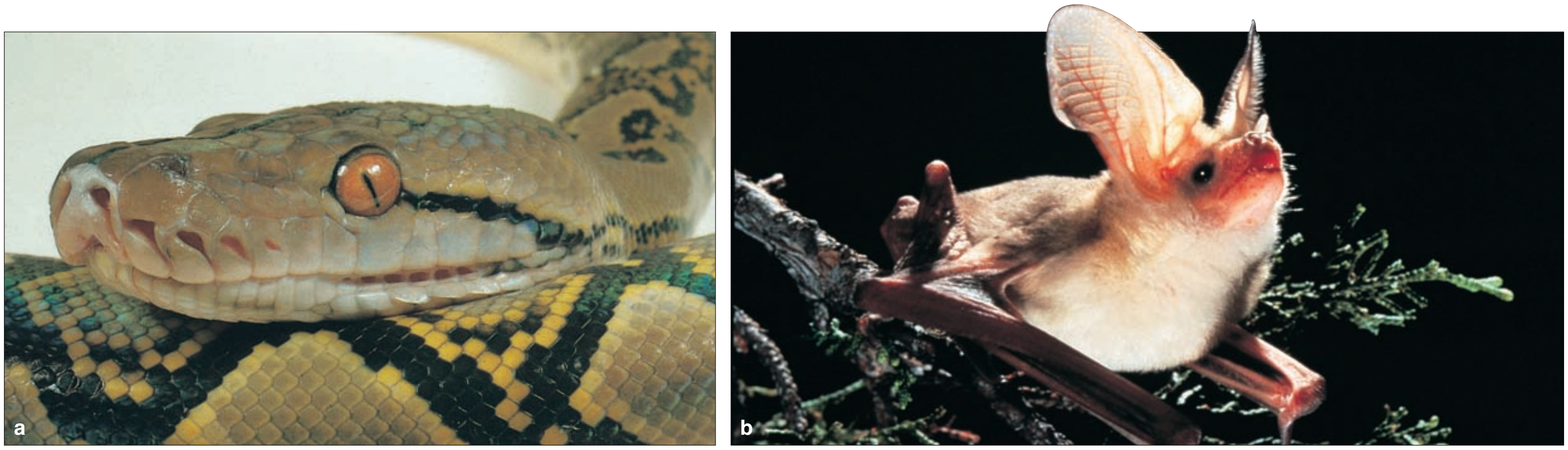


Figure 35.25 Examples of sensory receptors. (**a**) Thermoreceptors in pits above and below a python's mouth detect body heat, or infrared energy, of nearby prey. (**b**) Some bats listen to echoes of their own high-frequency sounds. Their brain constructs a sound map from the echoes that bounce back from prey and other objects in the surroundings. Such maps help this night-flying bat capture insects in midair without the help of eyes.

range of sound waves that receptors in human ears can detect. When a bat hears a pattern of distant echoes from, say, an airborne mosquito, it increases the rate of ultrasonic clicks to as many as 200 per second. That is faster than a machine gun can fire bullets. In the few milliseconds of silence between the clicks, sensory receptors in the bat's pair of inner ears detect the echoes. The bat brain swiftly constructs a "map" of the sounds, which the bat follows during its maneuvers through the night world.

Which part of the cochlear duct inside the bat ear do the ultrasounds stimulate?

4. The vestibular apparatus of all modern whales and dolphins is much smaller, relative to their body size, than it is in other mammals (Figure 35.26). Whales, remember, are descended from land-dwelling mammals (page 281). Fossils of early whales show that the vestibular apparatus became modified as their ancestors made the transition back to a life in the seas.

Think about how the sense of balance in an aquatic animal might differ from that of a land mammal that walks on four legs. Speculate on why natural selection might have favored a rapid reduction in the size of the vestibular apparatus during the transition from a terrestrial to an aquatic life-style.

5. Are organs of dynamic equilibrium, static equilibrium, or both activated during a heart-thumping roller coaster ride, as in Figure 35.27?

6. In humans, photoreceptors are most concentrated at the very back of the eyeball. In birds of prey, such as owls and hawks, the greatest density of photoreceptors is in a region closer to the eyeball's roof. When these birds are on the ground, they cannot see objects even slightly above them unless they turn their head almost upside down. What is the adaptive advantage of this peculiar type of retinal organization?

7. The strength of Earth's magnetic field and its angle relative to the surface vary with latitude. Diverse species sense these differences and use them as cues for assessing their location and direction of movement. Behavioral experiments have shown that sea turtles, salamanders, and spiny lobsters use information from Earth's magnetic field during their migrations. Whales and some burrowing rodents also seem to have a magnetic sense. Evidence about humans is contradictory. Is it likely that humans have such a sense? Suggest an experiment that might support or disprove the possibility.

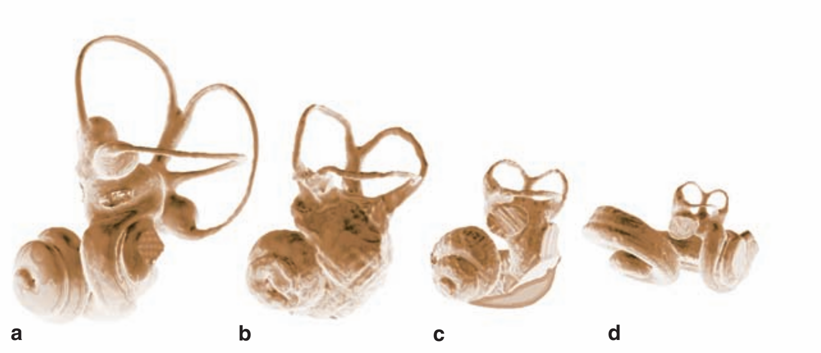


Figure 35.26 Inner ear structures from (**a**) a bushbaby, a notably agile land mammal, (**b**) a forerunner of whales (*Ichthyolestes*) that lived on land 50 million years ago, (**c**) a marine whale (*Indocetus*) that lived 45 million years ago, and (**d**) a dolphin. These computer reconstructions are adjusted to account for differences in body size.

Figure 35.27 One way to test whether your organs of equilibrium are working.