Chapter 50

Sensory and Motor Mechanisms

Lecture Outline

Overview: Sensing and Acting

- The detection and processing of sensory information and the generation of motor output provide the physiological basis for all animal activity.

Concept 50.1 Sensory receptors transduce stimulus energy and transmit signals to the central nervous system

- All sensory processes begin with stimuli, and all stimuli represent forms of energy.
- A sensory receptor converts stimulus energy to a change in membrane potential, thereby regulating the output of action potentials to the central nervous system.
- Activating a sensory receptor does not necessarily require a large amount of stimulus energy.
    - Some sensory receptors can detect the smallest possible unit of stimulus, such as most light receptors, which can detect a single quantum (photon) of light.
- When a stimulus's input to the nervous system is processed, a motor response may be generated.
    - One of the simplest such circuits is a reflex, such as the knee-jerk reflex.

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

- Sensory pathways begin with **sensory reception**, the detection of a stimulus by sensory cells.
- Most sensory cells are specialized neurons or epithelial cells that exist singly or in groups with other cell types in sensory organs, such as eyes or ears.
    - All sensory cells and organs, as well as subcellular structures that interact directly with stimuli, constitute **sensory receptors**.
- Many sensory receptors detect stimuli from outside the body, including heat, light, pressure, and chemicals.
    - There are also sensory receptors for stimuli from within the body, such as blood pressure and body position.
- Although animals use a range of sensory receptors to detect widely varying stimuli, the effect in all cases is to open or close ion channels.
    - Ion channels open or close when a substance outside the cell binds to a chemical receptor in the plasma membrane.
    - The resulting flow of ions across the membrane changes the membrane potential.

- The conversion of a physical or chemical stimulus to a change in the membrane potential of a sensory receptor is called **sensory transduction**; the change in the membrane potential is called a **receptor potential**.
- Receptor potentials are graded potentials; their magnitude varies with the strength of the stimulus.
- Sensory information travels through the nervous system as nerve impulses or action potentials.
- For many sensory receptors, transduction of the energy in a stimulus into a receptor potential initiates **transmission** of action potentials to the central nervous system (CNS).
- Some sensory receptors cells are specialized neurons, while others are specialized cells that regulate neurons.
    - Neurons that act directly as sensory receptors produce action potentials and have an axon that extends into the CNS.
    - Nonneuronal sensory receptor cells form chemical synapses with sensory neurons and usually increase the rate at which action potentials are produced.
- The response of a sensory receptor varies with stimuli of different intensities.
    - The primary difference is the magnitude of the receptor potential, which controls the rate at which action potentials are produced.
- If the receptor is a sensory neuron, a larger receptor potential results in more frequent action potentials.
    - If the receptor is not a sensory neuron, a larger receptor potential causes more neurotransmitter to be released, which usually increases the production of action potentials by the postsynaptic neuron.
- Many sensory neurons spontaneously generate action potentials at a low rate.
    - A stimulus does not switch the production of action potentials on or off: It changes *how often* an action potential is produced, alerting the CNS to changes in stimulus intensity.
- A difference in stimulus strength not only alters the activity of individual receptors, but also affects the number of receptors that are activated.
    - If a stronger stimulus triggers a response by more receptors, more axons transmit action potentials.
    - This increase in the number of axons transmitting action potentials is decoded by the nervous system as a stronger stimulus.
- Processing of sensory information can occur before, during, and after transmission of action potentials to the CNS.
- *Integration* of sensory information begins as soon as the information is received.
- Receptor potentials produced by stimuli delivered to different parts of a sensory receptor cell are integrated through summation, as are postsynaptic potentials in sensory neurons that form synapses with multiple receptors.

Processing of action potentials from sensory neurons generates perception of stimuli.

- When action potentials along sensory neurons reach the brain, circuits of neurons process this input to generate the **perception** of stimuli.
    - Perceptions—including colors, smells, sounds, and tastes—are constructions formed in the brain and do not exist outside it.

- Action potentials are all-or-none events.
  - An action potential triggered by light striking the eye is the same as an action potential triggered by air vibrating in the ear.
- We distinguish sights, sounds, and other stimuli by the connections that link sensory receptors to the brain.
  - Action potentials from sensory receptors travel along neurons that are dedicated to a particular stimulus and that synapse with particular neurons in the brain or spinal cord.
  - As a result, the brain distinguishes sensory stimuli based on where action potentials arrive in the brain.

The transduction of stimuli by sensory receptors is subject to two types of modification: amplification and adaptation.

- **Amplification** is the strengthening of a stimulus signal during transduction.
  - An action potential conducted from the eye to the human brain has about 100,000 times as much energy as the few photons of light that triggered it.
- Amplification that occurs in sensory receptor cells often requires signal transduction pathways involving second messengers.
  - Pathways including enzyme-catalyzed reactions amplify signal strength through the formation of many product molecules by a single enzyme molecule.
- Amplification may take place in accessory structures of a complex sense organ, as when the pressure associated with sound waves is enhanced by a factor of more than 20 before reaching receptors in the inner ear.
- Upon continued stimulation, many receptors undergo a decrease in responsiveness termed **sensory adaptation**, which enables the detection of changes in environments that vary in stimulus intensity.

Sensory receptors are categorized by the type of energy they transduce.

- A sensory cell typically has a single type of receptor specific for a particular stimulus, such as light or cold.
- Distinct cells and receptors may be responsible for particular qualities of a sensation, such as distinguishing red from blue.
- Sensory receptors are divided into five categories based on the nature of the stimuli they transduce: mechanoreceptors, chemoreceptors, electromagnetic receptors, thermoreceptors, and pain receptors.
- **Mechanoreceptors** respond to mechanical energy such as pressure, touch, stretch, motion, and sound.
- Mechanoreceptors typically consist of ion channels that are linked to external cell structures, such as “hairs” or cilia, as well as internal structures, such as the cytoskeleton.
  - Bending or stretching of the external structure generates tension that alters the permeability of ion channels, producing depolarization or hyperpolarization.
- Vertebrate stretch receptors are dendrites of sensory neurons that spiral around the middle of small skeletal muscle fibers.
  - Groups of 2 to 12 of these fibers, formed into a spindle shape and surrounded by connective tissue, are distributed throughout the muscle, parallel to other muscle fibers.
  - When the muscle is stretched, the spindle fibers are stretched, depolarizing sensory neurons and triggering action potentials that are transmitted to the spinal cord.

- The mammalian sense of touch relies on mechanoreceptors that are the dendrites of sensory neurons, embedded in layers of connective tissue.
  - Receptors that detect a light touch or vibration are close to the surface of the skin; they transduce very slight inputs of mechanical energy into receptor potentials.
  - Receptors that respond to stronger pressure and vibrations are in deep skin layers.
- Other receptors sense the movement of hairs.
  - Cats and rodents have sensitive mechanoreceptors at the base of their whiskers.
  - Deflection of different whiskers triggers action potentials that reach different cells in the brain, allowing the whiskers to provide detailed information about nearby objects.
- **Chemoreceptors** respond to chemical stimuli.
- General chemoreceptors transmit information about the total solute concentration of a solution, while specific chemoreceptors respond to specific types of molecules.
  - Osmoreceptors in the mammalian brain are general receptors that detect changes in the solute concentration of the blood and stimulate thirst when osmolarity increases.
  - Internal chemoreceptors respond to glucose, O_2, CO_2, and amino acids.
  - Two of the most sensitive and specific chemoreceptors known are in the antennae of the male silkworm moth and detect the components of the female moth sex pheromone.
- In chemoreceptors, the stimulus molecule binds to a specific receptor on the membrane of the sensory cell and initiates changes in ion permeability.
- **Electromagnetic receptors** detect electromagnetic energy such as visible light, electricity, and magnetism.
  - Snakes have infrared detectors that detect the body heat of prey.
  - The platypus has electroreceptors on its bill to detect electric field generated by prey.
- Some animals detecting an electromagnetic stimulus are also the source: Some fishes generate electrical currents and use electroreceptors to locate prey that disturb those currents.
- Many animals use Earth's magnetic field lines to orient themselves as they migrate.
  - The iron-containing mineral magnetite is found in many vertebrates, in bees, in molluscs, and in certain protists and prokaryotes that orient to Earth's magnetic field.
- **Thermoreceptors** detect heat or cold and help regulate body temperature by signaling surface and body core temperature.
  - Thermoreceptors in the skin and in the anterior hypothalamus send information to the body's thermostat in the posterior hypothalamus.
- Jalapeno and cayenne peppers were crucial in helping scientists understand how sensory cells detect temperature.
  - Hot peppers taste "hot" because they contain a natural product called capsaicin.
  - Exposing sensory neurons to capsaicin triggers an influx of calcium.
  - The receptor protein that binds capsaicin responds not only to capsaicin but also to high temperatures (42°C or hotter).
  - Spicy foods are "hot" because they activate the same receptors as high temperatures.
- Mammals have a number of thermoreceptors, each specific for a particular temperature range.
  - The capsaicin receptor and at least five other thermoreceptors belong to the TRP (transient receptor potential) family of ion channel proteins.

- The TRP-type receptor specific for temperatures lower than 28°C can be activated by menthol, a plant product perceived as having a "cool" flavor.

- **Pain receptors**, or **nociceptors**, are a class of naked dendrites in the epidermis.
- Pain is an important sensation because the stimulus leads to a defensive reaction.
- Different types of pain receptors respond to different types of pain, such as excess heat, pressure, or chemicals released from damaged or inflamed tissues.
  - Nociceptor density is highest in skin, although pain receptors are associated with other organs.
- Some chemicals alter the perception of pain.
  - Damaged tissues produce prostaglandins, which act as local regulators of inflammation and also increase pain by sensitizing receptors, lowering their threshold.
  - Aspirin and ibuprofen reduce pain by inhibiting prostaglandin synthesis.

Concept 50.2 The mechanoreceptors responsible for hearing and equilibrium detect moving fluid or settling particles

- Hearing and balance are related in most animals.
- Both involve mechanoreceptor cells, which produce receptor potentials when settling particles or moving fluid cause deflection of cell surface structures.
- Most invertebrates rely on mechanoreceptors located in organs called **statocysts**, which sense gravity and maintain equilibrium.
  - A statocyst has a layer of ciliated receptor cells surrounding a chamber that contains one or more **statoliths**, grains of sand or other dense granules.
  - Gravity causes the statoliths to settle to a low point in the chamber, stimulating mechanoreceptors in that location.
- Sound sensitivity in insects depends on body hairs that vibrate in response to sound waves.
  - Hairs of different stiffness and length vibrate at different frequencies.
- Many insects have localized "ears," a tympanic membrane stretched over an internal air chamber.
  - Sound waves vibrate the tympanic membrane, stimulating receptor cells attached to the inside of the membrane and resulting in nerve impulses that are transmitted to the brain.

In mammals, the sensory organs for hearing are associated with the ear.

- In *hearing*, the ear transduces pressure waves into nerve impulses that the brain perceives as sound.
- Hearing relies on sensory receptors that are hair cells, a type of mechanoreceptor.
- Before vibrations reach the hair cells, they are amplified and transformed by several accessory structures.
- The first steps in hearing involve structures in the ear that convert the vibrations of moving air to fluid pressure waves.
  - Moving air reaching the outer ear causes the tympanic membrane to vibrate.
  - The three bones of the middle ear transmit the vibrations to the oval window, a membrane on the cochlea's surface.

- When one of those bones, the stapes, vibrates against the oval window, it creates pressure waves in the fluid (perilymph) within the cochlea.
- The pressure waves push down on the cochlear duct and basilar membrane, causing the membrane and attached hair cells to vibrate up and down.
  - Hairs projecting from the moving basilar membrane are deflected by the tectorial membrane, which lies in a fixed position immediately above.
  - With each vibration, the hairs bend first in one direction and then the other.
- Mechanoreceptors in the hair cells respond by opening or closing ion channels.
  - Bending of the hairs in one direction depolarizes hair cells, increasing neurotransmitter release and the frequency of action potentials directed to the brain along the auditory nerve.
  - Bending of the hairs in the other direction hyperpolarizes hair cells, reducing neurotransmitter release and the frequency of auditory nerve sensations.
- Pressure waves travel through the vestibular canal and pass around the apex of the cochlea.
  - The waves continue through the tympanic canal, dissipating as they strike the **round window**.
  - This damping of sound waves resets the apparatus for the next vibrations.
- The ear conveys information to the brain about two important sound variables: volume and pitch.
- *Volume* is determined by the amplitude of the sound wave.
  - A large-amplitude sound wave causes more vigorous vibration of the basilar membrane, more bending of the hairs on the hair cells, and more action potentials in the sensory neurons.
- *Pitch* is a function of a sound wave's frequency, the number of vibrations per unit time.
  - High-frequency waves produce high-pitched sounds, whereas low-frequency waves produce low-pitched sounds.
- Pitch is commonly expressed in cycles per second, or hertz (Hz).
  - Healthy children can hear in the range of 20–20,000 Hz; dogs can hear sounds as high as 40,000 Hz; and bats can emit and hear clicking sounds at frequencies higher than 100,000 Hz, using this ability to locate objects.
- The cochlea can distinguish pitch because the basilar membrane is not uniform along its length: It is relatively narrow and stiff at the base of the cochlea near the oval window, and it is wider and more flexible at the apex.
  - Every region of the basilar membrane is tuned to a particular vibration frequency.
  - At any instant, the region of the membrane vibrating most vigorously triggers the highest frequency of action potentials in the neuronal pathway leading to the brain.
- The actual perception of pitch occurs within the cerebral cortex.
  - Axons in the auditory nerve project into auditory areas of the cerebral cortex according to the region of the basilar membrane in which the signal originated.
  - When a particular site in our cortex is stimulated, we perceive a particular pitch.

The inner ear also contains the organs of equilibrium.

- Several organs in the mammalian inner ear detect body movement, position, and balance.
- Behind the oval window is a vestibule with two chambers: the **utricle** and the **saccule**.

  - Each chamber contains a sheet of hair cells that project into a gelatinous material.
  - Embedded in the gel are many small calcium carbonate particles called otoliths.
- When you tilt your head, the otoliths press on the hairs protruding into the gel.
  - This deflection of the hairs changes the output of sensory neurons, signaling the brain that your head is at an angle.
- The otoliths are also responsible for the ability to perceive acceleration.
- Because the utricle is oriented horizontally and the saccule is positioned vertically, the inner ear can detect forward and back, or up and down, motion.
- Three semicircular canals connected to the utricle detect turning of the head and other forms of angular acceleration.
  - Within each canal, the hair cells form a single cluster, with the hairs projecting into a gelatinous cap called the cupula.
  - Because the three canals are arranged in the three spatial planes, they can detect angular motion of the head in any direction.

A lateral line system and the inner ear detect pressure waves in most fishes and aquatic amphibians.

- The ears of fishes lack cochlea, eardrums, and openings to the outside.
- Water vibrations caused by sound waves are conducted through the skeleton of the head to a pair of inner ears, setting otoliths in motion and stimulating hair cells.
  - The fish's air-filled swim bladder contributes to the transfer of sound to the inner ear.
  - Some fishes have a series of bones that conduct vibrations from the swim bladder to the inner ear.
- Most fishes and aquatic amphibians have a **lateral line system** along both sides of their body.
  - The system contains mechanoreceptors that detect low-frequency waves by a mechanism similar to the function of a mammalian inner ear.
- Water enters the lateral line system through pores and flows along a tube past mechanoreceptors formed from a cluster of hair cells, whose hairs are embedded in a gelatinous cupula.
- Water movement bends the cupula, depolarizing the hair cells and producing action potentials that are transmitted along the axons of sensory neurons to the brain.
  - This process provides a fish with information concerning its movement through water or the direction and velocity of water flowing over its body.
  - The lateral line system also detects water movements or vibrations generated by prey, predators, and other moving objects.
- In terrestrial vertebrates, the inner ear has evolved as the main organ of hearing and equilibrium.
  - Some amphibians have a lateral line as juveniles but not as terrestrial adults.
  - In frogs and toads, sound vibrations are conducted to the inner ear by a tympanic membrane on the body surface and a single middle ear bone.
- Birds and other reptiles also have a cochlea. As in amphibians, sound is conducted from the tympanic membrane to the inner ear of reptiles by a single bone.

Concept 50.3 Diverse visual systems rely on light-absorbing pigments

- The ability to detect light is important in the interaction of most animals with their environment.
- Although animals use a diverse set of organs for vision, the underlying mechanism for capturing light is the same, suggesting a common evolutionary origin.
- Light detectors in the animal kingdom range from simple clusters of cells that detect only the direction and intensity of light to complex organs that form images.
  - These diverse light detectors all contain photoreceptors, cells that contain light-absorbing pigment molecules.
- The genes that specify where and when photoreceptors arise during embryonic development are shared among animals as diverse as flatworms, annelids, arthropods, and vertebrates.
  - The genetic underpinnings of all photoreceptors were likely present in the earliest bilaterian animals.

A diversity of photoreceptors has evolved among invertebrates.

- Most invertebrates have some kind of light-detecting organ.
- The ocelli of planarians are among the simplest photoreceptors.
  - Ocelli are surrounded on three sides by a layer of darkly pigmented cells that block light.
  - Photoreceptors in each ocellus receive light only through the opening where there are no pigmented cells.
- Because the opening of one ocellus faces left and slightly forward, and the other opening faces right and forward, light shining from one side of the planarian stimulates the ocellus only on that side.
  - The planarian brain compares the rate of action potentials coming from the two ocelli and directs turning movements that minimize the rates of stimulation for both ocelli.
  - As a result, the planarian moves away from the light source until it reaches a shaded location where a rock or other object is likely to hide the animal from predators.
- Insects and crustaceans have compound eyes.
  - A **compound eye** consists of several thousand **ommatidia**, each with its own light-focusing lens.
  - Each ommatidium detects light from a tiny portion of the visual field.
  - The compound eye is very good at detecting movement, an important adaptation that reduces the risks of predation.
  - Whereas the human eye can distinguish only about 50 flashes of light per second, the compound eyes of some insects can detect flickering at a rate six times faster.
  - Insects have excellent color vision, and some can see ultraviolet light.
- **Single-lens eyes** are found in some invertebrates such as jellies, polychaetes, spiders, and many molluscs.
  - In the eye of an octopus or squid, light enters through the **pupil**, with the **iris** changing the diameter to let in more or less light.
  - Behind the pupil, a single lens focuses light on a layer of photoreceptors.
  - The muscles in an invertebrate's single-lens eye move the lens to focus at different distances.

Vertebrates have single-lens eyes.

- Vision begins when photons of light enter the eye and strike the rods and cones.
  - The energy of each photon is captured by a shift in configuration of a single chemical bond in retinal.
- Although light detection in the eye is the first stage in vision, it is actually the brain that "sees."
  - To understand vision, we must examine how the capture of light by retinal changes the production of action potentials and then follow these signals to the visual centers of the brain, where images are perceived.
- Transduction of visual information to the nervous system begins with the light-induced conversion of *cis*-retinal to *trans*-retinal.
  - *Trans*-retinal activates rhodopsin, which activates a G protein, which in turn activates an enzyme that can hydrolyze cyclic GMP.
  - In the dark, cyclic GMP in photoreceptor cells binds to sodium channels and keeps them open.
  - When the G protein dependent pathway is activated, cyclic GMP is broken down, sodium channels close, and the cell becomes hyperpolarized.
- The signal transduction pathway in photoreceptor cells shuts off as enzymes convert retinal back to the *cis* form, returning rhodopsin to its inactive state.
  - In very bright light, rhodopsin remains active, and the response in the rods becomes saturated.
- If the amount of light entering the eyes decreases abruptly, the rods do not regain full responsiveness for several minutes.
  - This is why you are temporarily blinded if you pass quickly from the bright sunshine into a movie theater or other dark environment.

Visual information is processed in the retina and the brain.

- Processing of visual information begins in the retina itself, where both rods and cones form synapses with bipolar cells.
  - In the dark, rods and cones are depolarized and continually release the neurotransmitter glutamate at these synapses.
- Some bipolar cells depolarize in response to glutamate, while others hyperpolarize.
  - Which of the two responses a bipolar cell exhibits depends on the type of glutamate receptor present on its surface at the synapse.
  - When light strikes the rods and cones, they hyperpolarize, shutting off their release of glutamate.
  - In response, the bipolar cells that are depolarized by glutamate hyperpolarize, and those that are hyperpolarized by glutamate depolarize.
- In addition to bipolar cells, information processing in the retina requires three other types of neurons—ganglion, horizontal, and amacrine cells.
- Signals from rods and cones can follow several different pathways in the retina.
  - Some information passes directly from photoreceptors to bipolar cells to ganglion cells.
  - In other cases, horizontal cells carry signals from one rod or cone to other photoreceptors and to several bipolar cells.
- When an illuminated rod or cone stimulates a horizontal cell, the horizontal cell inhibits more distant photoreceptors and bipolar cells that are not illuminated.

- The result is that the light spot appears lighter and the dark surroundings even darker.
- This form of integration, called **lateral inhibition**, sharpens edges and enhances contrast in the image.

- Amacrine cells distribute some information from one bipolar cell to several ganglion cells.
  - Lateral inhibition is repeated by the interactions of the amacrine cells with the ganglion cells and occurs at all levels of visual processing in the brain.
- A single ganglion cell receives information from an array of rods and cones, each of which responds to light coming from a particular location.
- Together, the rods or cones that feed information to one ganglion cell define a *receptive field*—the part of the visual field to which the ganglion can respond.
  - The fewer rods or cones that supply a single ganglion cell, the smaller the receptive field.
  - A smaller receptive field results in a sharper image, because the information as to where light struck the retina is more precise.
  - The ganglion cells of the fovea have very small receptive fields, so visual acuity in the fovea is high.
- Axons of ganglion cells form the optic nerves that transmit sensations from the eyes to the brain.
  - The two optic nerves meet at the **optic chiasm** near the center of the base of the cerebral cortex.
  - Axons in the optic nerves are routed at the optic chiasm such that sensations from the left visual field of both eyes are transmitted to the right side of the brain, and sensations from the right visual field are transmitted to the left side of the brain.
- Within the brain, most ganglion cell axons lead to the **lateral geniculate nuclei**, which have axons that reach the **primary visual cortex** in the cerebrum.
  - Additional neurons carry the information to higher-order visual processing and integrating centers elsewhere in the cortex.
- How does the cortex convert a complex set of action potentials representing two-dimensional images focused on the retina to three-dimensional perceptions of our surroundings?
  - 30% of the cerebral cortex, comprising hundreds of millions of neurons in perhaps dozens of integrating centers, takes part in formulating what we actually “see.”
- The brain not only processes visual information, but also controls what information is captured.
- One important type of control is focusing, which occurs by changing the shape of the lens.
  - When you focus on a close object, your lens becomes almost spherical.
  - When you view a distant object, your lens is flattened.
- By turning your head and pointing your eyes in a particular direction, your brain determines what lies in your field of vision.
- Peripheral vision allows humans to see objects over a nearly 180° range, but the distribution of photoreceptors across the eye limits both what we see and how well we see it.
- The human retina contains about 125 million rods and about 6 million cones.
  - At the **fovea**, the center of the visual field, there are no rods but a very high density of cones—about 150,000 cones per square millimeter.

- The ratio of rods to cones increases with distance from the fovea, with the peripheral regions having only rods.

- In daylight, you achieve your sharpest vision by looking directly at an object, such that light shines on the tightly packed cones in your fovea.
  - At night, looking directly at a dimly lit object is ineffective, since the rods—the more sensitive light receptors—are found outside the fovea.

Many vertebrates have good color vision.

- Among vertebrates, most fishes, amphibians, and reptiles, including birds, have very good color vision.
  - Humans and other primates are among the minority of mammals with this ability.
  - Many mammals are nocturnal, and having a high proportion of rods in the retina gives them keen night vision.
- In humans, the perception of color is based on three types of cones, each with a different visual pigment—red, green, or blue.
  - The three visual pigments, called *photopsins*, are formed from the binding of retinal to three distinct opsin proteins.
  - Slight differences in the opsin proteins are sufficient for each photopsin to absorb light optimally at a different wavelength.
- Abnormal color vision typically results from alterations in the genes for one or more photopsin proteins.
- Because the human genes for the red and green pigments are located on the X chromosome, a single defective copy of either gene can disrupt color vision in males.
  - For this reason, color blindness is more common in males than females (5-8% of males, but <1% of females, are affected) and nearly always disrupts perception of red or green (the blue pigment gene is on human chromosome 7).

Concept 50.4 The senses of taste and smell rely on similar sets of sensory receptors

- Many animals use their chemical senses to find mates, to recognize territory that has been marked by some chemical substance, and to help navigate during migration.
- Chemical conversation is especially important for social insects such as ants and bees.
- In all animals, chemical senses are important in feeding behavior.
  - For example, a hydra begins to make ingestive movements when it detects the compound glutathione, which is released from prey captured by the hydra's tentacles.
- The perceptions of **gustation** (taste) and **olfaction** (smell) are both dependent on chemoreceptors that detect specific chemicals in the environment.
- In terrestrial animals, taste is the detection of chemicals called **tastants** that are present in solution and smell is the detection of **odorant** chemicals in the air.
  - There is no distinction between taste and smell in aquatic animals.
- Taste receptors in insects are located on their feet and in mouthparts, within sensory hairs called sensilla.
  - A tasting hair contains chemoreceptors responsive to particular classes of tastant, such as sugar or salt.

- Insects are also capable of smelling airborne odorants using olfactory hairs, usually located on the antennae.

Mammalian receptor cells for taste are organized into taste buds.

- Mammals recognize five types of tastant.
  - Four represent the familiar taste perceptions: sweet, sour, salty, and bitter.
  - The fifth, called umami, is elicited by the amino acid glutamate.
- An individual taste cell expresses a single receptor type and detects tastants representing only one of the five tastes.
- The receptor cells for taste in mammals are modified epithelial cells organized into **taste buds**, which are scattered in several areas of the tongue and mouth.
  - Most taste buds on the tongue are associated with nipple-shaped projections called papillae.
  - Any region of the tongue with taste buds can detect any of the five types of taste.
- Taste receptors fall into two categories, each evolutionarily related to receptors for other senses.
- The sensation of sweet, umami, and bitter tastes requires a G-protein-coupled receptor, or GPCR.
  - In humans, there are more than 30 different bitter taste receptors, each able to recognize multiple bitter tastants.
  - Humans have one sweet and one umami receptor, each assembled from a different pair of GPCR proteins.
  - Other GPCR proteins are critical for the sense of smell.
- Unlike the other identified taste receptors, the receptor for sour tastants belongs to the TRP (transient receptor protein) family.
  - Formed from a pair of TRP proteins, the sour receptor is similar to the capsaicin receptor and other thermoreceptor proteins.
  - In taste buds, the TRP proteins of the sour receptor assemble into a channel in the taste cell plasma membrane.
  - Binding of an acid or other sour-tasting substance to the receptor triggers a change in the ion channel, leading to depolarization and activation of a sensory neuron.

Olfactory receptor cells line the upper portion of the nasal cavity.

- In olfaction, unlike gustation, the sensory cells are neurons.
- Olfactory receptor cells line the upper portion of the nasal cavity and send impulses along their axons directly to the olfactory bulb of the brain.
  - The receptive ends of the cells contain cilia that extend into the layer of mucus coating the nasal cavity.
- When an odorant diffuses into this region, it binds to a specific GPCR protein called an odorant receptor (OR) on the plasma membrane of the olfactory cilia.
  - These events trigger signal transduction leading to the production of cyclic AMP.
- In olfactory cells, cyclic AMP opens channels in the plasma membrane that are permeable to both Na^+ and Ca^{2+} ions.

- The flow of these ions into the receptor cell depolarizes the membrane, generating action potentials.

- Humans can distinguish thousands of different odors, each caused by a structurally distinct odorant.
  - There are more than 1,000 OR genes, about 3% of all human genes.
  - Each OR cell appears to express a single OR gene.
- Cells with different odorant selectivities are interspersed in the nasal cavity.
  - Cells that express the same OR gene transmit action potentials to the same small region of the olfactory bulb.
- Taste and smell interact with each other, although the receptors and brain pathways for the two senses are independent.

Concept 50.5 The physical interaction of protein filaments is required for muscle function

- Muscle cell function relies on microfilaments, which are the actin-containing components of the cytoskeleton.
- Microfilament movement brings about contraction, whereas muscle extension occurs passively.
- Vertebrate **skeletal muscle** is attached to the bones and is responsible for their voluntary movement.
- A skeletal muscle consists of a bundle of long fibers running parallel to the length of the muscle.
  - Each fiber is a single cell with multiple nuclei, formed by the fusion of many embryonic cells.
  - A muscle fiber is a bundle of smaller **myofibrils** arranged longitudinally.
- The myofibrils are composed of two kinds of **myofilaments**: thin and thick filaments.
  - **Thin filaments** consist of two strands of actin and one strand of regulatory protein coiled around each other.
  - **Thick filaments** are staggered arrays of myosin molecules.

Interactions between myosin and actin generate force during muscle contractions.

- Skeletal muscle is called **striated muscle** because the regular arrangement of the filaments creates a pattern of light and dark bands.
- Repeated units called **sarcomeres** are the functional units of muscle contraction.
  - The borders of the sarcomere, the Z lines, are lined up in adjacent myofibrils and form the striations.
  - Thin filaments are attached to the Z lines and project toward the center of the sarcomere, while the thick filaments are centered in the sarcomere.
- In a muscle fiber at rest, thick and thin filaments do not overlap completely.
  - Near the edge of the sarcomere are only thin filaments; the zone in the center contains only thick filaments.

- According to the **sliding-filament model** of muscle contraction, neither the thin nor the thick filaments change in length when the sarcomere shortens.
  - Instead, thin and thick filaments slide past each other, increasing their overlap.
- The longitudinal sliding relies on the interaction of actin and myosin.
  - Each myosin molecule has a long "tail" region and a globular "head" region.
  - The tail adheres to the tails of other myosin molecules that form the thick filament.
  - The head, which extends to the side, can bind and hydrolyze ATP to ADP.
- Hydrolysis of ATP converts myosin to a high-energy form.
  - This form of myosin binds to actin, forms a cross-bridge, and pulls the thin filament toward the center of the sarcomere.
- The cross-bridge is broken when a new molecule of ATP binds to the myosin head.
- Muscle contraction requires repeated cycles of binding and release.
  - In each cycle, the myosin head freed from a cross-bridge cleaves the newly bound ATP and binds again to actin.
  - Because the thin filament moved toward the center of the sarcomere in the previous cycle, the myosin head now attaches to a new binding site farther along the thin filament.
  - Each of the approximately 350 heads of a thick filament forms and reforms about five cross-bridges per second, driving filaments past each other.
- A typical muscle fiber at rest contains only enough ATP for a few contractions.
- To power repetitive contractions, the muscle cell relies on two other storage compounds: creatine phosphate and glycogen.
  - Transfer of a phosphate group from creatine phosphate to ADP in an enzyme-catalyzed reaction synthesizes additional ATP.
- The resting supply of creatine phosphate can sustain contractions for about 15 seconds.
  - ATP stores are also replenished when glycogen is broken down to glucose by either aerobic respiration or glycolysis and lactic acid fermentation.
- Using a typical muscle fiber's glycogen store, glycolysis can support about 1 minute of sustained contraction, whereas aerobic respiration can power contractions for nearly an hour.

Calcium ions and regulatory proteins control muscle contraction and relaxation.

- The regulatory proteins **tropomyosin** and the **troponin complex** bind to thin filaments.
- In a muscle fiber at rest, tropomyosin covers the myosin binding sites along the thin filament and prevents the interaction of actin and myosin.
  - When Ca^{2+} is present in the cytosol, it binds to the troponin complex, causing the proteins bound along the thin filament to shift position, exposing the myosin-binding sites on the thin filament.
  - The thin and thick filaments slide past each other, and the muscle fiber contracts.
- When the Ca^{2+} concentration falls, the binding sites are covered and contraction stops.
- Motor neurons cause muscle contraction by triggering the release of Ca^{2+} into the cytosol of muscle cells with which they synapse.
- The arrival of an action potential at the synaptic terminal of a motor neuron releases the neurotransmitter acetylcholine.

- Acetylcholine binds to receptors on the muscle fiber, depolarizing the membrane and triggering an action potential.

- The action potential spreads deep into the muscle fiber along infoldings of the plasma membrane called **transverse (T) tubules.**
  - The T tubules meet the muscle cell's **sarcoplasmic reticulum (SR)**, and Ca^{2+} stored within the interior of the SR is released into the cytosol.
  - Ca^{2+} binds to the troponin complex, triggering contractions of the muscle fiber.
- When the motor neuron input stops, the muscle cell relaxes and transport proteins in the SR pump Ca^{2+} out of the cytosol.
- As the Ca^{2+} concentration in the cytosol drops, the regulatory proteins bound to the thin filament again block the myosin-binding sites on the thin filaments.
- Several diseases cause paralysis by interfering with the excitation of skeletal muscle fibers by motor neurons.
  - In amyotrophic lateral sclerosis (ALS), motor neurons in the spinal cord and brain stem degenerate, and the muscle fibers with which they synapse atrophy.
  - ALS is progressive and is usually fatal within five years; there is no treatment or cure.
  - Myasthenia gravis is a treatable autoimmune disease in which a person produces antibodies to the acetylcholine receptors on skeletal muscle fibers.
  - As the number of receptors decreases, synaptic transmission between motor neurons and muscle fibers declines.

Diverse body movements require variation in muscle activity.

- A single skeletal muscle fiber contracts completely in a brief all-or-none twitch, or not at all.
- Contraction of a whole muscle, composed of many individual muscle fibers, is graded.
  - Graded contraction is due to variation in the number of muscle fibers that contract and variation in the rate at which muscle fibers are stimulated.
- In vertebrates, each branched motor neuron may form synapses with many skeletal muscle fibers, although each fiber is controlled by only one motor neuron.
- A **motor unit** consists of a single motor neuron and all the muscle fibers it controls.
  - When a motor neuron produces an action potential, all the muscle fibers in its motor unit contract as a group.
  - The strength of the contraction depends on how many muscle fibers the motor neuron controls, from a few to hundreds.
- The nervous system can thus regulate the strength of contraction in a whole muscle by determining how many motor units are activated at a given instant and by selecting large or small motor units to activate.
- As more and more of the motor neurons controlling the muscle are activated, a process of recruitment increases the force developed by the muscle.
- Prolonged contraction of muscles can result in fatigue, caused by depletion of ATP and dissipation of ion gradients.
  - Accumulation of lactate, once thought to contribute to muscle fatigue, actually has beneficial effects on muscle function.
- The nervous system can also produce graded whole-muscle contractions by varying the rate of muscle fiber stimulation.

- A single action potential will produce a twitch lasting for 100 msec or less.
- If a second action potential arrives before the muscle fiber has completely relaxed, the two twitches sum, resulting in greater tension.
- Further summation occurs as the rate of stimulation increases.
- When the rate is so high that the muscle fiber cannot relax between stimuli, the twitches fuse into one smooth, sustained contraction called **tetanus**.

- Because muscle fibers are connected to bones via tendons and connective tissues, a contracting muscle fiber stretches these elastic structures, transmitting tension to the bones.
  - In a single twitch, a muscle fiber begins to relax before connective tissues are fully stretched.
  - During summation, high-frequency action potentials maintain an elevated concentration of calcium in the cytosol of the muscle fiber, prolonging cross-bridge cycling and causing greater stretching of the elastic structures.
  - During tetanus, the elastic structures are fully stretched, and all of the tension generated by the muscle fiber is transmitted to the bones.

Muscle fibers are specialized.

- There are several distinct types of skeletal muscle fibers, each adapted to a characteristic set of functions.
- Fiber types are classified either by the source of ATP used to power muscle activity or by the speed of muscle contraction.
- Fibers that rely on aerobic respiration are called oxidative fibers.
  - These fibers have many mitochondria, a rich blood supply, and a large amount of an oxygen-storing protein called **myoglobin** that binds oxygen more tightly than does hemoglobin.
- Fibers that rely on glycolysis are called glycolytic fibers.
  - These fibers have a larger diameter and less myoglobin than oxidative fibers and fatigue more readily.
- **Fast-twitch fibers** develop tension two to three times faster than **slow-twitch fibers**.
  - Fast-twitch fibers enable brief, rapid, powerful contraction.
  - Slow-twitch fibers, characteristic of muscles that maintain posture, can sustain long contractions.
- Relative to fast-twitch fibers, slow-twitch fibers have less sarcoplasmic reticulum, so Ca^{2+} remains in the cytosol longer.
  - As a result, a muscle twitch in a slow-twitch fiber lasts about five times as long as one in a fast-twitch fiber.
- Although all slow-twitch fibers are oxidative, fast-twitch fibers can be either glycolytic or oxidative.
- Most human skeletal muscles contain both fast and slow-twitch fibers, although the muscles of the eye and hand are exclusively fast twitch.
  - In a muscle with a mixture of fast and slow-twitch fibers, the relative proportions of each are genetically determined.
  - If a muscle is used repeatedly for activities requiring high endurance, some fast glycolytic fibers develop into fast oxidative fibers, producing a muscle that is more resistant to fatigue.

In addition to skeletal muscle, vertebrates have cardiac and smooth muscle.

- Although **cardiac muscle** is striated like skeletal muscle, structural differences between skeletal and cardiac muscle fibers result in differences in their electrical and membrane properties.
- Cardiac muscle cells can generate their own action potentials without nervous system input.
  - Action potentials of cardiac muscles can last up to 20 times longer than action potentials of skeletal muscle fibers.
- Plasma membranes of adjacent cardiac muscle cells interlock at specialized regions called **intercalated discs**, where gap junctions provide direct electrical coupling between the cells.
  - The action potential generated in a specialized region of the heart spreads to all other cardiac muscle cells, causing the whole heart to contract.
  - A long refractory period prevents summation and tetanus.
- **Smooth muscle** lines the walls of blood vessels and digestive system organs.
- Smooth muscle lacks the striations seen in skeletal and cardiac muscle.
- In smooth muscle, thick filaments are scattered throughout the cytoplasm, and thin filaments are attached to structures called dense bodies tethered to the plasma membrane.
  - There is less myosin in smooth muscle than in striated muscle fibers, and the myosin is not associated with specific actin strands.
- Some smooth muscle cells contract only when stimulated by neurons of the autonomic nervous system, whereas others are electrically coupled to one another and can generate action potentials without neural input.
- Smooth muscle contraction and relaxation are slower than for striated muscle.
- Although Ca^{2+} regulates smooth contraction, the mechanism for regulation is different from that in skeletal and cardiac muscle.
  - Smooth muscle cells lack troponin complexes and T tubules and have poorly developed SR.
- During an action potential, Ca^{2+} enters the cytosol through the plasma membrane.
  - Calcium ions cause contraction by binding to the protein calmodulin, activating an enzyme that phosphorylates the myosin head and enables cross-bridge activity.

Invertebrate muscle cells are similar to vertebrate skeletal and smooth muscle cells.

- The flight muscles of insects are capable of independent, rhythmic contraction, so the wings of some insects can actually beat faster than action potentials can arrive from the CNS.
- The thick filaments in the muscles that hold clam shells closed contain a protein called paramyosin that enables the muscles to remain contracted for as long as a month, with only a low rate of energy consumption.

Concept 50.6 Skeletal systems transform muscle contraction into locomotion

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

- Because muscles exert force only during contraction, moving a body part requires two muscles attached to the same section of the skeleton.
  - The nervous system coordinates the function of the two muscles in an antagonistic pair.
- Skeletons function in support and protection as well as facilitating movement.
  - In many animals, a hard skeleton also protects soft tissues.

Skeletons come in many different forms.

- Hardened support structures can be external (as in exoskeletons), internal (as in endoskeletons), or even absent (as in fluid-based or hydrostatic skeletons).
- A **hydrostatic skeleton**, characteristic of cnidarians, flatworms, nematodes, and annelids, consists of fluid held under pressure in a closed body compartment.
  - Form and movement are controlled by using muscles to change the shape of the compartment.
- Among the cnidarians, a hydra can elongate by closing its mouth and using contractile cells in the body wall to constrict the central gastrovascular cavity.
  - Because water cannot be compressed, decreasing the diameter of the cavity forces it to increase in length.
- In flatworms, movement results mainly from muscles in the body wall exerting localized forces the interstitial fluid.
- Nematodes contract longitudinal muscles around the fluid-filled body cavity.
- In annelids, circular and longitudinal muscles act together to change the shape of individual fluid-filled segments.
  - Earthworms use their hydrostatic skeletons to move by **peristalsis**.
- Hydrostatic skeletons are advantageous in aquatic environments and support crawling and burrowing in terrestrial animals.
  - Hydrostatic skeletons do not allow the body to be held off the ground for running or walking.
- An **exoskeleton** is a hard encasement deposited on the surface of an animal.
- Many molluscs are enclosed in a calcium carbonate shell secreted by the mantle.
  - As the animal grows, it enlarges the shell by adding to its outer edge.
  - Clams and other bivalves close their hinged shell using muscles attached to the inside.
- The jointed exoskeleton of arthropods is composed of a cuticle, with muscles attached to the interior surface.
  - About 30–50% of the cuticle consists of **chitin**.
- Fibrils of chitin are embedded in a protein matrix, forming a composite material that combines strength and flexibility.
  - The cuticle can be hardened with organic compounds that cross-link the proteins of the exoskeleton or by adding calcium salts.
  - It remains unhardened in body parts that must be flexible, such as leg joints.
- With each growth spurt, an arthropod sheds its exoskeleton (molts) and produces a larger one.
- An **endoskeleton** consists of hard supporting elements held within the soft tissues of the animal.
  - Sponges are reinforced by needlelike structures of inorganic material or protein fibers.

- Echinoderms' bodies are reinforced by hard plates called ossicles, composed of magnesium carbonate and calcium carbonate crystals.

- Chordate endoskeletons are composed of cartilage, bone, or some combination of the two.
  - The mammalian skeleton is built from more than 200 bones, some connected at joints by ligaments and others fused together.

Movement in water, on land, and in air depends on adaptations of body shape and posture.

- How thick does an endoskeleton need to be? Let's apply ideas from civil engineering.
  - The weight of a building increases with the cube of its dimensions.
  - The strength of a building support depends on its cross-sectional area, which increases with the square of its diameter.
- If we scaled up a mouse to the size of an elephant, the legs of the giant mouse would be too thin to support its weight.
  - Large animals have very different body proportions from those of small animals.
- In supporting body weight, body posture—the position of the legs relative to the main body—is more important than leg size, at least in mammals and birds.
  - Muscles and tendons (connective tissue that joins muscle to bone) hold the legs of large mammals straight and positioned under the body and actually bear most of the load.
- Most animals are mobile and spend a considerable portion of their time and energy actively searching for food.
  - These activities involve **locomotion**, active travel from place to place.
- An animal must expend energy to overcome two forces that tend to keep it stationary: friction and gravity.
  - The amount of energy required to oppose friction or gravity is reduced by an animal body plan adapted for movement in a particular environment.
- For locomotion on land, powerful muscles and skeletal support are more important than a streamlined shape.
- When a kangaroo hops, the tendons in its legs store and release energy like a spring that is compressed and released.
  - The kangaroo's large tail helps it maintain balance.
- When a quadruped walks, it keeps three feet (or one foot, for bipeds) on the ground to maintain balance.
- When an animal runs, all four feet (or both feet, for bipeds) may be off the ground briefly, but at running speeds, it is momentum more than foot contact that keeps the body upright.
- Crawling requires a considerable expenditure of energy to overcome friction.
  - Earthworms crawl by peristalsis.
  - Many snakes undulate the entire body from side to side, assisted in movement by large, moveable scales on the underside of the body that push against the ground.
- Because water is buoyant, gravity poses less of a problem for swimming than for other modes of locomotion.
  - Since water is dense, friction is more of a problem.
  - Fast swimmers have sleek, fusiform (torpedo-shaped) bodies.

- Animals swim in diverse ways.
  - Many insects and four-legged vertebrates use their legs as oars to push against the water.
  - Squids and scallops are jet-propelled, taking in and squirting out water.
  - Sharks and bony fishes move their bodies and tails from side to side, while whales undulate their bodies and tails up and down.
- Active flight has evolved in only a few animal groups: insects, reptiles (including birds), and, among the mammals, bats.
  - One group of flying reptiles, the pterosaurs, died out millions of years ago, leaving birds and bats as the only flying vertebrates.
- Gravity poses a major problem for flight because wings must develop enough lift to overcome gravity's downward force.
  - The key to flight is the aerodynamic shape of wings as airfoils.
- Flying animals are light, with body masses ranging from less than a gram for some insects to 20 kg for the largest flying birds.
  - Many flying animals have structural adaptations that contribute to low body mass.
  - Birds have no urinary bladder or teeth and have bones with air-filled regions that reduce weight.

The energy cost of locomotion depends on the mode of locomotion and the environment.

- Swimming is the most energy efficient mode of locomotion, assuming that the animal is specialized for swimming.
  - Running animals generally expend more energy per meter than equivalent-sized swimming animals, partly because running or walking requires energy to overcome gravity.
  - Flying animals use more energy than swimming or running animals with the same body mass.
- Larger animals travel more efficiently than smaller animals specialized for the same mode of transportation.
  - A 450-kg horse expends less energy *per kilogram of body mass* than a 4-kg cat running the same distance.
  - Of course, the total amount of energy expended in locomotion is greater for the larger animal.
- An animal's use of energy for movement determines how much energy in food is available for other activities, such as growth and reproduction.
  - Thus, structural and behavioral adaptations that maximize the efficiency of locomotion increase an animal's evolutionary fitness.