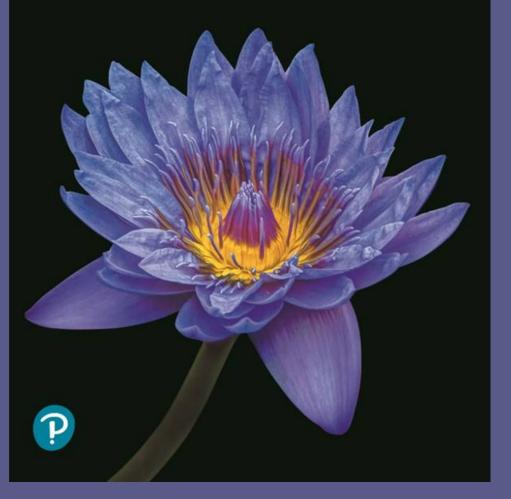
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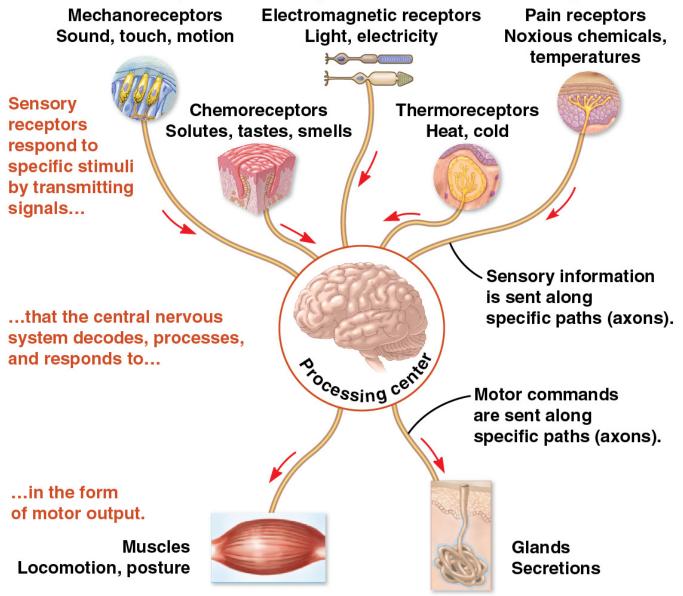
Chapter 50

Sensory and Motor Mechanisms

> Lecture Presentations by Nicole Tunbridge and Kathleen Fitzpatrick

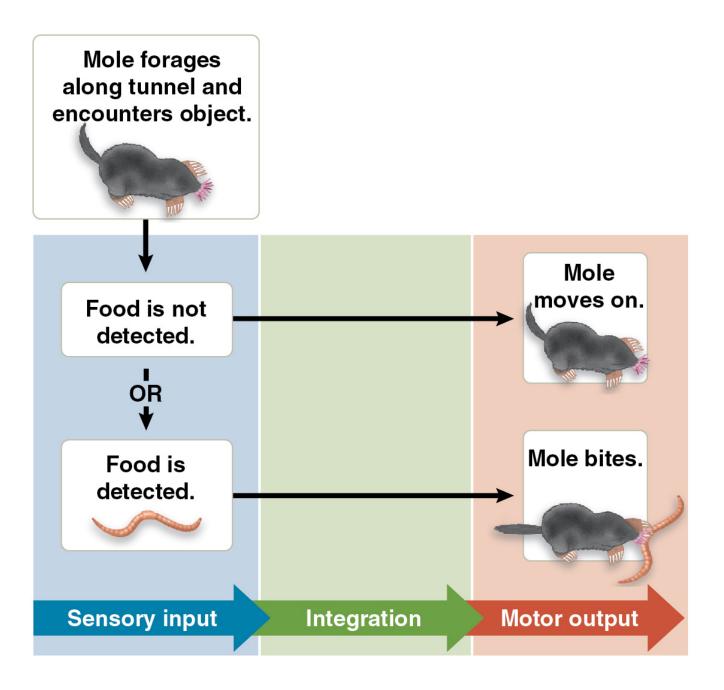


What steps link sensory stimuli to animal activity?



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

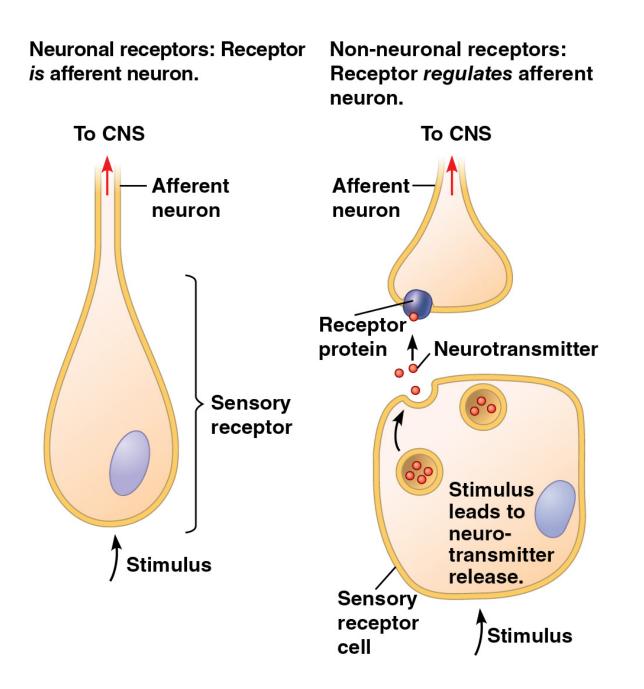
- All stimuli represent forms of energy
- A sensory receptor converts stimulus energy into a change in the membrane potential
- When a stimulus is received and processed by the nervous system, a motor response may be generated
- This may involve a simple reflex or more elaborate processing



- Sensory pathways have four basic functions in common
 - Sensory reception
 - Transduction
 - Transmission
 - Perception

Sensory Reception and Transduction

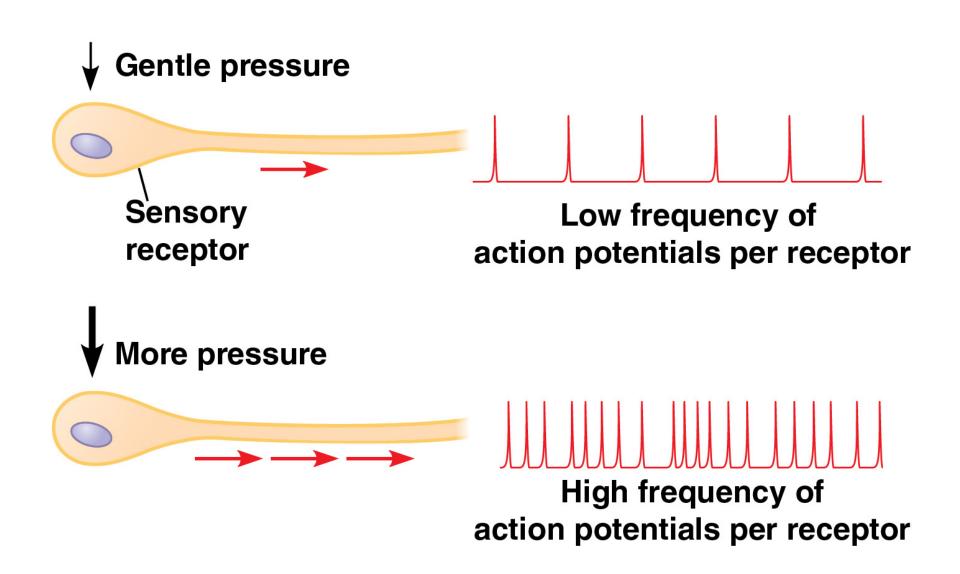
- A sensory pathway begins with sensory reception, detection of stimuli by sensory receptors
- Sensory receptors are sensory cells or organs
- They interact with stimuli, both inside and outside the body



- Sensory transduction is the conversion of stimulus energy into a change in the membrane potential of a sensory receptor
- This change in membrane potential is called a receptor potential
- Receptor potentials are graded potentials: Their magnitude varies with the strength of the stimulus

Transmission

- Sensory information travels through the nervous system as action potentials
- Sensory receptors may be neurons or nonneuronal receptors
- The size of a receptor potential increases with the intensity of the stimulus
- In sensory neurons that spontaneously generate action potentials at a low rate, a stimulus changes how often an action potential is produced



- Processing of sensory information can occur before, during, and after transmission of action potentials to the central nervous system (CNS)
- Integration often begins as soon as the information is received

Perception

- Perceptions are the brain's construction of stimuli
- Stimuli from different sensory receptors travel as action potentials along dedicated neural pathways
- The brain distinguishes stimuli from different receptors based on the path by which the action potentials arrive

Amplification and Adaptation

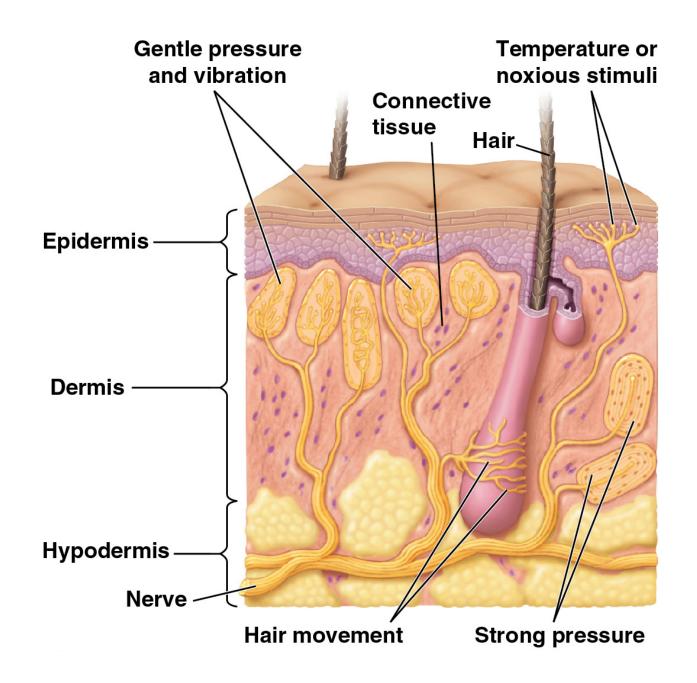
- Amplification is the strengthening of a sensory signal during transduction
- Sensory adaptation is a decrease in responsiveness to continued stimulation

Types of Sensory Receptors

- Based on energy transduced, sensory receptors fall into five categories
 - Mechanoreceptors
 - Chemoreceptors
 - Electromagnetic receptors
 - Thermoreceptors
 - Pain receptors

Mechanoreceptors

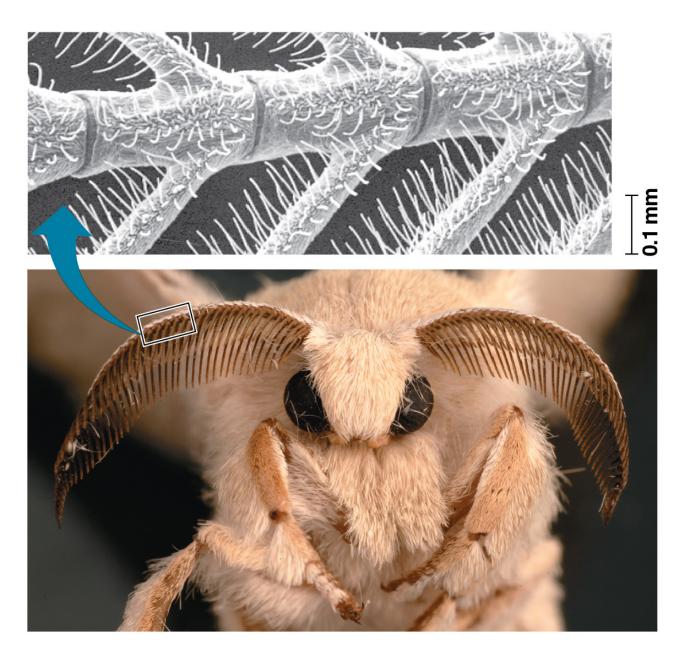
- Mechanoreceptors sense physical deformation caused by forms of mechanical energy
- They typically consist of ion channels linked to structures that end outside the cell, such as "hairs" (cilia)
- The mammalian sense of touch relies on mechanoreceptors that are dendrites of sensory neurons



Chemoreceptors

- Some chemoreceptors transmit information about the total solute concentration of a solution
- Others respond to specific molecules in body fluids
- When a stimulus molecule binds to a chemoreceptor, the chemoreceptor becomes more or less permeable to ions
- The antennae of the male silkworm moth have very sensitive specific chemoreceptors

Figure 50.6



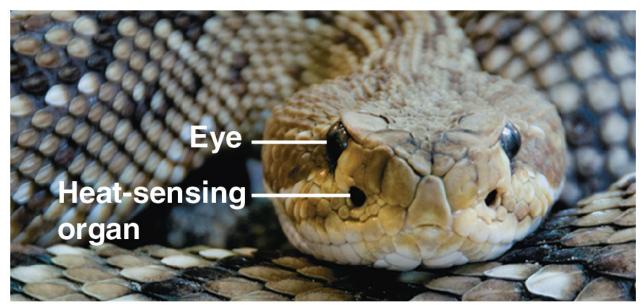
Electromagnetic Receptors

- Electromagnetic receptors detect electromagnetic energy such as light, electricity, and magnetism
- The platypus has electroreceptors on its bill that can detect the electric field generated by prey
- Many animals can migrate using Earth's magnetic field to orient themselves

Figure 50.7



(a) Beluga whales



(b) Rattlesnake

Thermoreceptors

- Thermoreceptors detect heat and cold
- Certain snakes rely on thermoreceptors to detect infrared radiation emitted by warm prey
- Jalapeno and cayenne peppers contain a substance called capsaicin
- Receptors that respond to capsaicin respond to high temperatures also, by opening a calcium channel
- Mammals have a variety of thermoreceptors, each specific for a particular temperature range

Pain Receptors

- In humans, pain receptors, or nociceptors, detect stimuli that reflect harmful conditions
- They respond to extreme pressure or temperature, or chemicals released from damaged or inflamed tissues
- Chemicals produced in an animal's body sometimes enhance the perception of pain

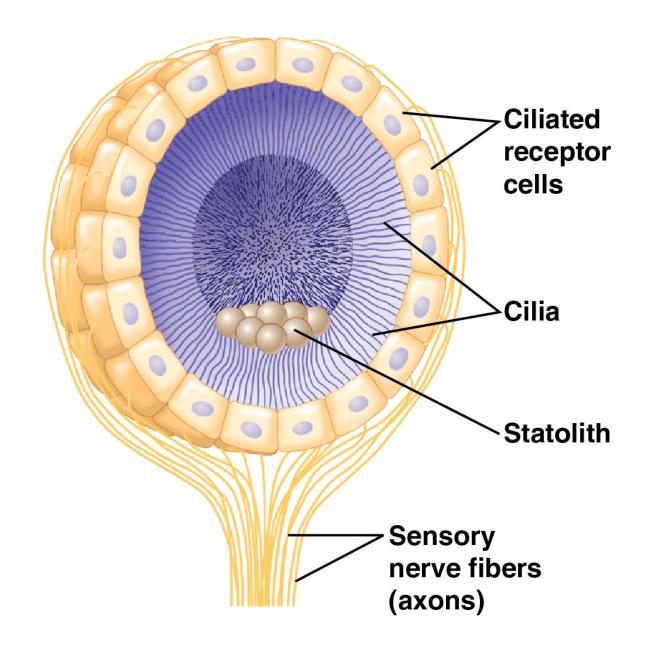
CONCEPT 50.2: In hearing and equilibrium, mechanoreceptors detect moving fluid or settling particles

- Hearing and perception of body equilibrium (sense of balance) are related in most animals
- For both senses, settling particles or moving fluid is detected by mechanoreceptors

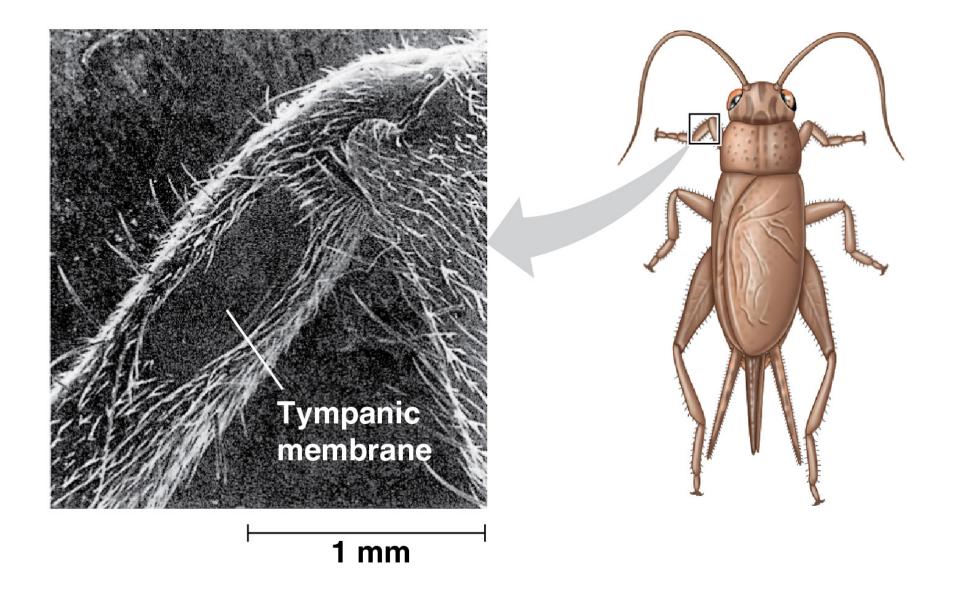
Sensing of Gravity and Sound in Invertebrates

- Most invertebrates maintain equilibrium using mechanoreceptors located in organs called statocysts
- Statocysts contain mechanoreceptors that detect the movement of granules called statoliths
- Statoliths provide information about the body position with respect to gravity

Figure 50.8



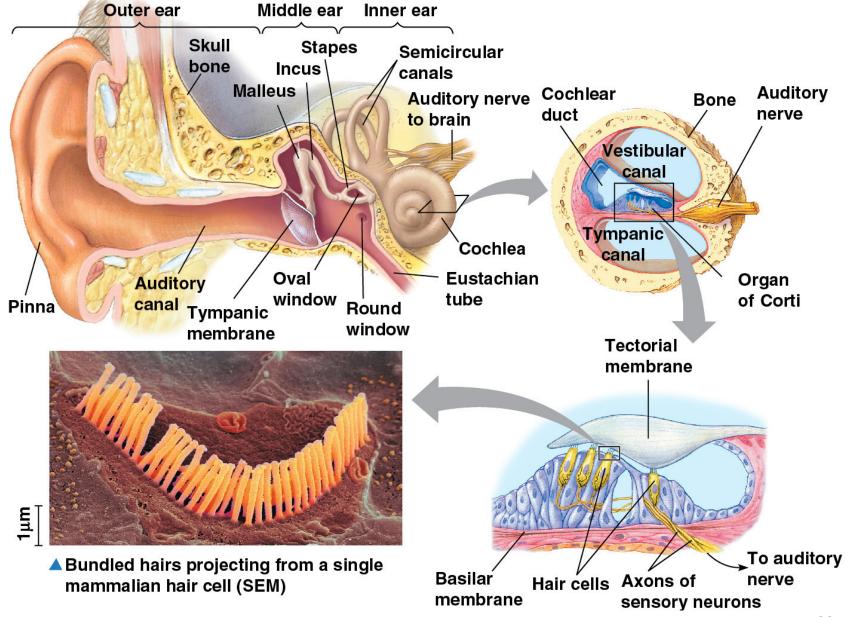
- Many insects have body hairs that vibrate in response to sound waves
- Many also detect sound with localized organs consisting of a tympanic membrane stretched over an internal air chamber



Hearing and Equilibrium in Mammals

 In most terrestrial vertebrates, sensory organs for hearing and equilibrium are closely associated in the ear

Figure 50.10

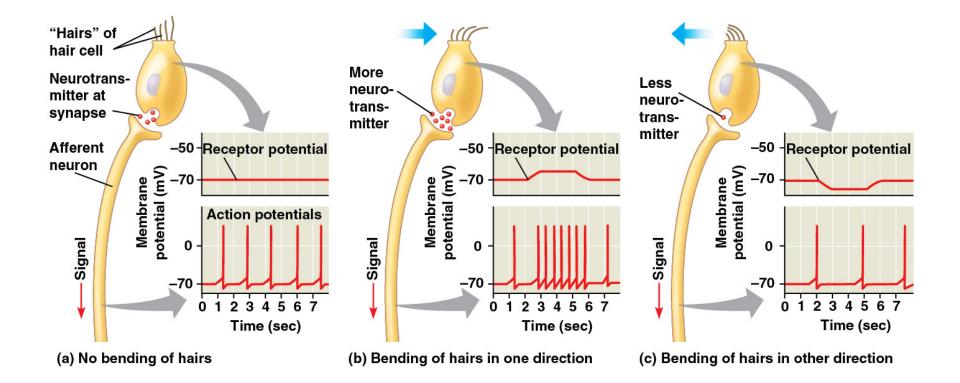


Hearing

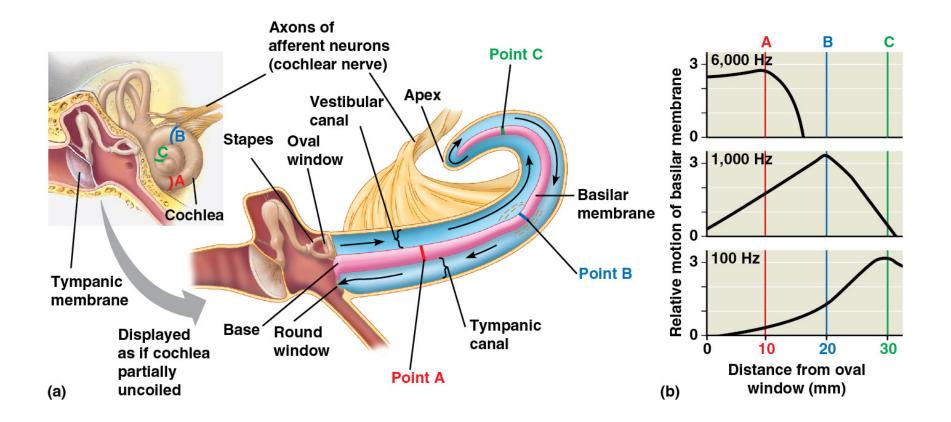
- Vibrating objects create pressure waves in the air
- The ear transduces this stimulus into nerve impulses
- To hear sounds, we rely on hair cells, sensory cells with hairlike projections that detect motion
- Moving air reaches the outer ear and causes vibration of the tympanic membrane
- The three bones of the middle ear transmit the vibrations to the oval window

- When one of the three bones, the stapes, vibrates again the oval window, it creates pressure waves in the fluid inside the cochlea
- Fluid pressure waves push down on the cochlear duct and basilar membrane
- The basilar membrane and the attached hair cells vibrate up and down

- The bending of hair cells depolarizes the membranes of mechanoreceptors and sends action potentials to the brain via the auditory nerve
- The fluid waves dissipate when they strike the round window at the end of the tympanic canal
- This damping of sound resets the apparatus for the next vibrations that arrive

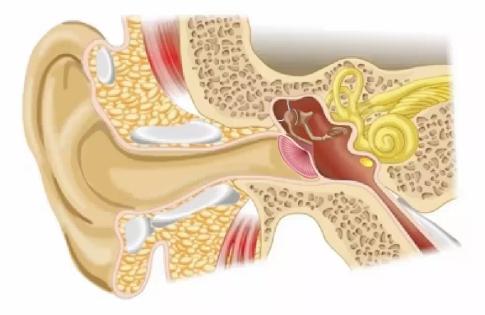


- The ear captures information about
 - Volume (loudness), the amplitude of the sound wave
 - Pitch, the frequency of the sound wave
- The cochlea can distinguish pitch because the basilar membrane is not uniform along its length
- Each region of the basilar membrane is tuned to a particular vibration frequency



Animation: The Human Ear

The Human Ear

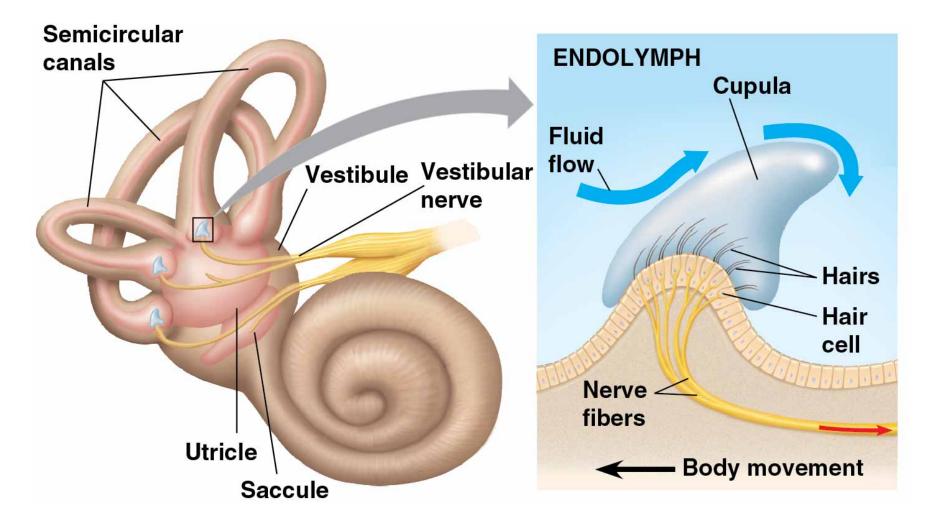




Equilibrium

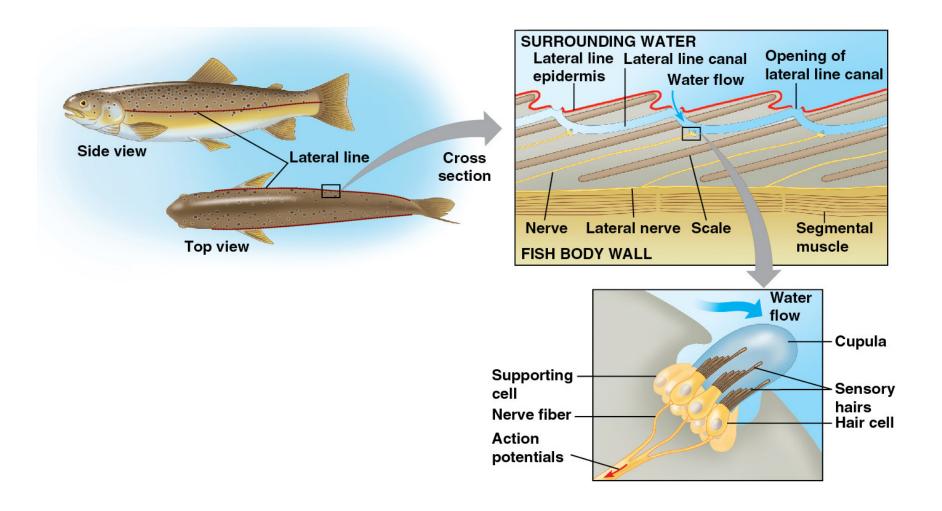
- Several organs in the inner ear detect body movement, position, and balance
 - The utricle and saccule contain hair cells projecting into a gelatinous material
 - Embedded in the gel are granules called otoliths that allow us to perceive position relative to gravity or linear movement
 - Three semicircular canals contain hair cells and fluid

- The hair cells in the semicircular canals form a cluster in a cap called a cupula
- The three canals are arranged in the three spatial planes
- This allows the detection of angular motion of the head in any direction



Hearing and Equilibrium in Other Vertebrates

- Unlike mammals, fishes have only a pair of inner ears near the brain
- Most fishes and aquatic amphibians also have a lateral line system along both sides of their body
- The lateral line system contains mechanoreceptors with hair cells that detect and respond to water movement



CONCEPT 50.3: The diverse visual receptors of animals depend on light-absorbing pigments

 Animals use a diverse set of organs for vision, but the underlying mechanism for capturing light is the same, suggesting a common evolutionary origin

Evolution of Visual Perception

- Light detectors in the animal kingdom range from simple clusters of cells that detect direction and intensity of light to complex organs that form images
- Light detectors all contain photoreceptors, cells that contain light-absorbing pigment molecules

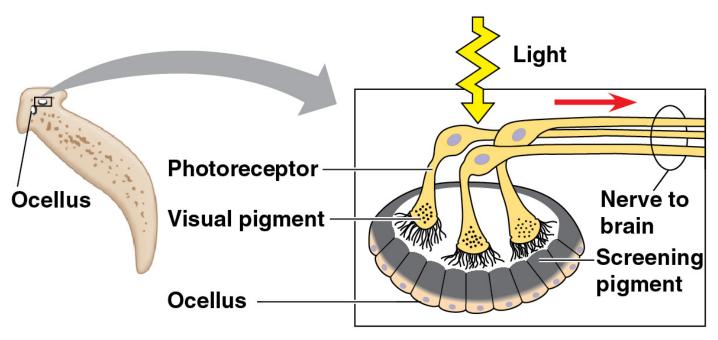
Light-Detecting Organs

- Most invertebrates have a light-detecting organ
- One of the simplest light-detecting organs is that of planarians
- A pair of ocelli called eyespots are located in the head region
- These allow planarians to move away from light and seek shaded locations

Figure 50.15

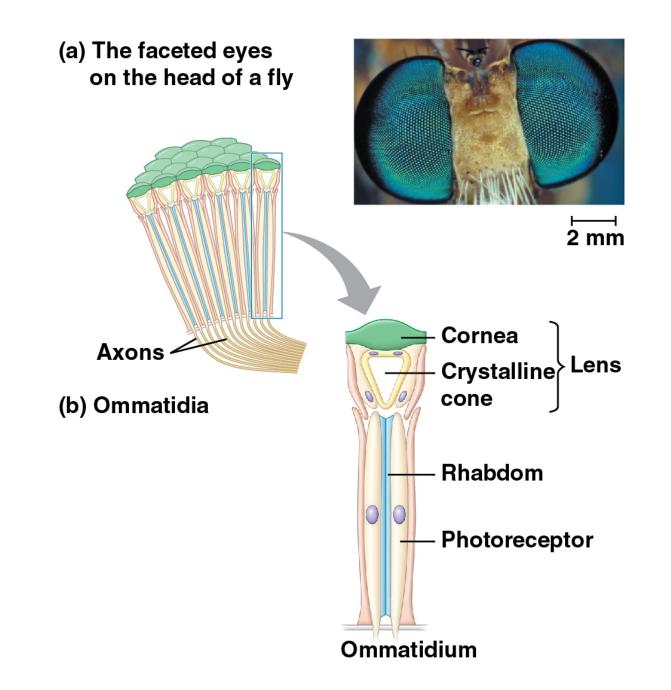


(a)



Compound Eyes

- Insects, crustaceans, and some polychaete worms have compound eyes, consisting of up to several thousand light detectors called ommatidia
- Compound eyes are very effective at detecting movement
- Insects have excellent color vision, and some can see into the ultraviolet range



Single-Lens Eyes

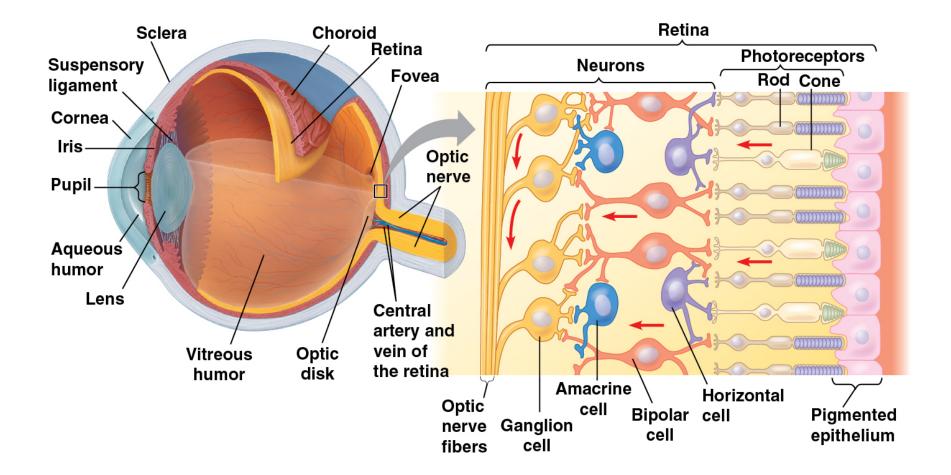
- Among invertebrates, single-lens eyes are found in some jellies and polychaete worms, as well as spiders and many molluscs
- They work on a camera-like principle: The iris changes the diameter of the pupil to control how much light enters
- The eyes of all vertebrates have a single lens

The Vertebrate Visual System

 In vertebrates, the eye detects color and light, but the brain assembles the information and perceives the image

- The human eye is surrounded by several layers
- Just inside the choroid (a thin, pigmented layer) are the neurons and photoreceptors of the retina
- The lens is a transparent disk of protein
- In front of the lens is the clear and watery aqueous humor and behind it is the jellylike vitreous humor

- Light entering the eye strikes the retina, reaching the rods and cones, two types of photoreceptors
- The neurons of the retina then relay visual information to the optic nerve and brain
- The optic disk, in the retina, lacks photoreceptors and thus forms a blind spot, where light is not detected



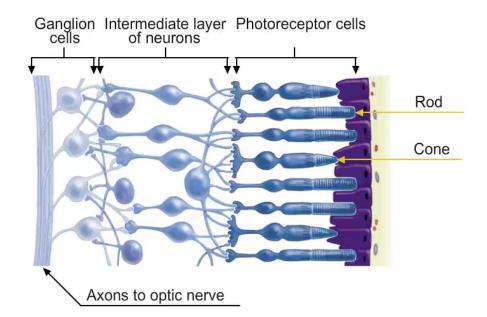
Animation: Structure and Function of the Eye

Structure and Function of the Eye

- Humans have two main types of photoreceptor cells
 - Rods are more sensitive to light, but do not distinguish colors
 - Cones provide color vision, but contribute very little to night vision

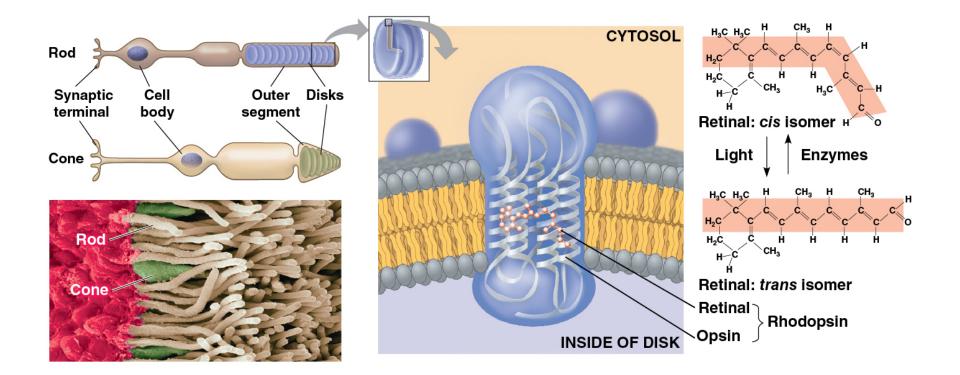
Animation: Photoreception

Photoreception





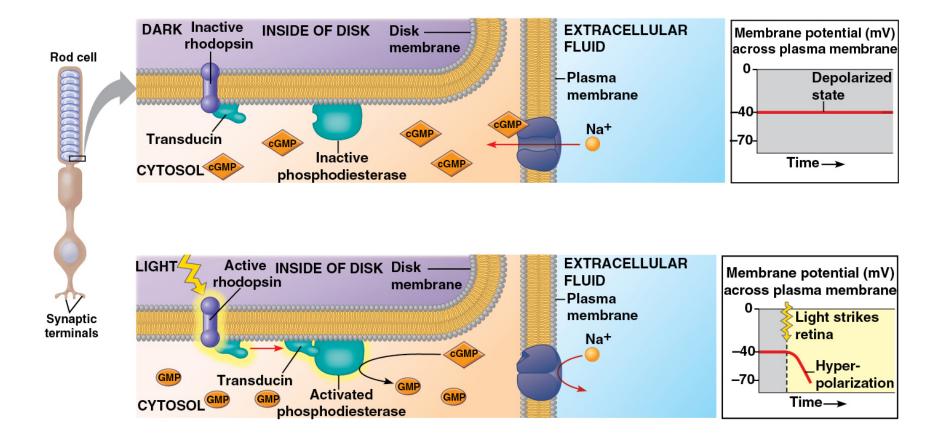
- Vertebrate visual pigments consist of retinal, a light-absorbing pigment bound to a membrane protein called an opsin
- One such pigment is called **rhodopsin**
- Absorption of light causes a shape change in retinal, from the *trans*- to the *cis*- form



Sensory Transduction in the Eye

- Transduction of visual information to the nervous system begins when light induces the conversion of *cis*-retinal to *trans*-retinal
- Trans-retinal activates rhodopsin, which activates a G protein, eventually leading to hydrolysis of cyclic GMP
- Cyclic GMP in the dark binds sodium ion channels and keeps them open

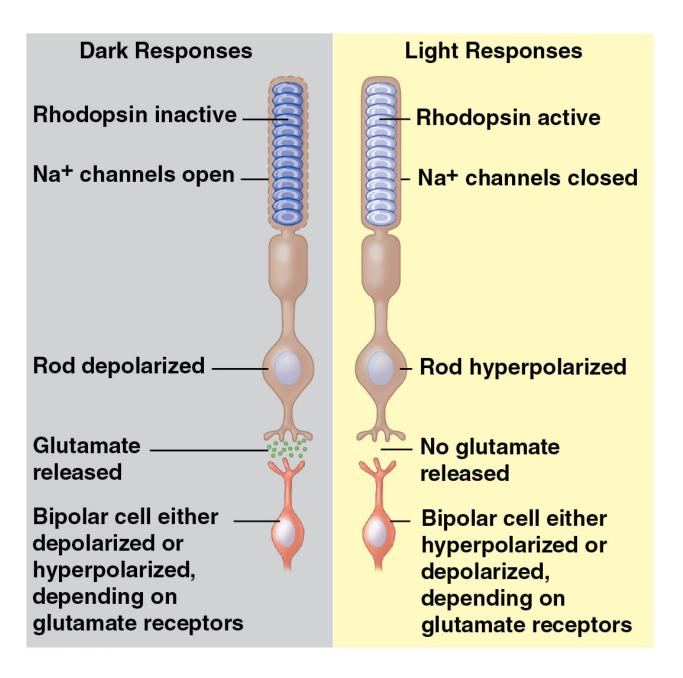
- When cyclic GMP breaks down, Na⁺ channels close
- This hyperpolarizes the cell
- The signal transduction pathway usually shuts off again as enzymes convert retinal back to the *cis* form



Processing of Visual Information in the Retina

- Processing of visual information begins in the retina
- In the dark, rods and cones continually release the neurotransmitter glutamate into synapses with neurons called bipolar cells
- When light strikes the rods and cones, they hyperpolarize, shutting off their release of glutamate
- The decrease in glutamate changes the membrane potential of bipolar cells

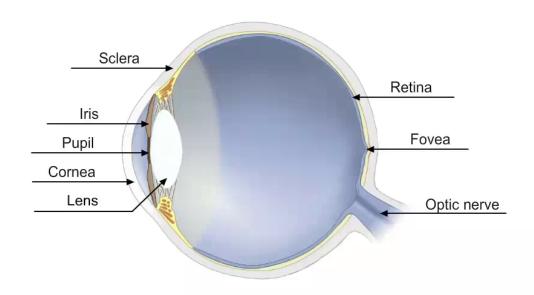
- Lateral inhibition is when a rod or cone stimulates a horizontal cell and the horizontal cell then inhibits more distant photoreceptors and bipolar cells
- In this way, regions receiving light appear lighter and dark surroundings even darker
- This enhances contrast in an image



- A single ganglion receives information from an array of rods and cones
- Together, the rods and cones that are feeding information to one ganglion cell define a receptive field
- A smaller receptive field typical results in a sharper image

Animation: Function of the Retina

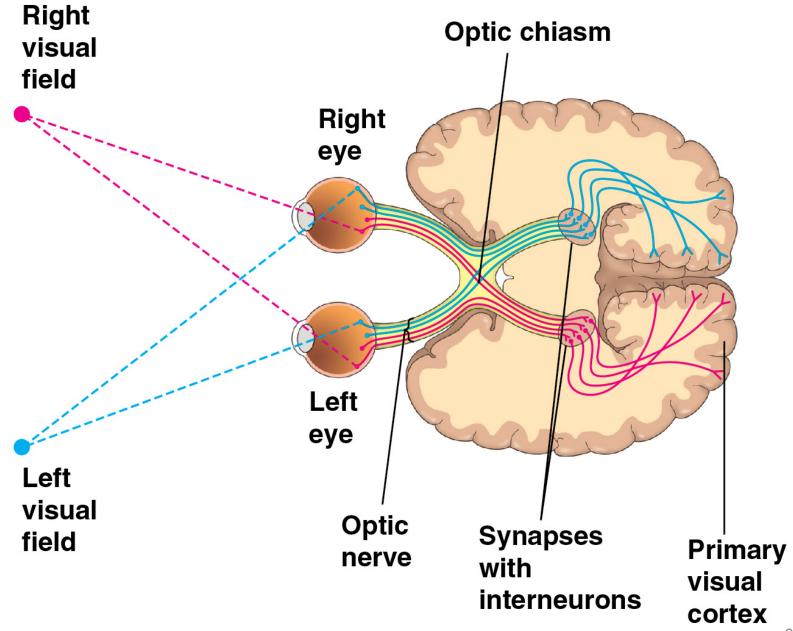
Function of the Retina



Processing of Visual Information in the Brain

- The optic nerves meet at the optic chiasm near the center of the base of the cerebral cortex
- Sensations from the left visual field of both eyes are transmitted to the right side of the brain
- Sensations from the right visual field of both eyes are transmitted to the left side of the brain

- Most ganglion cell axons lead to the lateral geniculate nuclei
- The lateral geniculate nuclei relay information to the primary visual cortex in the cerebrum
- At least 30% of the cerebral cortex, in dozens of integrating centers, is active in creating visual perceptions

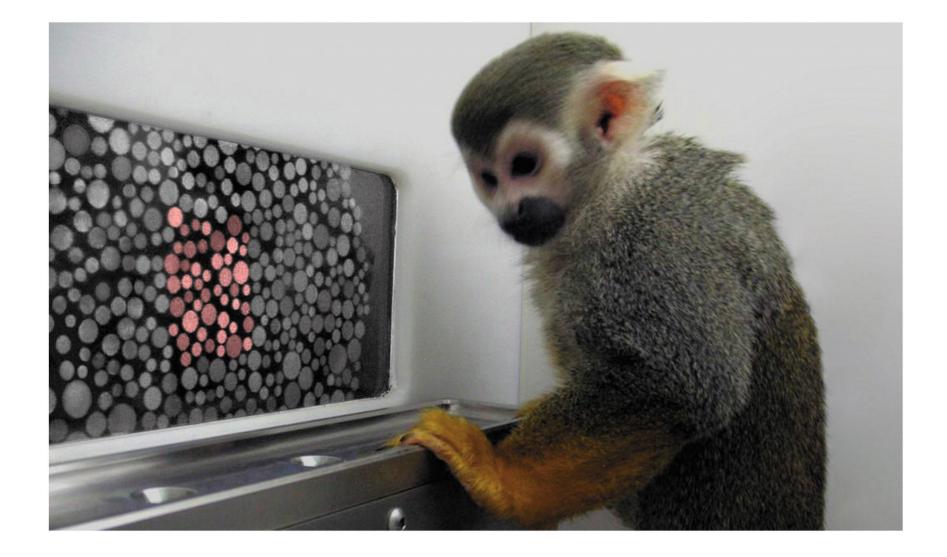


Color Vision

- 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 the ability to see color well
- Mammals that are nocturnal, such as cats, usually have a high proportion of rods in the retina and probably see a pastel world during the day

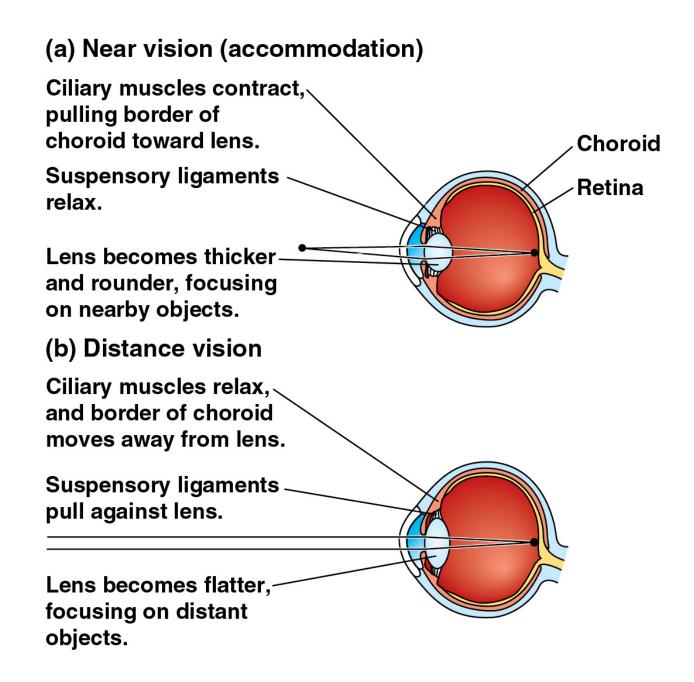
- In humans, perception of color is based on three types of cones, each with a different visual pigment: red, green, or blue
- These pigments are called photopsins and are formed when retinal binds to three distinct opsin proteins

- Abnormal color vision results from mutations in the genes for one or more photopsin proteins
- Researchers studying color vision in squirrel monkeys made a breakthrough in gene therapy
- Male squirrel monkeys are red-green color-blind
- When researchers introduced the missing gene using a virus, full color vision was apparent

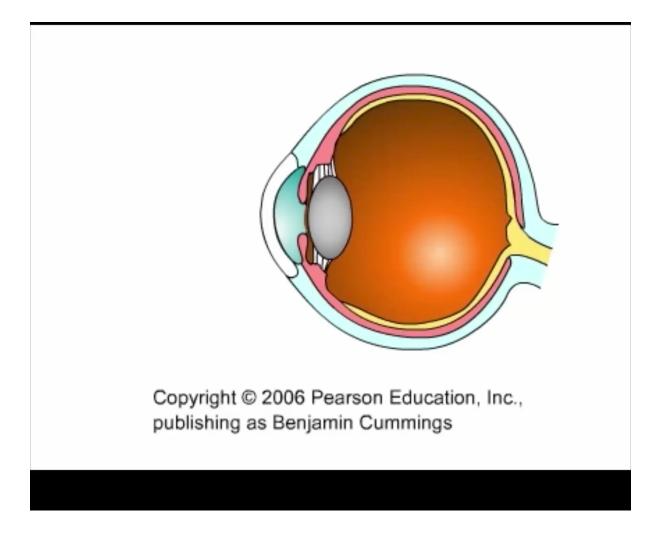


The Visual Field

- The brain processes visual information and controls what information is captured
- Focusing occurs by changing the shape of the lens
- The **fovea** is the center of the visual field and contains no rods, but a high density of cones



Animation: Near and Distance Vision



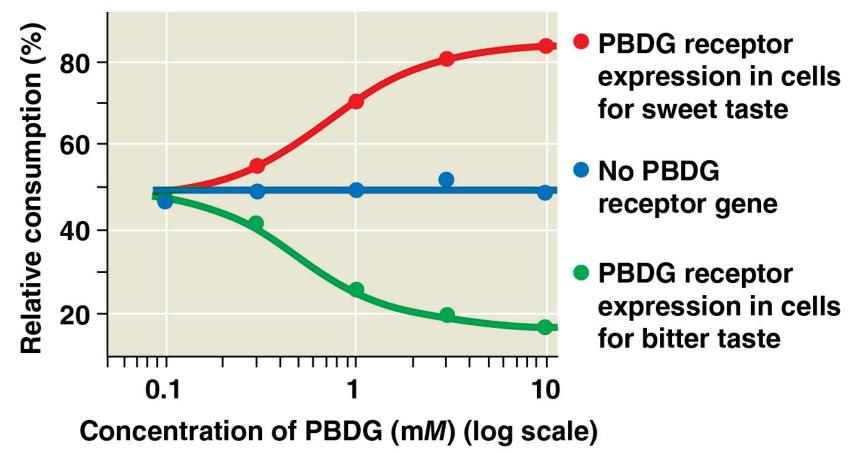
CONCEPT 50.4: The senses of taste and smell rely on similar sets of sensory receptors

- In terrestrial animals
 - Gustation (taste) is dependent on the detection of chemicals called tastants, present in a solution
 - Olfaction (smell) is dependent on the detection of odorant molecules, carried through the air
- In aquatic animals there is no distinction between taste and smell
- Taste receptors of insects are in sensory hairs located on feet and in mouthparts

Taste in Mammals

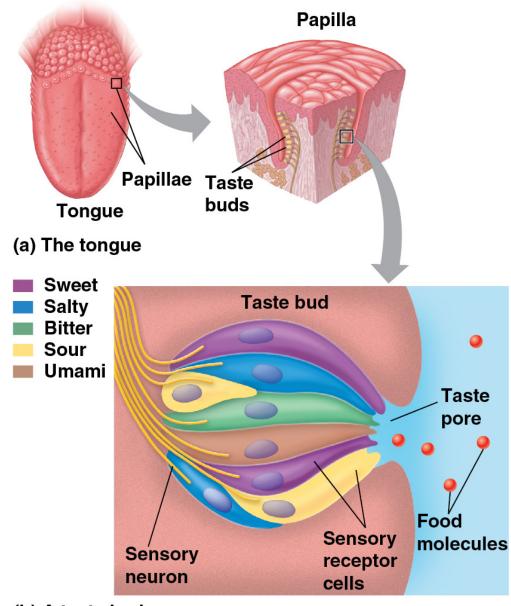
- In humans and other mammals, there are five taste perceptions: sweet, sour, salty, bitter, and umami (elicited by glutamate)
- Researchers have identified receptors for all five tastes
- Experiments show that an individual taste cell expresses one receptor type and detects one of the five tastes





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

- Receptor cells for taste in mammals are modified epithelial cells organized into taste buds, located in several areas of the tongue and mouth
- Most taste buds are associated with projections called papillae
- Any region with taste buds can detect any of the five types of taste



(b) A taste bud

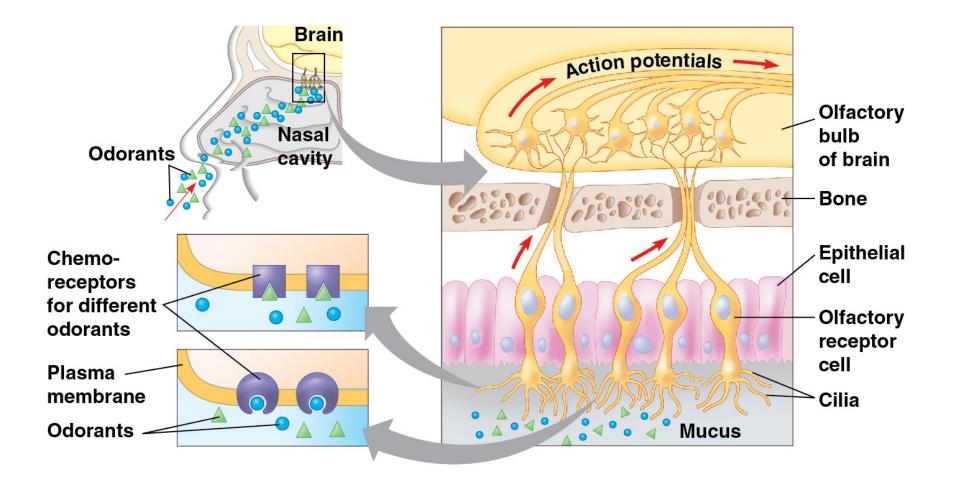
- Taste receptors are of three types
 - The sensations of sweet, umami, and bitter each require one or more genes encoding a G proteincoupled receptor (GPCR)
 - The receptor for sour belongs to the TRP family and is similar to the capsaicin receptor and other thermoreceptor proteins
 - The taste receptor for salt is a sodium channel

Smell in Humans

- Olfactory receptor cells are neurons that line the upper portion of the nasal cavity
- Binding of odorant molecules to receptors triggers a signal transduction pathway, generating action potentials that travel to the olfactory bulb of the brain

- Mammals can distinguish thousands of different odors; they have hundreds, or thousands of genes that encode olfactory receptors (ORs)
- Identification of particular odors relies on two properties of the olfactory system
 - Each olfactory receptor cell expresses on OR (olfactory receptor) gene
 - Those cells that express the same OR gene transmit action potentials to the same small region of the olfactory bulb

- After odorants are detected, information from olfactory receptors is collected and integrated
- Signals from the nervous system regulate this process, increasing or decreasing the response to particular odorants
- Although receptors and brain pathways for taste and smell are independent, the two senses do interact
- Much of the flavor experienced by humans is due to our sense of smell



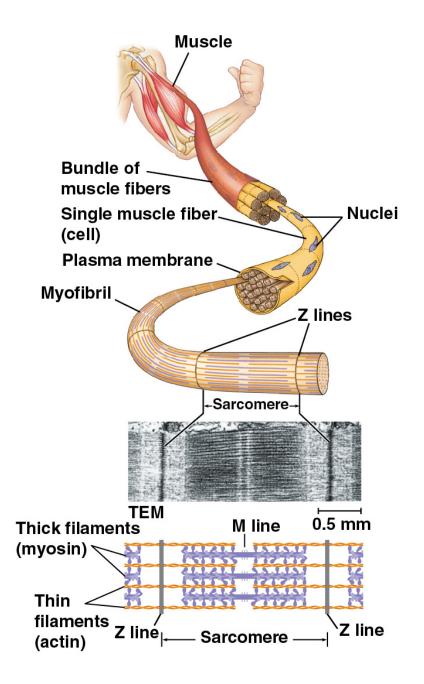
CONCEPT 50.5: The physical interaction of protein filaments is required for muscle function

- Muscle activity is a response to input from the nervous system
- Muscle cell contraction relies on the interaction between thin filaments, composed mainly of actin, and thick filaments, staggered arrays of myosin

Vertebrate Skeletal Muscle

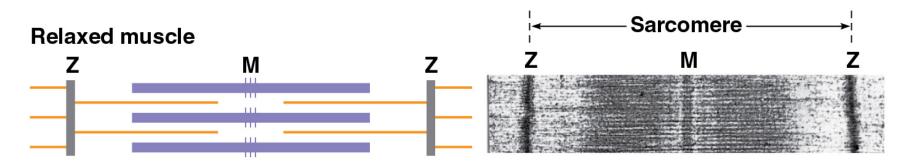
- Vertebrate skeletal muscle moves bones and the body and is characterized by a hierarchy of smaller and smaller units
- A skeletal muscle consists of a bundle of long fibers, each a single cell, running along the length of the muscle
- Each muscle fiber is itself a bundle of smaller myofibrils arranged longitudinally

- Skeletal muscle is also called striated muscle because the regular arrangement of myofilaments creates a pattern of light and dark bands
- The functional unit of a muscle is called a sarcomere and is bordered by Z lines, where thin filaments attach

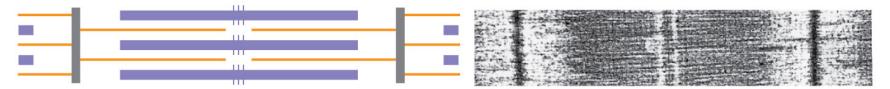


The Sliding-Filament Model of Muscle Contraction

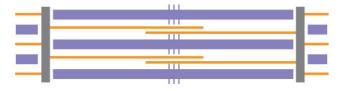
 According to the sliding-filament model, thin and thick filaments ratchet past each other longitudinally, powered by the myosin molecules

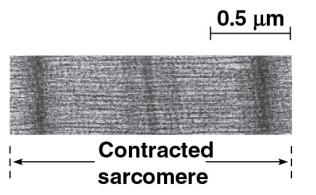


Contracting muscle



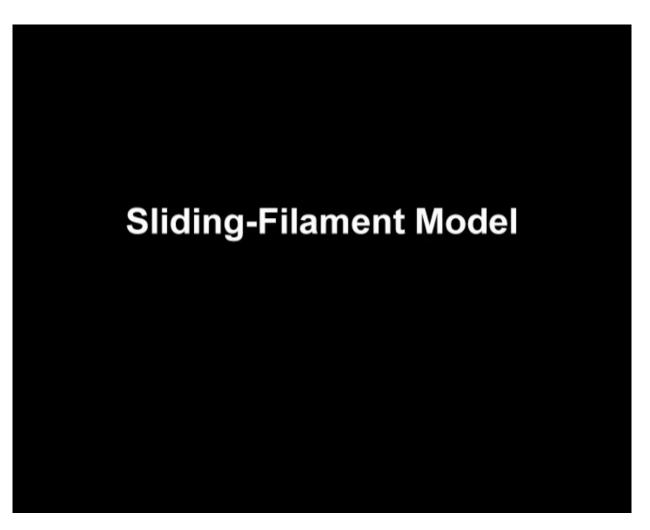
Fully contracted muscle



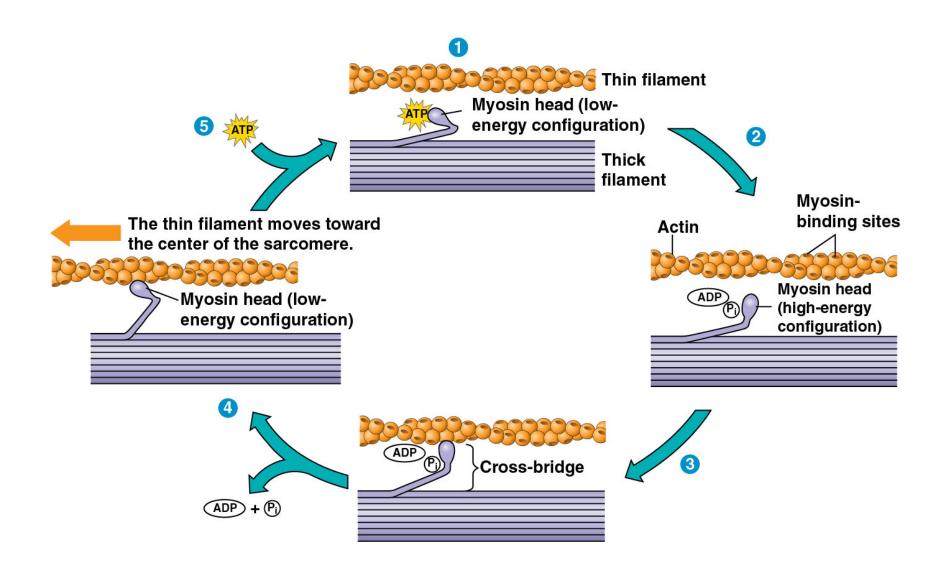


- Each myosin has a long "tail" region and a globular "head" region
- The head of a myosin molecule binds to an actin filament, forming a cross-bridge and pulling the thin filament toward the center of the sarcomere
- Muscle contraction requires repeated cycles of this binding and release

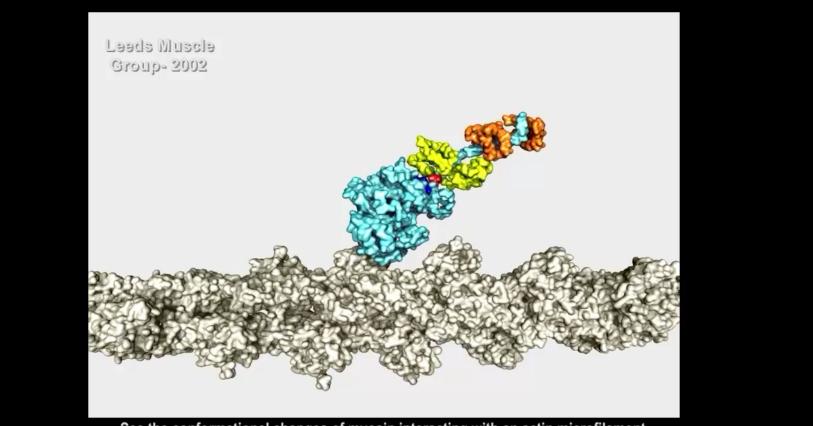
BioFlix® Animation: Sliding-filament model of muscle contraction



- Glycolysis and aerobic respiration generate the ATP needed to sustain muscle contraction
- During intense muscle activity, oxygen becomes limiting and ATP is generated instead by lactic acid fermentation
- This activity generates less ATP per glucose than glycolysis and can sustain contraction for only about 1 minute



Video: Myosin-Actin Interaction

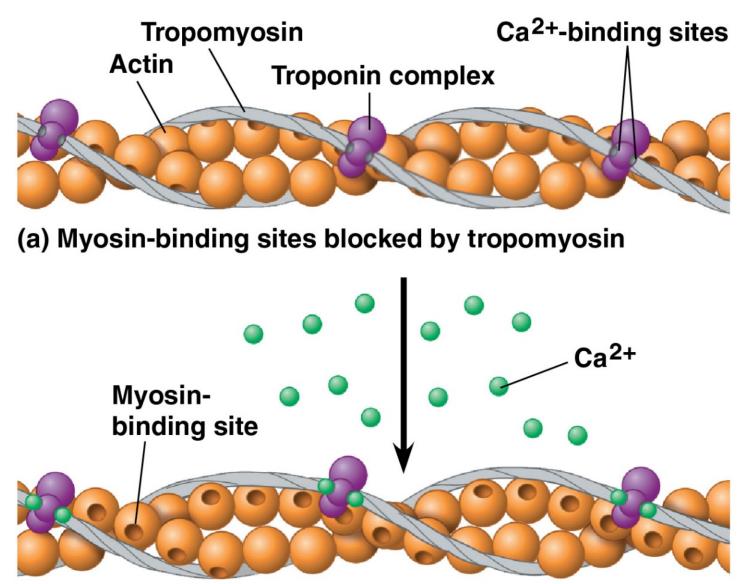


See the conformational changes of myosin interacting with an actin microfilament.

The Role of Calcium and Regulatory Proteins

- The regulatory protein tropomyosin and the troponin complex, a set of additional proteins, bind to actin strands on thin filaments when a muscle fiber is at rest
- This prevents actin and myosin from interacting

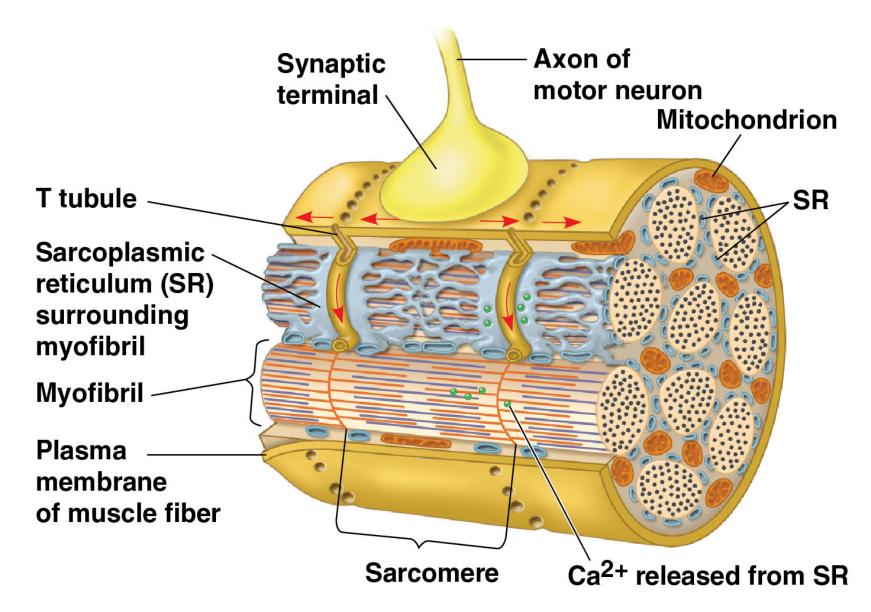
- For a muscle fiber to contract, myosin-binding sites must be exposed
- This occurs when calcium ions (Ca²⁺) bind to the troponin complex and expose the myosin-binding sites
- Contraction occurs when the concentration of Ca²⁺ is high; muscle fiber contraction stops when the concentration of Ca²⁺ is low



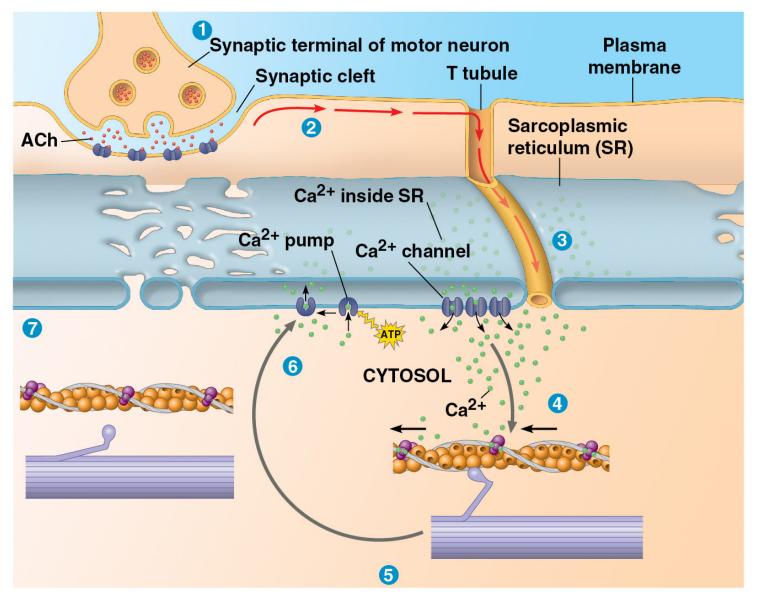
(b) Myosin-binding sites exposed

- The stimulus leading to contraction of a muscle fiber is an action potential in a motor neuron that makes a synapse with the muscle fiber
- The synaptic terminal of the motor neuron releases the neurotransmitter acetylcholine
- Acetylcholine depolarizes the muscle, causing it to produce an action potential

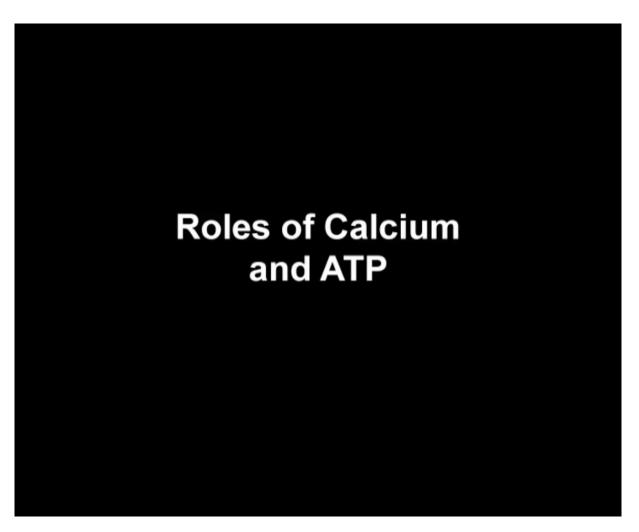
- Action potentials travel to the interior of the muscle fiber along transverse (T) tubules
- The action potential along T tubules causes the sarcoplasmic reticulum (SR) to release Ca²⁺
- The Ca²⁺ binds to the troponin complex, initiating the muscle fiber contraction



- When motor neuron input stops, the muscle cell relaxes
- Transport proteins in the SR pump Ca²⁺ out of the cytosol back into the SR
- Regulatory proteins bound to thin filaments shift back to their starting positions



BioFlix® Animation: Roles of Calcium and ATP in Muscle Contraction

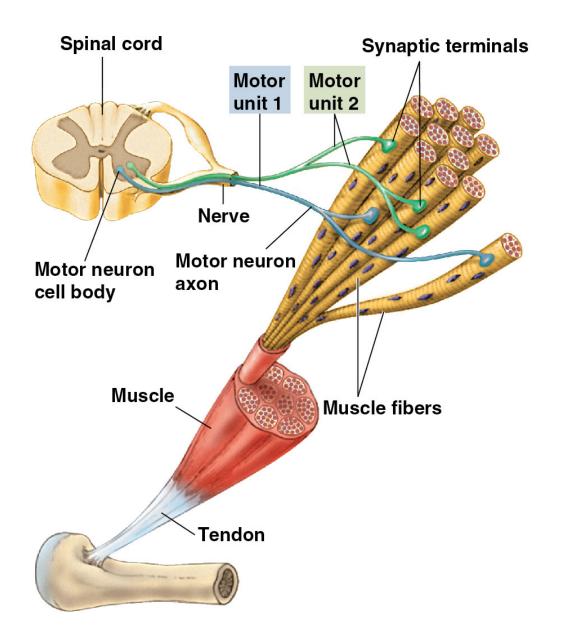


- Amyotrophic lateral sclerosis (ALS) interferes with the excitation of skeletal muscle fibers
- This disease is progressive and usually fatal within five years of symptoms appearing
- Myasthenia gravis is an autoimmune disease that attacks acetylcholine receptors on muscle fibers
- It can generally be controlled with drugs that inhibit acetylcholinesterase or suppress the immune system

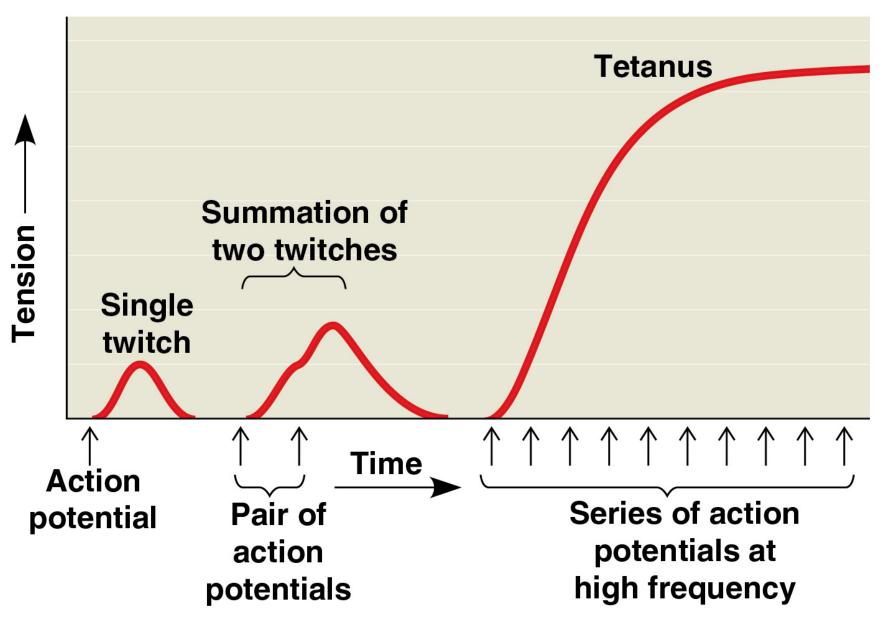
Nervous Control of Muscle Tension

- Contraction of a whole muscle is graded; the extent and strength of its contraction can be voluntarily altered
- There are two basic mechanisms by which the nervous system produces graded contractions
 - Varying the number of fibers that contract
 - Varying the rate at which fibers are stimulated

- In vertebrates, each motor neuron may synapse with multiple 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



- Recruitment is the process by which more and more motor neurons are activated
- As recruitment proceeds, the force developed by a muscle increases
- A twitch results from a single action potential in a motor neuron
- More rapidly delivered action potentials produce a graded contraction through summation



 Tetanus is a state of smooth and sustained contraction produced when the rate of stimulation is so high that muscle fibers cannot relax between stimuli

Types of Skeletal Muscle Fibers

- There are several distinct types of skeletal muscles, each of which is adapted to a particular set of functions
- They are classified by the source of ATP powering the muscle activity or by the speed of muscle contraction

Table 50.1 Types of Skeletal Muscle Fibers			
	Slow-Twitch	Fast-Twitch	
	Oxidative	Oxidative	Glycolytic
Contraction speed	Slow	Fast	Fast
Major ATP source	Aerobic respiration	Aerobic respiration	Glycolysis
Rate of fatigue	Slow	Intermediate	Fast
Mitochondria	Many	Many	Few
Myoglobin content	High (red muscle)	High (red muscle)	Low (white muscle)

Oxidative and Glycolytic Fibers (1 of 2)

- Oxidative fibers rely mostly on aerobic respiration to generate ATP
- These fibers have many mitochondria, a rich blood supply, and a large amount of myoglobin
- Myoglobin is a protein that binds oxygen more tightly than hemoglobin does

Oxidative and Glycolytic Fibers (2 of 2)

- Glycolytic fibers use glycolysis as their primary source of ATP
- Glycolytic fibers have less myoglobin and a larger diameter than oxidative fibers
- They also tire more easily
- In poultry and fish, light meat is composed of glycolytic fibers, while dark meat is composed of oxidative fibers

Fast-Twitch and Slow-Twitch Fibers (1 of 3)

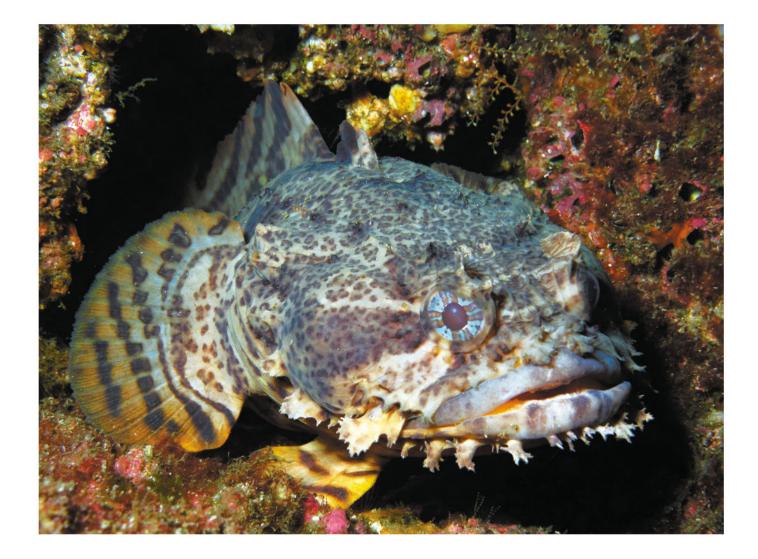
- Fast-twitch fibers enable brief, rapid, powerful contractions
- Fast-twitch fibers can be either glycolytic or oxidative

Fast-Twitch and Slow-Twitch Fibers (2 of 3)

- Slow-twitch fibers contract more slowly but sustain longer contractions
- Slow fibers have less sarcoplasmic reticulum than fast fibers and pump Ca²⁺ more slowly
- All slow-twitch fibers are oxidative

Fast-Twitch and Slow-Twitch Fibers (3 of 3)

- Most human skeletal muscles contain both slowtwitch and fast-twitch fibers in varying ratios
- Some vertebrates have muscles that twitch at rates much faster than human muscles
- In producing its characteristic mating call, the male oyster toadfish can contract and relax certain muscles more than 200 times per second



Other Types of Muscle

- In addition to skeletal muscle, vertebrates have cardiac muscle and smooth muscle
- Cardiac muscle, found only in the heart, consists of striated cells electrically connected by intercalated disks
- Cardiac muscle can generate action potentials without neural input

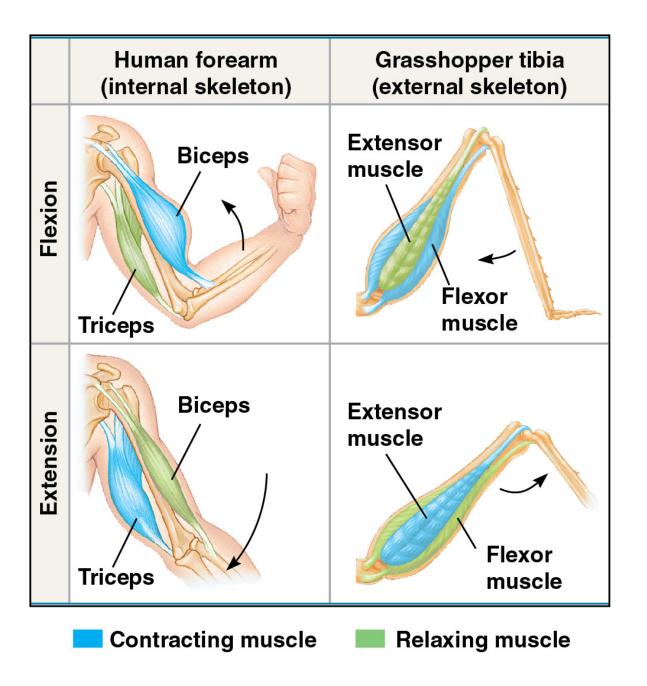
- Smooth muscle is found mainly in walls of hollow organs such as those of the circulatory, digestive, and reproductive systems
- Smooth muscle lacks striations, because the actin and myosin filaments are not regularly arrayed
- Contractions are slow and may be caused by stimulation from neurons in the autonomic nervous system
- Contractions may also be initiated by the muscles themselves

- Calcium regulates smooth muscle contraction but smooth muscle cells have no troponin complex or T tubules
- Their sarcoplasmic reticulum is not well developed
- Calcium ions enter the cytosol through the plasma membrane; they cause contraction by binding the protein calmodulin
- Calmodulin activates an enzyme that phosphorylates the myosin head, enabling crossbridge activity

CONCEPT 50.6: Skeletal systems transform muscle contraction into locomotion

- The skeleton provides a rigid structure to which muscles attach
- Skeletal muscles are attached in antagonistic pairs, the actions of which are coordinated by the nervous system
- The paired muscles work cooperatively
- Skeletons function in support, protection, and movement

Figure 50.35

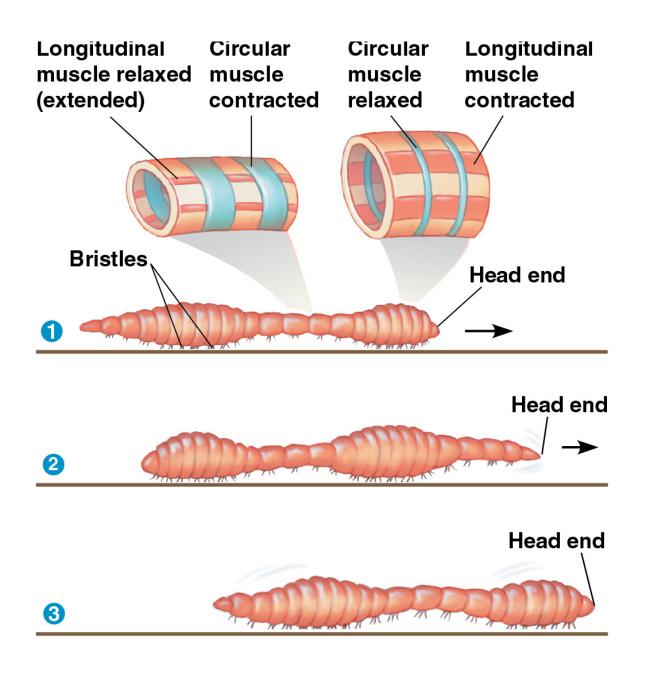


Types of Skeletal Systems

- The three main types of skeletons are
 - Exoskeletons (external hard parts)
 - Endoskeletons (internal hard parts)
 - Hydrostatic skeletons (fluid-based support)

Hydrostatic Skeletons

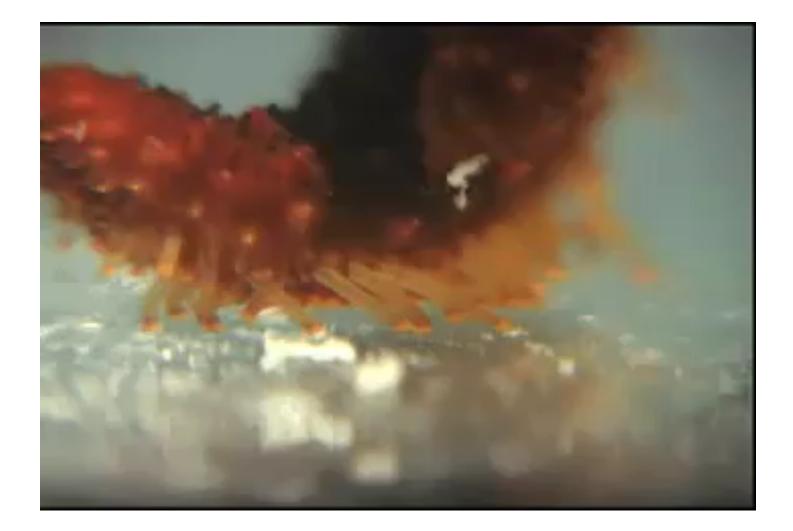
- A hydrostatic skeleton consists of fluid held under pressure in a closed body compartment
- This is the main type of skeleton in most cnidarians, flatworms, nematodes, and annelids
- Annelids use their hydrostatic skeleton for peristalsis, a type of movement produced by rhythmic waves of muscle contractions from front to back
- Hydrostatic skeletons are well suited for aquatic life



Video: Earthworm Locomotion



Video: Echinoderm tube feet



Video: Jelly Swimming



Video: Thimble Jellies

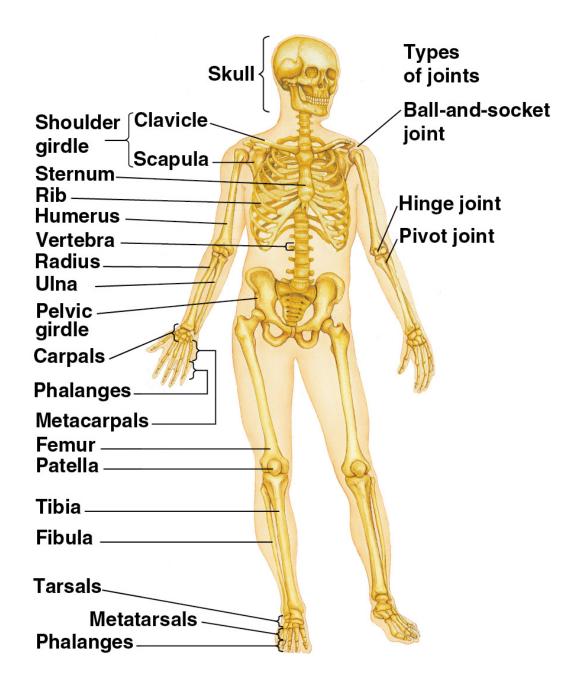


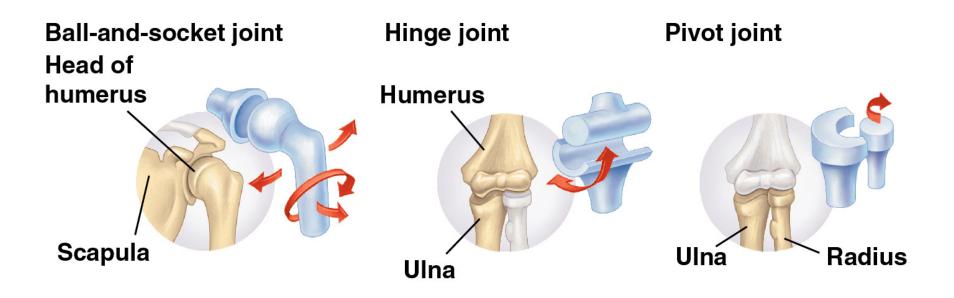
Exoskeletons

- An exoskeleton is a hard covering deposited on the surface of an animal
- Exoskeletons are found in most molluscs and arthropods
- Arthropods have a jointed exoskeleton called a cuticle, which can be both strong and flexible
- The polysaccharide chitin is often found in the arthropod cuticle

Endoskeletons

- An endoskeleton consists of a hard internal skeleton buried in soft tissue
- Endoskeletons are found in organisms ranging from sponges to mammals
- Vertebrate endoskeletons consist of cartilage, bone, or a combination of these
- A mammalian skeleton has more than 200 bones, some fused together, others connected at joints by ligaments





- The skeletons of small and large animals have different proportions
- In mammals and birds, the position of legs relative to the body is very important in determining how much weight the legs can bear

Types of Locomotion

- Most animals are capable of **locomotion**, active travel from place to place
- In locomotion, energy is expended to overcome friction and gravity

Locomotion on Land

- Walking, running, hopping, or crawling on land requires an animal to support itself and move against gravity
- Diverse adaptations for locomotion on land have evolved in vertebrates



- Air poses relatively little resistance for land locomotion
- Maintaining balance is a prerequisite to walking, running, or hopping
- Crawling poses a different challenge; a crawling animal must exert energy to overcome friction

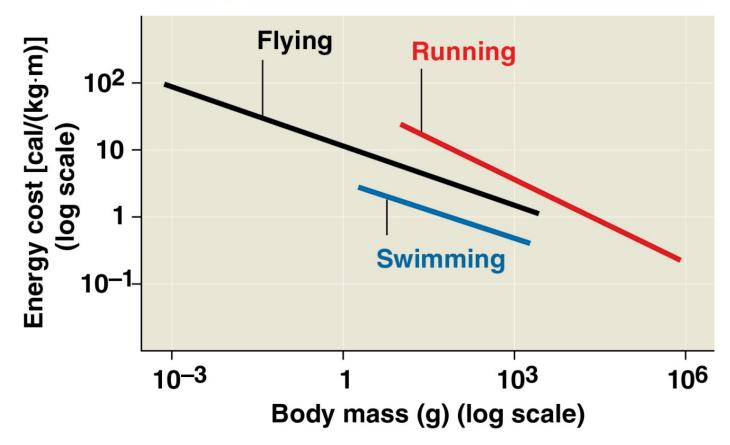
Swimming

- In water, friction is a bigger problem than gravity
- Fast swimmers usually have a sleek, torpedo-like shape to minimize friction
- Animals swim in diverse ways
 - Paddling with their legs as oars
 - Jet propulsion
 - Undulating their body and tail from side to side or up and down

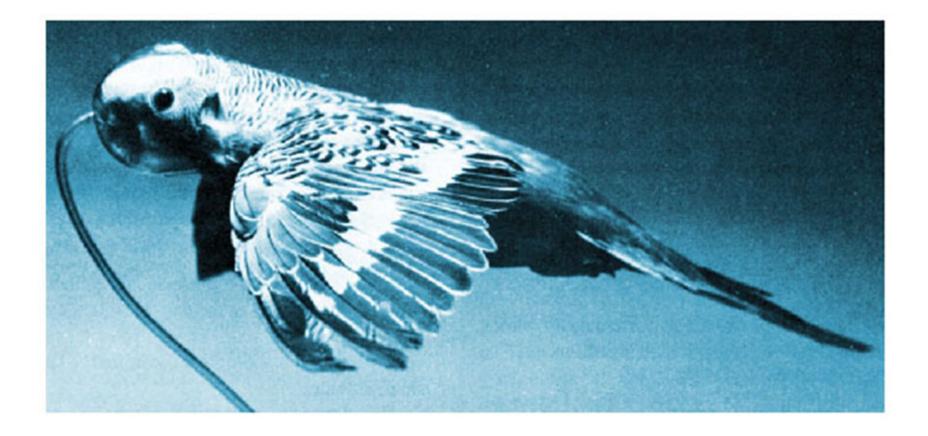
Flying

- Active flight requires that wings develop enough lift to overcome the downward force of gravity
- Many flying animals have adaptations that reduce body mass
 - For example, birds have no urinary bladder or teeth and have relatively large bones with air-filled regions

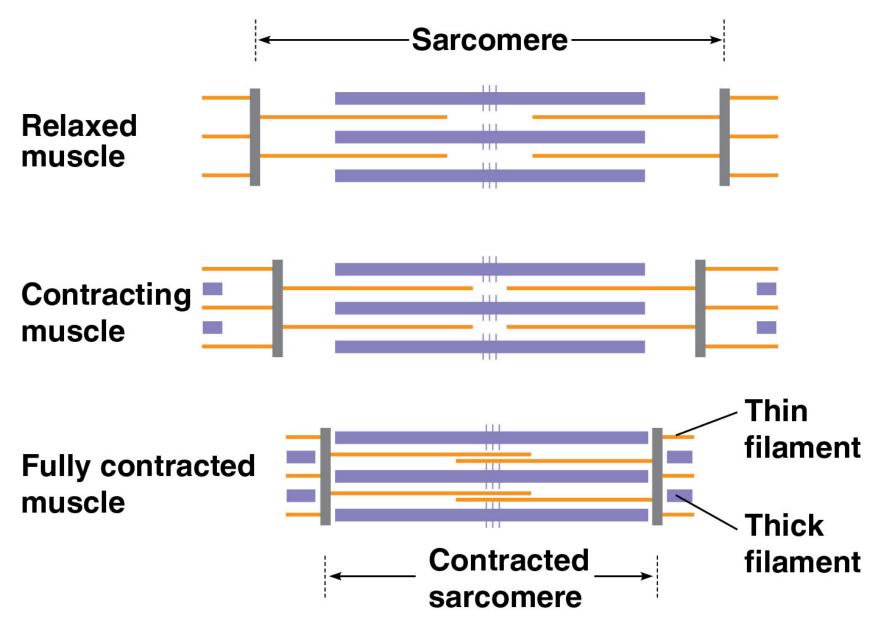


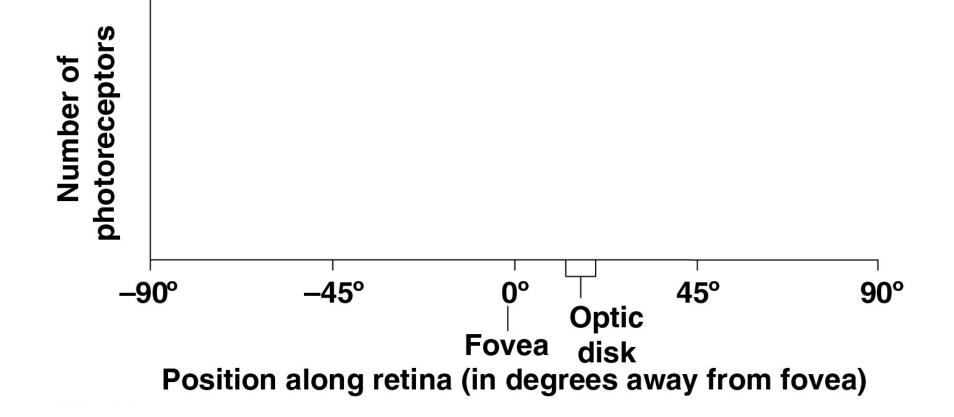


Data from K. Schmidt-Nielsen, Locomotion: Energy cost of swimming, flying, and running, *Science* 177:222–228 (1972). Reprinted with permission from AAAS









Frequency (hops/sec)	Energy used (joules/sec)	
1.85	735	
0.92	716	

