50

Locomotion

Concept Outline

50.1 A skeletal system supports movement in animals.

Types of Skeletons. There are three types of skeletal systems found in animals: hydrostatic skeletons, exoskeletons, and endoskeletons. Hydrostatic skeletons function by the movement of fluid in a body cavity. Exoskeletons are made of tough exterior coverings on which muscles attach to move the body. Endoskeletons are rigid internal bones or cartilage which move the body by the contraction of muscles attached to the skeleton.

The Structure of Bone. The human skeleton, an example of an endoskeleton, is made of bone that contains cells called osteocytes within a calcified matrix.

50.2 Skeletal muscles contract to produce movements at joints.

Types of Joints. The joints where bones meet may be immovable, slightly movable, or freely movable.

Actions of Skeletal Muscles. Synergistic and antagonistic muscles act on the skeleton to move the body.

50.3 Muscle contraction powers animal locomotion.

The Sliding Filament Mechanism of Contraction. Thick and thin myofilaments slide past one another to cause muscle shortening.

The Control of Muscle Contraction. During contraction Ca^{++} moves aside a regulatory protein which had been preventing cross-bridges from attaching to the thin filaments. Nerves stimulate the release of Ca^{++} from its storage depot so that contraction can occur.

Types of Muscle Fibers. Muscle fibers can be categorized as slow-twitch (slow to fatigue) or fast-twitch (fatigue quickly but can provide a fast source of power).

Comparing Cardiac and Smooth Muscles. Cardiac muscle cells are interconnected to form a single functioning unit. Smooth muscles lack the myofilament organization found in striated muscle but they still contract via the sliding filament mechanism.

Modes of Animal Locomotion. Animals rarely move in straight lines. Their movements are adjusted both by mechanical feedback and by neural control. Muscles generate power for movement, and also act as springs, brakes, struts, and shock absorbers.

FIGURE 50.1
On the move. The movements made by this sidewinder rattlesnake are the result of strong muscle contractions acting on the bones of the skeleton. Without muscles and some type of skeletal system, complex locomotion as shown here would not be possible.

Plants and fungi move only by growing, or as the passive passengers of wind and water. Of the three multicellular kingdoms, only animals explore their environment in an active way, through locomotion. In this chapter we examine how vertebrates use muscles connected to bones to achieve movement. The rattlesnake in figure 50.1 slithers across the sand by a rhythmic contraction of the muscles sheathing its body. Humans walk by contracting muscles in their legs. Although our focus in this chapter will be on vertebrates, it is important to realize that essentially all animals employ muscles. When a mosquito flies, its wings are moved rapidly through the air by quickly contracting flight muscles. When an earthworm burrows through the soil, its movement is driven by strong muscles pushing its body past the surrounding dirt.

50.1 A skeletal system supports movement in animals.

Types of Skeletons

Animal locomotion is accomplished through the force of muscles acting on a rigid skeletal system. There are three types of skeletal systems in the animal kingdom: hydraulic skeletons, exoskeletons, and endoskeletons.

Hydrostatic skeletons are primarily found in soft-bodied invertebrates such as earthworms and jellyfish. In this case, a fluid-filled cavity is encircled by muscle fibers. As the muscles contract, the fluid in the cavity moves and changes the shape of the cavity. In an earthworm, for example, a wave of contractions of circular muscles begins anteriorly and compresses each segment of the body, so that the fluid pressure pushes it forward. Contractions of longitudinal muscles then pull the rear of the body forward (figure 50.2).

Exoskeletons surround the body as a rigid hard case in most animals. Arthropods, such as crustaceans and insects, have exoskeletons made of the polysaccharide *chitin* (figure 50.3*a*). An exoskeleton offers great protection to internal organs and resists bending. However, in order to grow, the animal must periodically molt. During molting, the animal is particularly vulnerable to predation because its old exoskeleton has been shed. Having an exoskeleton also limits the size of the animal. An animal with an exoskeleton cannot get too large because its exoskeleton would have to become thicker and heavier, in order to prevent collapse, as the animal grew larger. If an insect were the size of a human being, its exoskeleton would have to be so thick and heavy it would be unable to move.

Endoskeletons, found in vertebrates and echinoderms, are rigid internal skeletons to which muscles are attached. Vertebrates have a flexible exterior that accommodates the movements of their skeleton. The endoskeleton of vertebrates is composed of cartilage or bone. Unlike chitin, bone is a cellular, living tissue capable of growth, self-repair, and remodeling in response to physical stresses.

The Vertebrate Skeleton

A vertebrate endoskeleton (figure 50.3*b*) is divided into an axial and an appendicular skeleton. The axial skeleton's bones form the axis of the body and support and protect the organs of the head, neck, and chest. The appendicular skeleton's bones include the bones of the limbs, and the pectoral and pelvic girdles that attach them to the axial skeleton.

The bones of the skeletal system support and protect the body, and serve as levers for the forces produced by contraction of skeletal muscles. Blood cells form within the bone marrow, and the calcified matrix of bones acts as a reservoir for calcium and phosphate ions.

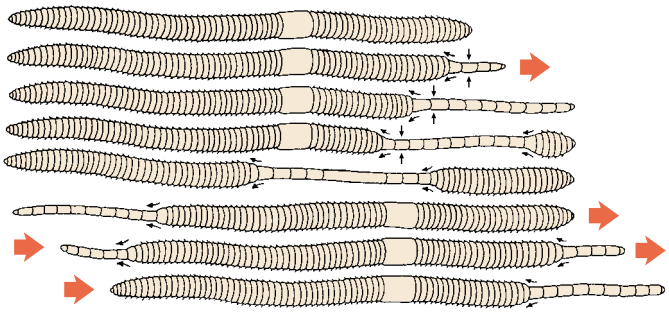


FIGURE 50.2
Locomotion in earthworms. The hydrostatic skeleton of the earthworm uses muscles to move fluid within the segmented body cavity changing the shape of the animal. When an earthworm's circular muscles contract, the internal fluid presses on the longitudinal muscles, which then stretch to elongate segments of the earthworms. A wave of contractions down the body of the earthworm produces forward movement.

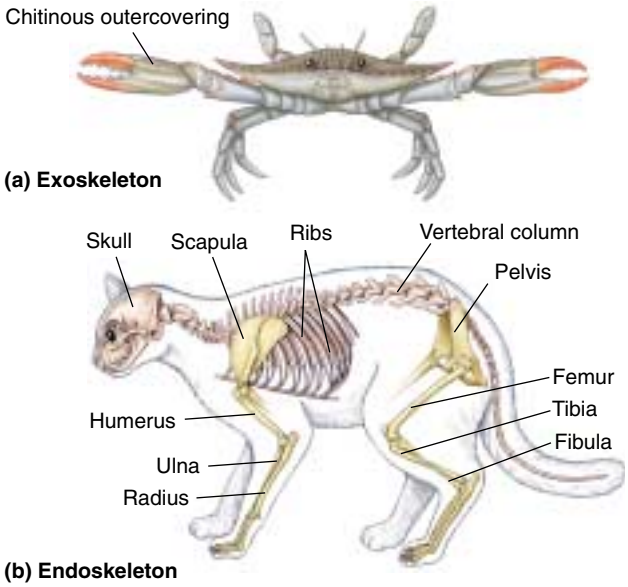


FIGURE 50.3
Exoskeleton and endoskeleton. (*a*) The hard, tough outcovering of an arthropod, such as this crab, is its exoskeleton. (*b*) Vertebrates, such as this cat, have endoskeletons. The axial skeleton is shown in the peach shade, the appendicular skeleton in the yellow shade. Some of the major bones are labeled.

There are three types of animal skeletons: hydrostatic skeleton, exoskeleton, and endoskeleton. The endoskeletons found in vertebrates are composed of bone or cartilage and are organized into axial and appendicular portions.

The Structure of Bone

Bone, the building material of the vertebrate skeleton, is a special form of connective tissue (see chapter 49). In bone, an organic extracellular matrix containing collagen fibers is impregnated with small, needle-shaped crystals of calcium phosphate in the form of hydroxyapatite crystals. Hydroxyapatite is brittle but rigid, giving bone great strength. Collagen, on the other hand, is flexible but weak. As a result, bone is both strong and flexible. The collagen acts to spread the stress over many crystals, making bone more resistant to fracture than hydroxyapatite is by itself.

Bone is a dynamic, living tissue that is constantly reconstructed throughout the life of an individual. New bone is formed by *osteoblasts*, which secrete the collagen-containing organic matrix in which calcium phosphate is later deposited. After the calcium phosphate is deposited, the cells, now known as osteocytes, are encased within spaces called *lacunae* in the calcified matrix. Yet another type of bone cells, called osteoclasts, act to dissolve bone and thereby aid in the remodeling of bone in response to physical stress.

Bone is constructed in thin, concentric layers, or *lamellae*, which are laid down around narrow channels called *Haversian canals* that run parallel to the length of the bone. Haversian canals contain nerve fibers and blood vessels, which keep the osteocytes alive even though they are entombed in a calcified matrix. The concentric lamellae of bone, with their entrapped osteocytes, that surround a Haversian canal form the basic unit of bone structure, called a Haversian system.

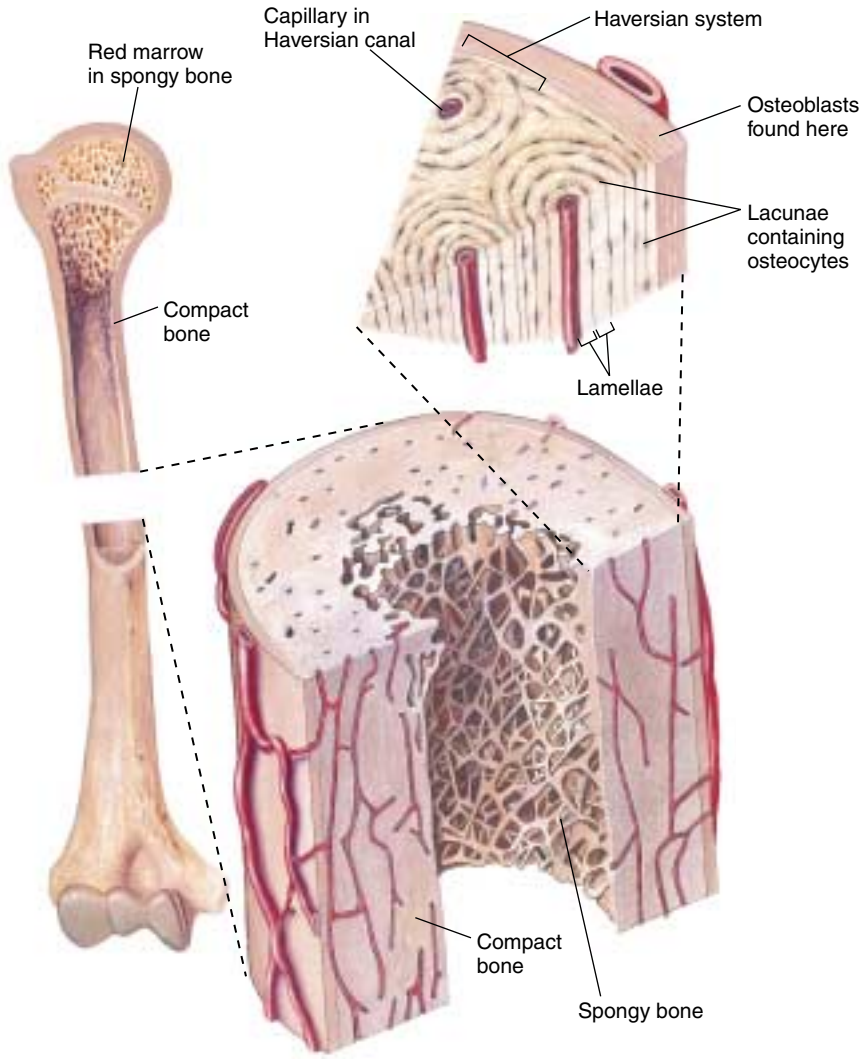


FIGURE 50.4
The organization of bone, shown at three levels of detail. Some parts of bone are dense and compact, giving the bone strength. Other parts are spongy, with a more open lattice; it is there that most blood cells are formed.

Bone formation occurs in two ways. In flat bones, such as those of the skull, osteoblasts located in a web of dense connective tissue produce bone within that tissue. In long bones, the bone is first "modeled" in cartilage. Calcification then occurs, and bone is formed as the cartilage degenerates. At the end of this process, cartilage remains only at the articular (joint) surfaces of the bones and at the growth plates located in the necks of the long bones. A child grows taller as the cartilage thickens in the growth plates and then is partly replaced with bone. A person stops growing (usually by the late teenage years) when the entire cartilage growth plate becomes replaced by bone. At this point, only the articular cartilage at the ends of the bone remains.

The ends and interiors of long bones are composed of an open lattice of bone called *spongy bone*. The spaces within contain marrow, where most blood cells are formed (figure 50.4). Surrounding the spongy bone tissue are concentric layers of *compact bone*, where the bone is much denser. Compact bone tissue gives bone the strength to withstand mechanical stress.

Bone consists of cells and an extracellular matrix that contains collagen fibers, which provide flexibility, and calcium phosphate, which provides strength. Bone contains blood vessels and nerves and is capable of growth and remodeling.

50.2 Skeletal muscles contract to produce movements at joints.

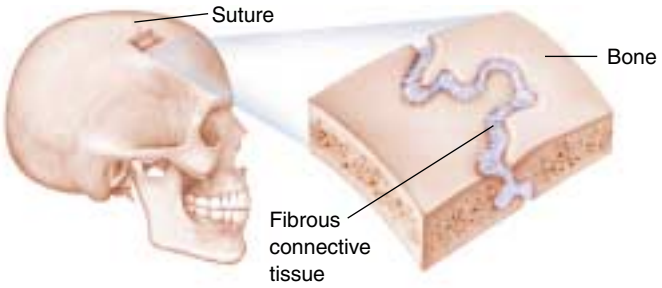
Types of Joints

The skeletal movements of the body are produced by contraction and shortening of muscles. Skeletal muscles are generally attached by tendons to bones, so when the muscles shorten, the attached bones move. These movements of the skeleton occur at joints, or articulations, where one bone meets another. There are three main classes of joints:

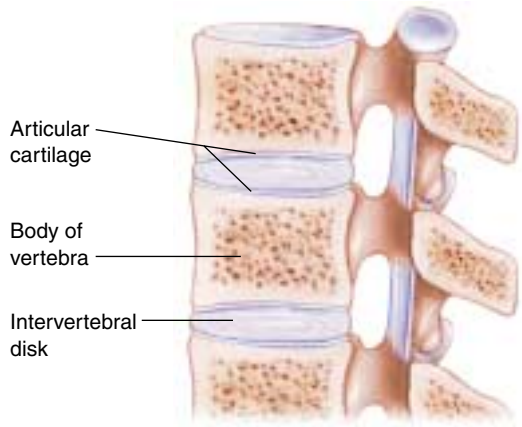
1. **Immovable joints** include the *sutures* that join the bones of the skull (figure 50.5*a*). In a fetus, the skull bones are not fully formed, and there are open areas of dense connective tissue ("soft spots," or *fontanels*) between the bones. These areas allow the bones to shift slightly as the fetus moves through the birth canal during childbirth. Later, bone replaces most of this connective tissue.
2. **Slightly movable joints** include those in which the bones are bridged by cartilage. The vertebral bones of the spine are separated by pads of cartilage called *intervertebral discs* (figure 50.5*b*). These *cartilaginous joints* allow some movement while acting as efficient shock absorbers.
3. **Freely movable joints** include many types of joints and are also called synovial joints, because the articulating ends of the bones are located within a *synovial capsule* filled with a lubricating fluid. The ends of the bones are capped with cartilage, and the synovial capsule is strengthened by ligaments that hold the articulating bones in place.

Synovial joints allow the bones to move in directions dictated by the structure of the joint. For example, a joint in the finger allows only a hingelike movement, while the joint between the thigh bone (femur) and pelvis has a ball-and-socket structure that permits a variety of different movements (figure 50.5*c*).

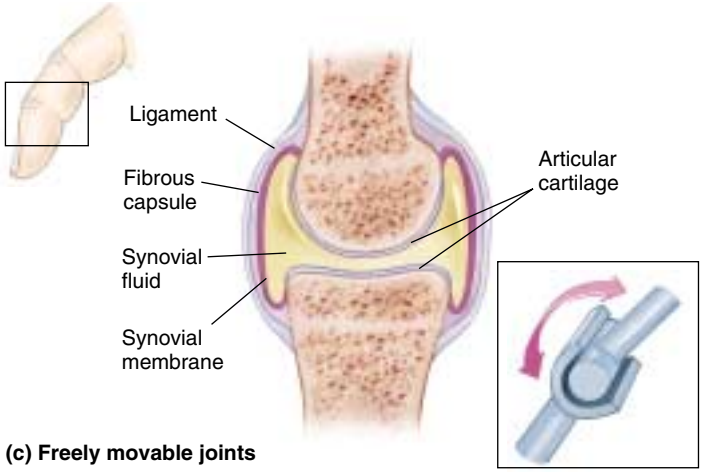
Joints confer flexibility to a rigid skeleton, allowing a range of motions determined by the type of joint.

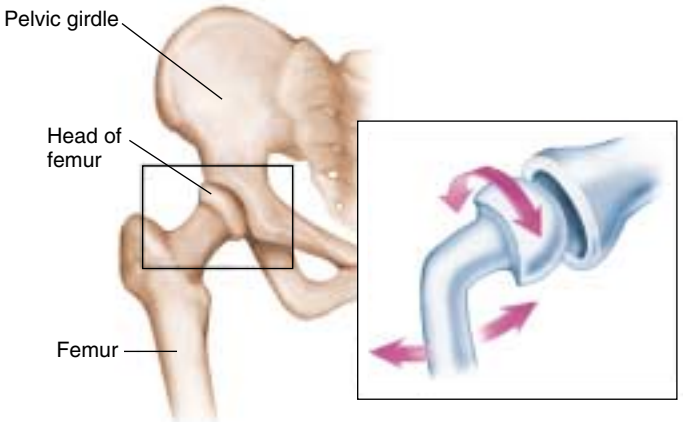


(a) Immovable joint



(b) Slightly movable joints





(c) Freely movable joints

FIGURE 50.5
Three types of joints. (*a*) Immovable joints include the sutures of the skull; (*b*) slightly movable joints include the cartilaginous joints between the vertebrae; and (*c*) freely movable joints are the synovial joints, such as a finger joint and or a hip joint.

Actions of Skeletal Muscles

Skeletal muscles produce movement of the skeleton when they contract. Usually, the two ends of a skeletal muscle are attached to different bones (although in some cases, one or both ends may be connected to some other kind of structure, such as skin). The attachments to bone are made by means of dense connective tissue straps called *tendons*. Tendons have elastic properties that allow "give-and-take" during muscle contraction. One attachment of the muscle, the **origin,** remains relatively stationary during a contraction. The other end of the muscle, the **insertion,** is attached to the bone that moves when the muscle contracts. For example, contraction of the biceps muscle in the upper arm causes the forearm (the insertion of the muscle) to move toward the shoulder (the origin of the muscle).

Muscles that cause the same action at a joint are **synergists**. For example, the various muscles of the quadriceps group in humans are synergists: they all act to extend the knee joint. Muscles that produce opposing actions are **antagonists.** For example, muscles that flex a joint are antagonist to muscles that extend that joint (figure 50.6*a*). In humans, when the hamstring muscles contract, they cause flexion of the knee joint (figure 50.6*b*). Therefore, the quadriceps and hamstrings are antagonists to each other. In general, the muscles that antagonize a given movement are relaxed when that movement is performed. Thus, when the hamstrings flex the knee joint, the quadriceps muscles relax.

Isotonic and Isometric Contractions

In order for muscle fibers to shorten when they contract, they must generate a force that is greater than the opposing forces that act to prevent movement of the muscle's insertion. When you lift a weight by contracting muscles in your biceps, for example, the force produced by the muscle is greater than the force of gravity on the object you are lifting. In this case, the muscle and all of its fibers shorten in length. This type of contraction is referred to as **isotonic contraction,** because the force of contraction remains relatively constant throughout the shortening process (*iso* = same; *tonic* = strength).

Preceding an isotonic contraction, the muscle begins to contract but the tension is absorbed by the tendons and other elastic tissue associated with the muscle. The muscle does not change in length and so this is called **isometric** (literally, "same length") **contraction.** Isometric contractions occur as a phase of normal muscle contraction but also exist to provide tautness and stability to the body.

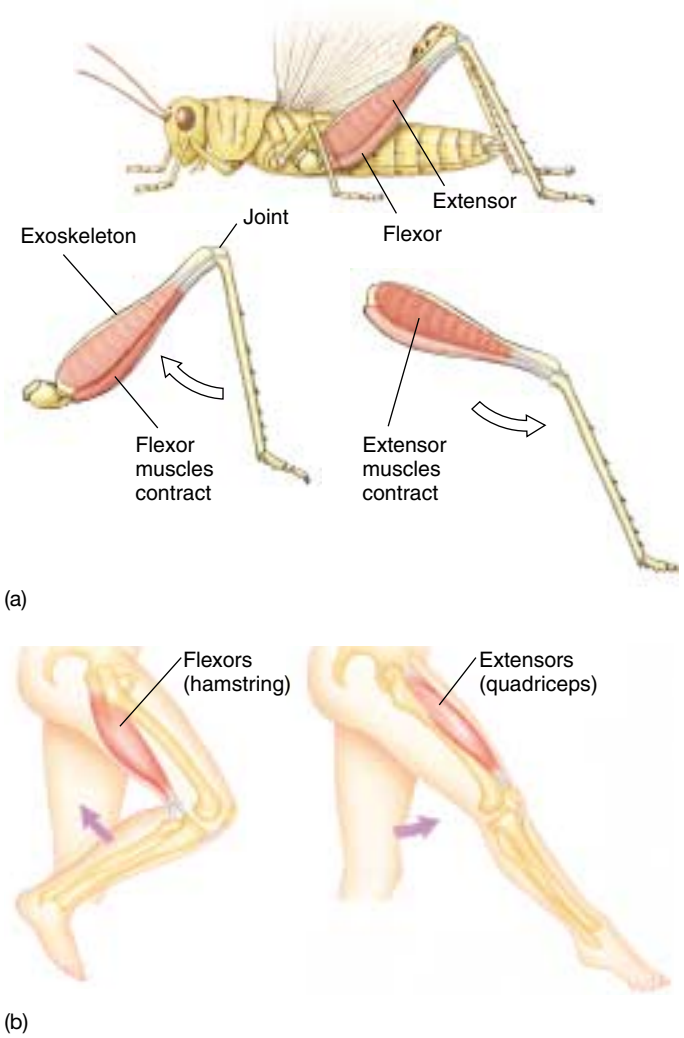


FIGURE 50.6
Flexor and extensor muscles of the leg. (*a*) Antagonistic muscles control the movement of an animal with an exoskeleton, such as the jumping of a grasshopper. When the smaller flexor tibia muscle contracts it pulls the lower leg in toward the upper leg. Contraction of the extensor tibia muscles straightens out the leg and sends the insect into the air. (*b*) Similarly, antagonistic muscles can act on an endoskeleton. In humans, the hamstrings, a group of three muscles, produce flexion of the knee joint, whereas the quadriceps, a group of four muscles, produce extension.

Synergistic muscles have the same action, whereas antagonistic muscles have opposite actions. Both muscle groups are involved in locomotion. Isotonic contractions involve the shortening of muscle, while isometric contractions do not alter the length of the muscle.

50.3 Muscle contraction powers animal locomotion.

The Sliding Filament Mechanism of Contraction

Each skeletal muscle contains numerous **muscle fibers,** as described in chapter 49. Each muscle fiber encloses a bundle of 4 to 20 elongated structures called **myofibrils.** Each myofibril, in turn, is composed of **thick** and **thin myofilaments** (figure 50.7). The muscle fiber is striated (has cross-striping) because its myofibrils are striated, with dark and light bands. The banding pattern results from the organization of the myofilaments within the myofibril. The thick myofilaments are stacked together to produce the dark bands, called *A bands;* the thin filaments alone are found in the light bands, or *I bands.*

Each I band in a myofibril is divided in half by a disc of protein, called a *Z line* because of its appearance in electron micrographs. The thin filaments are anchored to these discs of proteins that form the Z lines. If you look at an electron micrograph of a myofibril (figure 50.8), you will see that the structure of the myofibril repeats from Z line to Z line. This repeating structure, called a **sarcomere,** is the smallest subunit of muscle contraction.

The thin filaments stick partway into the stack of thick filaments on each side of an A band, but, in a resting

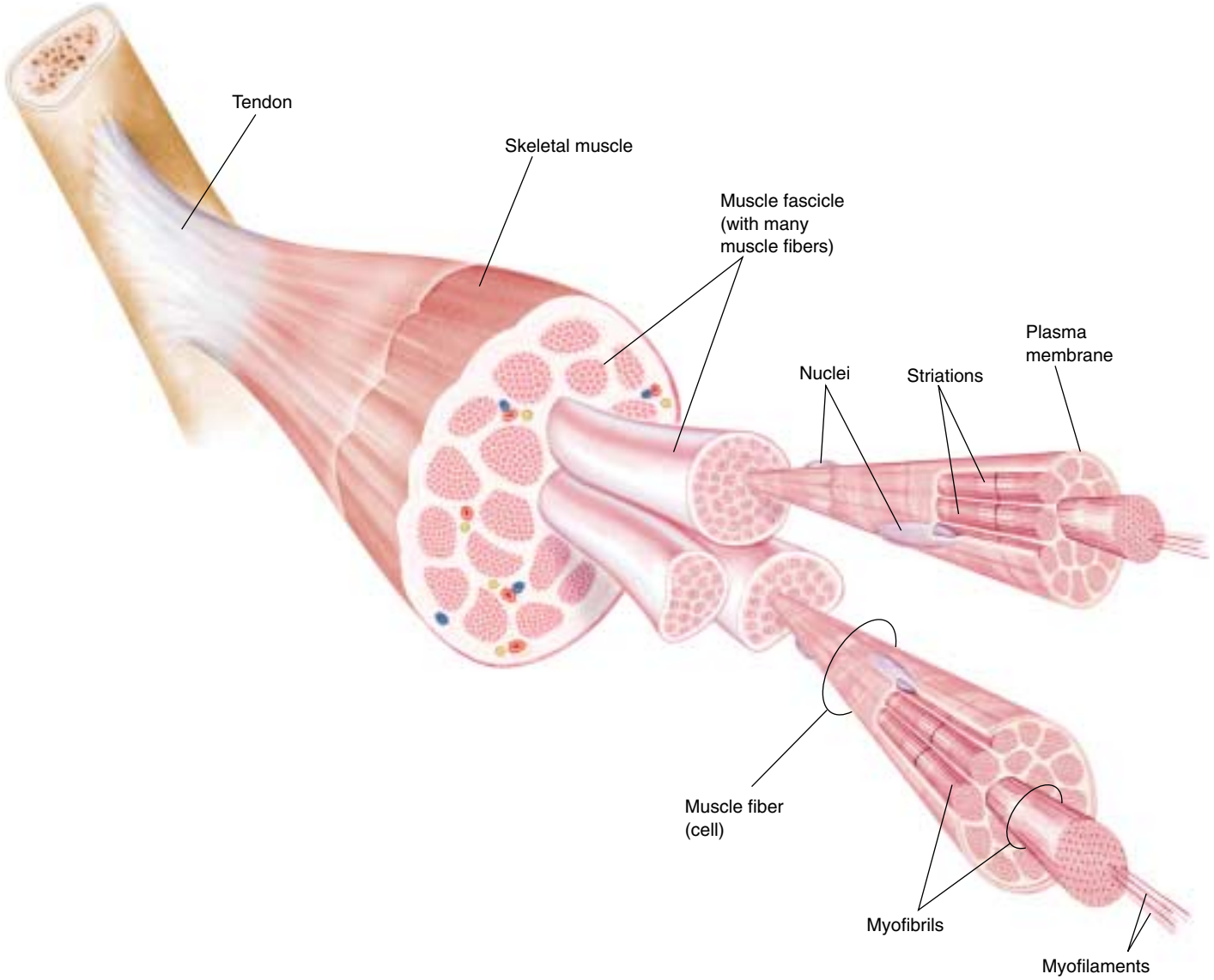


FIGURE 50.7
The organization of skeletal muscle. Each muscle is composed of many fascicles, which are bundles of muscle cells, or fibers. Each fiber is composed of many myofibrils, which are each, in turn, composed of myofilaments.

muscle, do not project all the way to the center of the A band. As a result, the center of an A band (called an *H band*) is lighter than each side, with its interdigitating thick and thin filaments. This appearance of the sarcomeres changes when the muscle contracts.

A muscle contracts and shortens because its myofibrils contract and shorten. When this occurs, the myofilaments do *not* shorten; instead, the thin filaments slide deeper into the A bands (figure 50.9). This makes the H bands narrower until, at maximal shortening, they disappear entirely. It also makes the I bands narrower, because the dark A bands are brought closer together. This is the **sliding filament mechanism** of contraction.

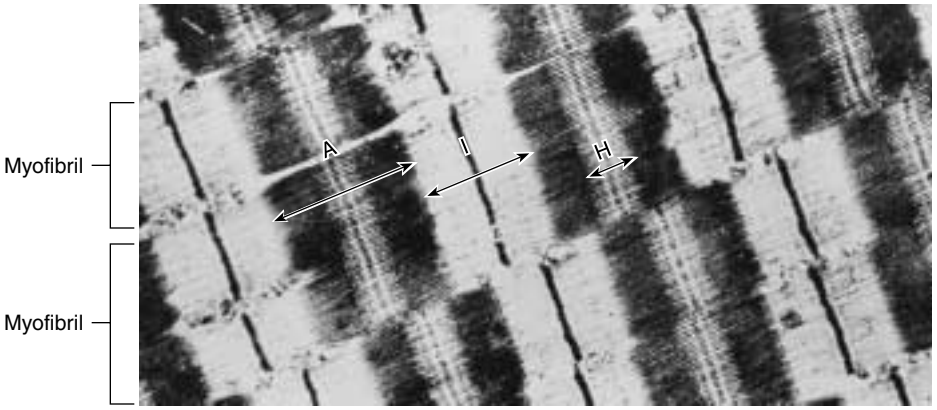


FIGURE 50.8
An electron micrograph of a skeletal muscle fiber. The Z lines that serve as the borders of the sarcomeres are clearly seen within each myofibril. The thick filaments comprise the A bands; the thin filaments are within the I bands and stick partway into the A bands, overlapping with the thick filaments. There is no overlap of thick and thin filaments at the central region of an A band, which is therefore lighter in appearance. This is the H band.

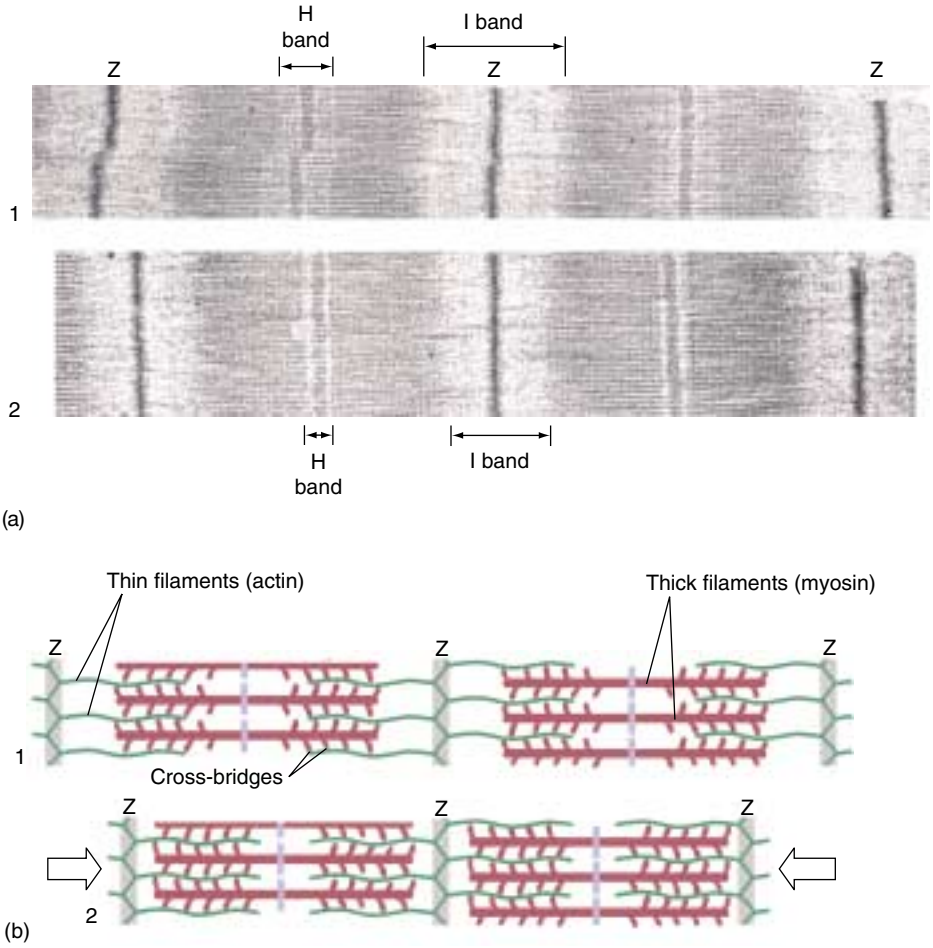


FIGURE 50.9
Electron micrograph (a) and diagram (b) of the sliding filament mechanism of contraction. As the thin filaments slide deeper into the centers of the sarcomeres, the Z lines are brought closer together. (*1*) Relaxed muscle; (*2*) partially contracted muscle.

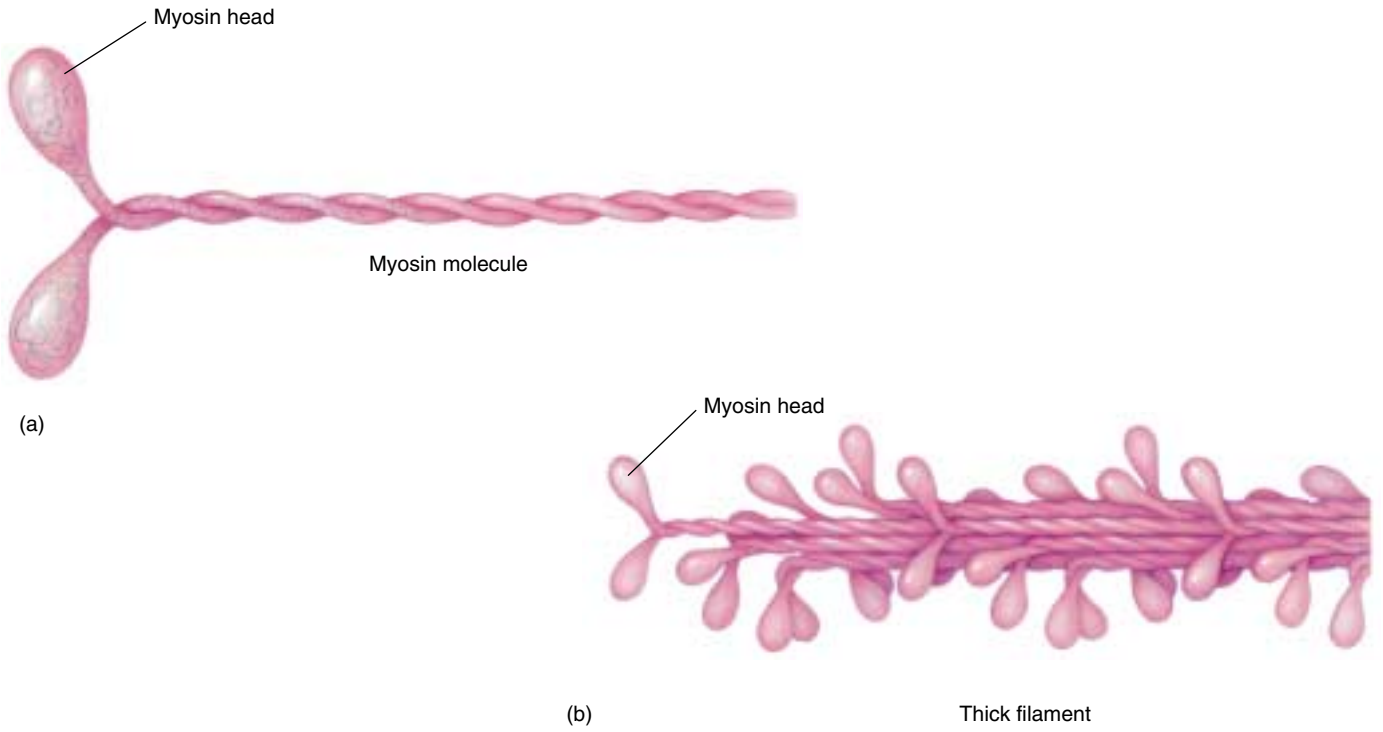


FIGURE 50.10
Thick filaments are composed of myosin. (*a*) Each myosin molecule consists of two polypeptide chains wrapped around each other; at the end of each chain is a globular region referred to as the "head." (*b*) Thick filaments consist of myosin molecules combined into bundles from which the heads protrude at regular intervals.

Electron micrographs reveal **cross-bridges** that extend from the thick to the thin filaments, suggesting a mechanism that might cause the filaments to slide. To understand how this is accomplished, we have to examine the thick and thin filaments at a molecular level. Biochemical studies show that each thick filament is composed of many **myosin** proteins packed together, and every myosin molecule has a "head" region that protrudes from the thick filaments (figure 50.10). These myosin heads form the cross-bridges seen in electron micrographs. Biochemical studies also show that each thin filament consists primarily of many globular **actin** proteins twisted into a double helix (figure 50.11). Therefore, if we were able to see a sarcomere at a molecular level, it would have the structure depicted in figure 50.12*a*.

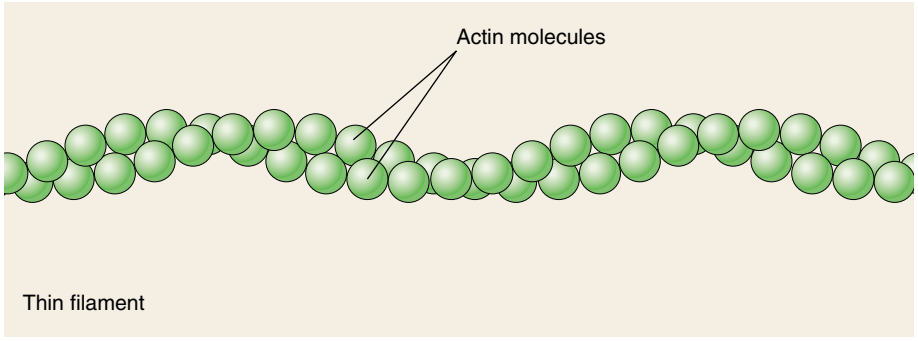


FIGURE 50.11
Thin filaments are composed of globular actin proteins. Two rows of actin proteins are twisted together in a helix to produce the thin filaments.

Before the myosin heads bind to the actin of the thin filaments, they act as ATPase enzymes, splitting ATP into ADP and P_i. This activates the heads, "cocking" them so that they can bind to actin and form cross-bridges. Once a myosin head binds to actin, it undergoes a conformational (shape) change, pulling the thin filament toward the center of the sarcomere (figure 50.12*b*) in a *power stroke*. At the end of the power stroke, the myosin head binds to a new molecule of ATP. This allows the head to detach from actin and continue the **cross-bridge cycle** (figure 50.13), which repeats as long as the muscle is stimulated to contract.

In death, the cell can no longer produce ATP and therefore the cross-bridges cannot be broken—this causes the muscle stiffness of death, or *rigor mortis*. A living cell, however, always has enough ATP to allow the

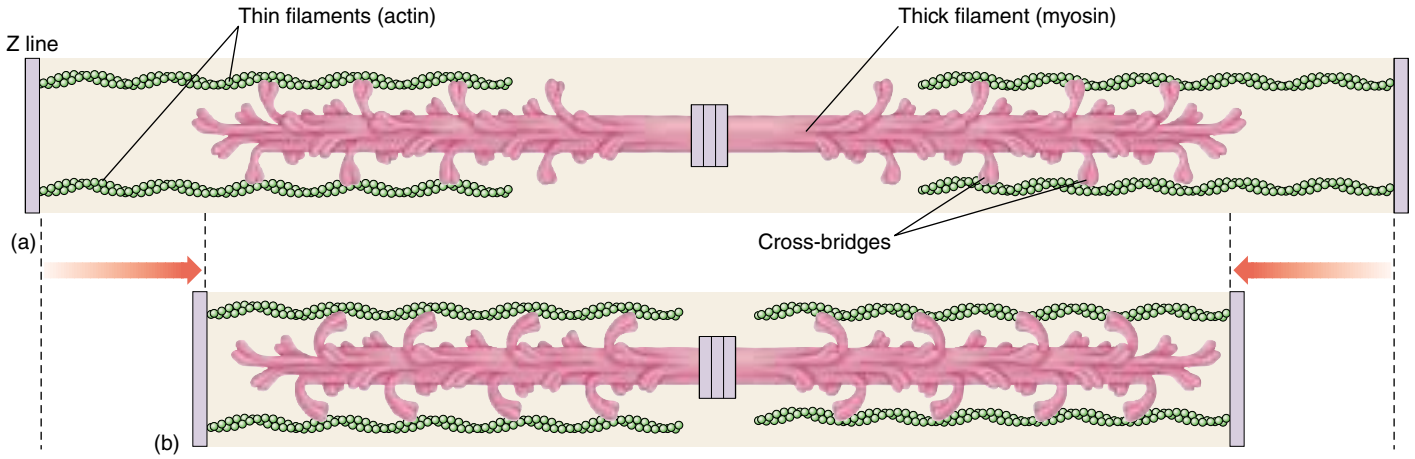


FIGURE 50.12
The interaction of thick and thin filaments in striated muscle sarcomeres. The heads on the two ends of the thick filaments are oriented in opposite directions (*a*), so that the cross-bridges pull the thin filaments and the Z lines on each side of the sarcomere toward the center. (*b*) This sliding of the filaments produces muscle contraction.

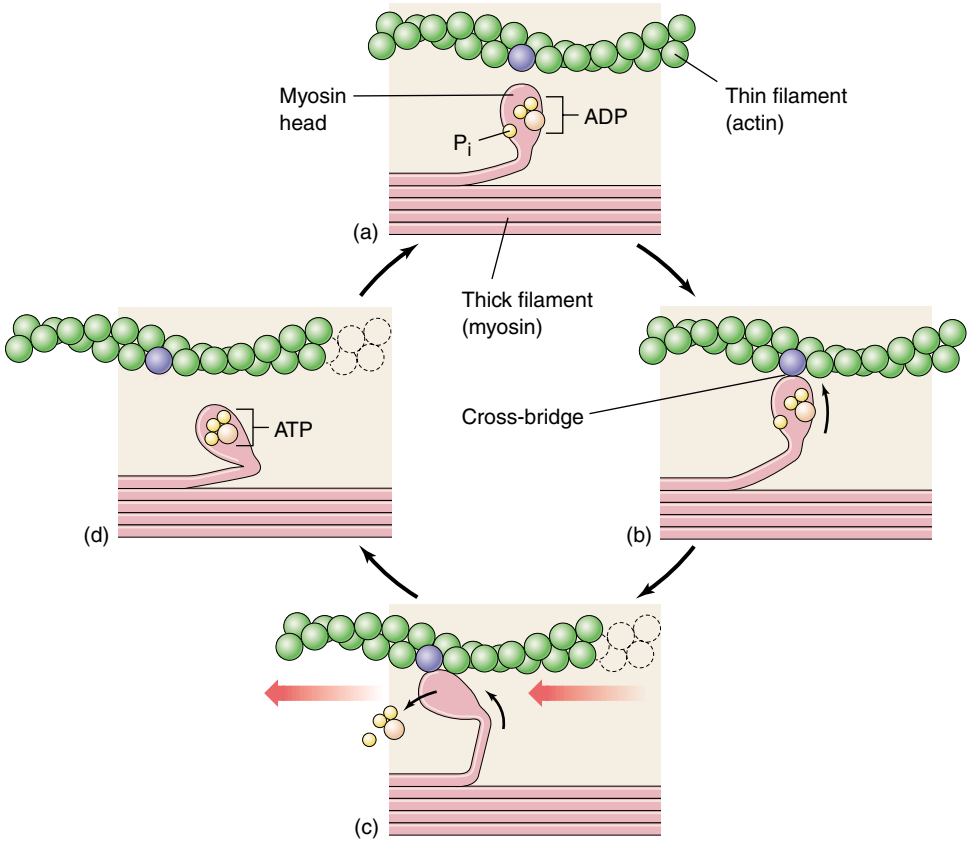


FIGURE 50.13
The cross-bridge cycle in muscle contraction. (*a*) With ADP and P_i attached to the myosin head, (*b*) the head is in a conformation that can bind to actin and form a cross-bridge. (*c*) Binding causes the myosin head to assume a more bent conformation, moving the thin filament along the thick filament (to the left in this diagram) and releasing ADP and P_i. (*d*) Binding of ATP to the head detaches the cross-bridge; cleavage of ATP into ADP and P_i puts the head into its original conformation, allowing the cycle to begin again.

myosin heads to detach from actin. How, then, is the cross-bridge cycle arrested so that the muscle can relax? The regulation of muscle contraction and relaxation requires additional factors that we will discuss in the next section.

Thick and thin filaments are arranged to form sarcomeres within the myofibrils. Myosin proteins comprise the thick filaments, and the heads of the myosin form cross-bridges with the actin proteins of the thin filaments. ATP provides the energy for the cross-bridge cycle and muscle contraction.

The Control of Muscle Contraction

The Role of Ca^{++} in Contraction

When a muscle is relaxed, its myosin heads are "cocked" and ready, through the splitting of ATP, but are unable to bind to actin. This is because the attachment sites for the myosin heads on the actin are physically blocked by another protein, known as **tropomyosin,** in the thin filaments. Cross-bridges therefore cannot form in the relaxed muscle, and the filaments cannot slide.

In order to contract a muscle, the tropomyosin must be moved out of the way so that the myosin heads can bind to actin. This requires the function of **troponin,** a regulatory protein that binds to the tropomyosin. The troponin and tropomyosin form a complex that is regulated by the calcium ion (Ca^{++}) concentration of the muscle cell cytoplasm.

When the Ca^{++} concentration of the muscle cell cytoplasm is low, tropomyosin inhibits cross-bridge formation and the muscle is relaxed (figure 50.14). When the Ca^{++} concentration is raised, Ca^{++} binds to troponin. This causes the troponin-tropomyosin complex to be shifted away from the attachment sites for the myosin heads on the actin. Cross-bridges can thus form, undergo power strokes, and produce muscle contraction.

Where does the Ca^{++} come from? Muscle fibers store Ca^{++} in a modified endoplasmic reticulum called a sarcoplasmic reticulum, or SR (figure 50.15). When a muscle fiber is stimulated to contract, an electrical impulse travels into the muscle fiber down invaginations called the **transverse tubules** (**T tubules**). This triggers the release of Ca^{++} from the SR. Ca^{++} then diffuses into the myofibrils, where it binds to troponin and causes contraction. The contraction of muscles is regulated by nerve activity, and so nerves must influence the distribution of Ca^{++} in the muscle fiber.

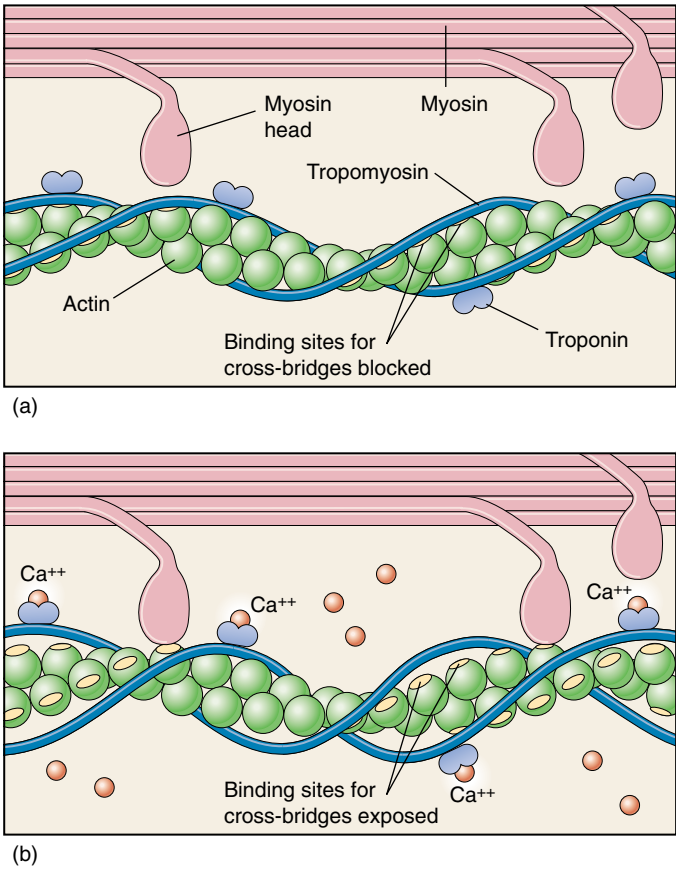


FIGURE 50.14
How calcium controls striated muscle contraction. (*a*) When the muscle is at rest, a long filament of the protein tropomyosin blocks the myosin-binding sites on the actin molecule. Because myosin is unable to form cross-bridges with actin at these sites, muscle contraction cannot occur. (*b*) When Ca^{++} binds to another protein, troponin, the Ca^{++}-troponin complex displaces tropomyosin and exposes the myosin-binding sites on actin, permitting cross-bridges to form and contraction to occur.

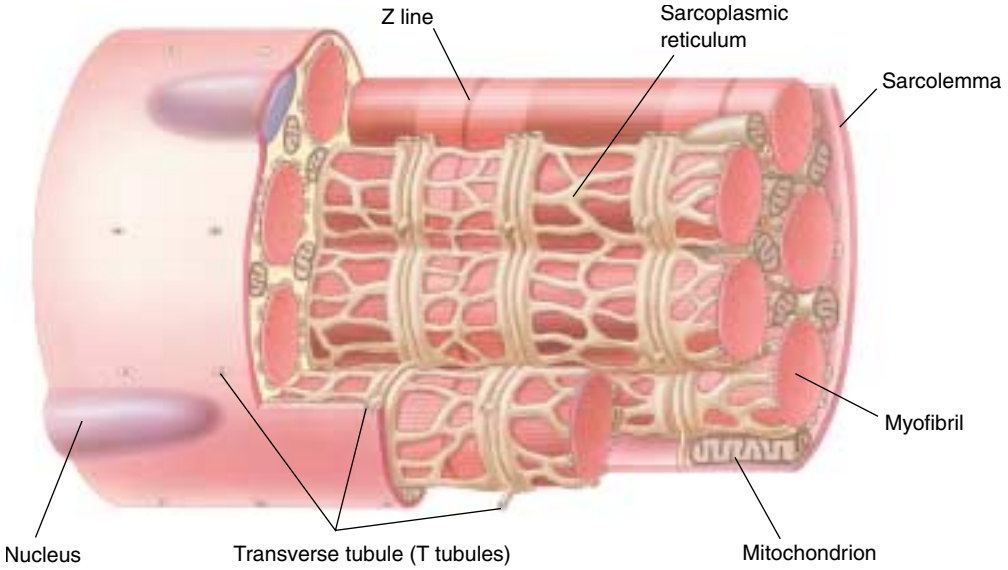


FIGURE 50.15
The relationship between the myofibrils, transverse tubules, and sarcoplasmic reticulum. Impulses travel down the axon of a motor neuron that synapses with a muscle fiber. The impulses are conducted along the transverse tubules and stimulate the release of Ca^{++} from the sarcoplasmic reticulum into the cytoplasm. Ca^{++} diffuses toward the myofibrils and causes contraction.

Nerves Stimulate Contraction

Muscles are stimulated to contract by motor neurons. The particular motor neurons that stimulate skeletal muscles, as opposed to cardiac and smooth muscles, are called *somatic motor neurons*. The axon (see figure 49.12) of a somatic motor neuron extends from the neuron cell body and branches to make functional connections, or *synapses*, with a number of muscle fibers. (Synapses are discussed in more detail in chapter 54.) One axon can stimulate many muscle fibers, and in some animals a muscle fiber may be innervated by more than one motor neuron. However, in humans each muscle fiber only has a single synapse with a branch of one axon.

When a somatic motor neuron produces electrochemical impulses, it stimulates contraction of the muscle fibers it innervates (makes synapses with) through the following events:

1. The motor neuron, at its synapse with the muscle fibers, releases a chemical known as a *neurotransmitter*. The specific neurotransmitter released by somatic motor neurons is **acetylcholine (ACh).** ACh acts on the muscle fiber membrane to stimulate the muscle fiber to produce its own electrochemical impulses.
2. The impulses spread along the membrane of the muscle fiber and are carried into the muscle fibers through the T tubules.
3. The T tubules conduct the impulses toward the sarcoplasmic reticulum, which then release Ca^{++}. As described earlier, the Ca^{++} binds to troponin, which exposes the cross-bridge binding sites on the actin myofilaments, stimulating muscle contraction.

When impulses from the nerve stop, the nerve stops releasing ACh. This stops the production of impulses in the muscle fiber. When the T tubules no longer produce impulses, Ca^{++} is brought back into the SR by active transport. Troponin is no longer bound to Ca^{++}, so tropomyosin returns to its inhibitory position, allowing the muscle to relax.

The involvement of Ca^{++} in muscle contraction is called, **excitation-contraction coupling** because it is the release of Ca^{++} that links the excitation of the muscle fiber by the motor neuron to the contraction of the muscle.

Motor Units and Recruitment

A single muscle fiber responds in an all-or-none fashion to stimulation. The response of an entire muscle depends upon the number of individual fibers involved. The set of muscle fibers innervated by all axonal branches of a given motor neuron is defined as a **motor unit** (figure 50.16). Every time the motor neuron produces impulses, all muscle fibers in that motor unit contract together. The division of the muscle into motor units allows the muscle's strength of contraction to be finely graded, a requirement for coordinated movements of the skeleton. Muscles that require a finer degree of control have smaller motor units (fewer muscle fibers per neuron) than muscles that require less precise control but must exert more force. For example, there are only a few muscle fibers per motor neuron in the muscles that move the eyes, while there are several hundred per motor neuron in the large muscles of the legs.

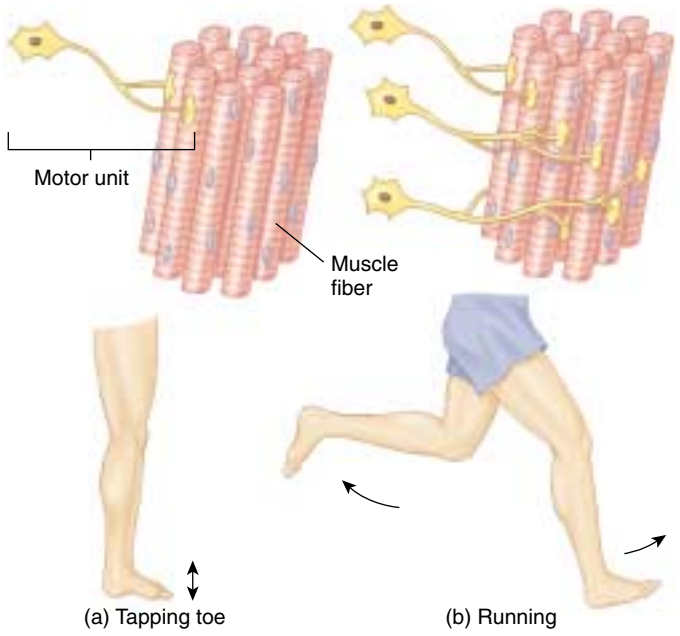


FIGURE 50.16
The number and size of motor units. (*a*) Weak, precise muscle contractions use smaller and fewer motor units. (*b*) Larger and stronger movements require additional motor units that are larger.

Most muscles contain motor units in a variety of sizes, which can be selectively activated by the nervous system. The weakest contractions of a muscle involve the activation of a few small motor units. If a slightly stronger contraction is necessary, additional small motor units are also activated. The initial increments to the total force generated by the muscle are therefore relatively small. As ever greater forces are required, more and larger motor units are brought into action, and the force increments become larger. The nervous system's use of increased numbers and sizes of motor units to produce a stronger contraction is termed **recruitment.**

The cross-bridges are prevented from binding to actin by tropomyosin in a relaxed muscle. In order for a muscle to contract, Ca^{++} must be released from the sarcoplasmic reticulum, where it is stored, so that it can bind to troponin and cause the tropomyosin to shift its position in the thin filaments. Muscle contraction is stimulated by neurons. Varying sizes and numbers of motor units are used to produce different types of muscle contractions.

Types of Muscle Fibers

Muscle Fiber Twitches

An isolated skeletal muscle can be studied by stimulating it artificially with electric shocks. If a muscle is stimulated with a single electric shock, it will quickly contract and relax in a response called a **twitch.** Increasing the stimulus voltage increases the strength of the twitch up to a maximum. If a second electric shock is delivered immediately after the first, it will produce a second twitch that may partially "ride piggyback" on the first. This cumulative response is called **summation** (figure 50.17).

If the stimulator is set to deliver an increasing frequency of electric shocks automatically, the relaxation time between successive twitches will get shorter and shorter, as the strength of contraction increases. Finally, at a particular frequency of stimulation, there is no visible relaxation between successive twitches. Contraction is smooth and sustained, as it is during normal muscle contraction in the body. This smooth, sustained contraction is called **tetanus.** (The term *tetanus* should not be confused with the disease of the same name, which is accompanied by a painful state of muscle contracture, or *tetany*.)

Skeletal muscle fibers can be divided on the basis of their contraction speed into **slow-twitch,** or **type I, fibers,** and **fast-twitch,** or **type II, fibers.** The muscles that move the eyes, for example, have a high proportion of fast-twitch fibers and reach maximum tension in about 7.3 milliseconds; the soleus muscle in the leg, by contrast, has a high proportion of slow-twitch fibers and requires about 100 milliseconds to reach maximum tension (figure 50.18).

Muscles like the soleus must be able to sustain a contraction for a long period of time without fatigue. The resistance to fatigue demonstrated by these muscles is aided by other characteristics of slow-twitch (type I) fibers that endow them with a high capacity for aerobic respiration. Slow-twitch fibers have a rich capillary supply, numerous mitochondria and aerobic respiratory enzymes, and a high concentration of **myoglobin** pigment. Myoglobin is a red pigment, similar to the hemoglobin in red blood cells, but its higher affinity for oxygen improves the delivery of oxygen to the slow-twitch fibers. Because of their high myoglobin content, slow-twitch fibers are also called *red fibers.*

The thicker, fast-twitch (type II) fibers have fewer capillaries and mitochondria than slow-twitch fibers and not as much myoglobin; hence, these fibers are also called *white fibers.* Fast-twitch fibers are adapted to respire anaerobically by using a large store of glycogen and high concentrations of glycolytic enzymes. Fast-twitch fibers are adapted for the rapid generation of power and can grow thicker and stronger in response to weight training. The "dark meat" and "white meat" found in meat such as chicken and turkey consists of muscles with primarily red and white fibers, respectively.

In addition to the type I (slow-twitch) and type II (fast-twitch) fibers, human muscles also have an intermediate form of fibers that are fast-twitch but also have a high oxidative capacity, and so are more resistant to fatigue. Endurance training increases the proportion of these fibers in muscles.

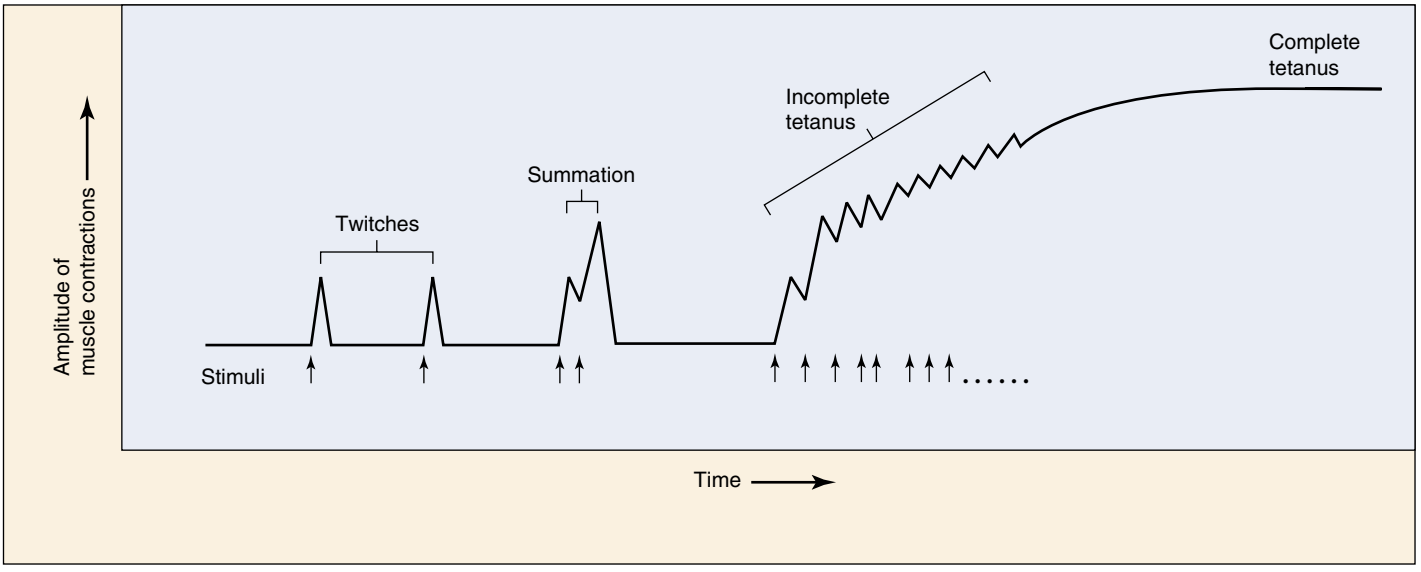


FIGURE 50.17
Muscle twitches summate to produce a sustained, tetanized contraction. This pattern is produced when the muscle is stimulated electrically or naturally by neurons. Tetanus, a smooth, sustained contraction, is the normal type of muscle contraction in the body.

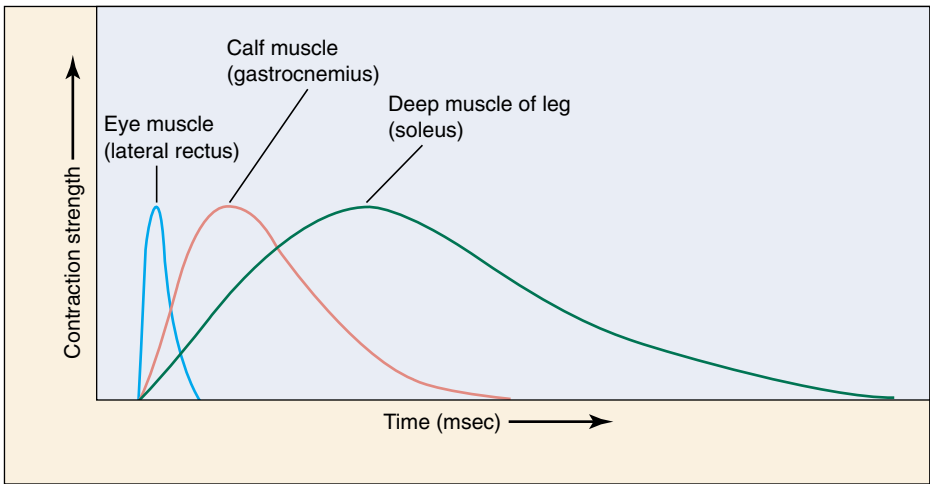


FIGURE 50.18
Skeletal muscles have different proportions of fast-twitch and slow-twitch fibers. The muscles that move the eye contain mostly fast-twitch fibers, whereas the deep muscle of the leg (the soleus) contains mostly slow-twitch fibers. The calf muscle (gastrocnemius) is intermediate in its composition.

Muscle Metabolism during Rest and Exercise

Skeletal muscles at rest obtain most of their energy from the aerobic respiration of fatty acids. During exercise, muscle glycogen and blood glucose are also used as energy sources. The energy obtained by cell respiration is used to make ATP, which is needed for (1) the movement of the cross-bridges during muscle contraction and (2) the pumping of Ca^{++} into the sarcoplasmic reticulum for muscle relaxation. ATP can be obtained by skeletal muscles quickly by combining ADP with phosphate derived from creatine phosphate. This compound was produced previously in the resting muscle by combining creatine with phosphate derived from the ATP generated in cell respiration.

Skeletal muscles respire anaerobically for the first 45 to 90 seconds of moderate-to-heavy exercise, because the cardiopulmonary system requires this amount of time to sufficiently increase the oxygen supply to the exercising muscles. If exercise is moderate, aerobic respiration contributes the major portion of the skeletal muscle energy requirements following the first 2 minutes of exercise.

Whether exercise is light, moderate, or intense for a given person depends upon that person's maximal capacity for aerobic exercise. The maximum rate of oxygen consumption in the body (by aerobic respiration) is called the maximal oxygen uptake, or the aerobic capacity. The intensity of exercise can also be defined by the lactate threshold. This is the percentage of the maximal oxygen uptake at which a significant rise in blood lactate levels occurs as a result of anaerobic respiration. For average, healthy people, for example, a significant amount of blood lactate appears when exercise is performed at about 50 to 70% of the maximal oxygen uptake.

Muscle Fatigue and Physical Training

Muscle fatigue refers to the use-dependant decrease in the ability of a muscle to generate force. The reasons for fatigue are not entirely understood. In most cases, however, muscle fatigue is correlated with the production of lactic acid by the exercising muscles. Lactic acid is produced by the anaerobic respiration of glucose, and glucose is obtained from muscle glycogen and from the blood. Lactate production and muscle fatigue are therefore also related to the depletion of muscle glycogen.

Because the depletion of muscle glycogen places a limit on exercise, any adaptation that spares muscle glycogen will improve physical endurance. Trained athletes have an increased proportion of energy derived from the aerobic respiration of fatty acids, resulting in a slower depletion of their muscle glycogen reserve. The greater the level of physical training, the higher the proportion of energy derived from the aerobic respiration of fatty acids. Because the aerobic capacity of endurance-trained athletes is higher than that of untrained people, athletes can perform more exercise before lactic acid production and glycogen depletion cause muscle fatigue.

Endurance training does not increase muscle size. Muscle enlargement is produced only by frequent periods of high-intensity exercise in which muscles work against high resistance, as in weight lifting. As a result of resistance training, type II (fast-twitch) muscle fibers become thicker as a result of the increased size and number of their myofibrils. Weight training, therefore, causes skeletal muscles to grow by **hypertrophy** (increased cell size) rather than by cell division and an increased number of cells.

Muscles contract through summation of the contractions of their fibers, producing tension that may result in shortening of the muscle. Slow-twitch skeletal muscle fibers are adapted for aerobic respiration and are slower to fatigue than fast-twitch fibers, which are more adapted for the rapid generation of power.

Comparing Cardiac and Smooth Muscles

Cardiac and smooth muscle are similar in that both are found within internal organs and both are generally not under conscious control. Cardiac muscle, however, is like skeletal muscle in that it is striated and contracts by means of a sliding filament mechanism. Smooth muscle (as its name implies) is not striated. Smooth muscle does contain actin and myosin filaments, but they are arranged less regularly within the cell.

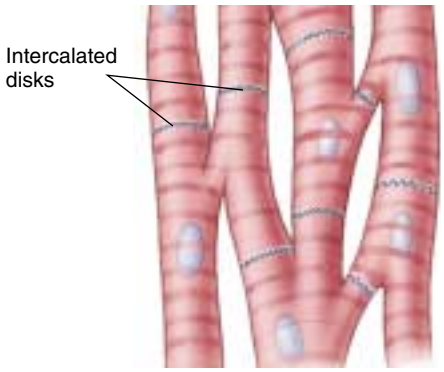


FIGURE 50.19
Cardiac muscle. Cells are organized into long branching chains that interconnect, forming a lattice; neighboring cells are linked by structures called intercalated discs.

Cardiac Muscle

Cardiac muscle in the vertebrate heart is composed of striated muscle cells that are arranged differently from the fibers in a skeletal muscle. Instead of the long, multinucleate cells that form skeletal muscle, cardiac muscle is composed of shorter, branched cells, each with its own nucleus, that interconnect with one another at intercalated discs (figure 50.19). Intercalated discs are regions where the membranes of two cells fuse together, and the fused membranes are pierced by **gap junctions** (chapter 7). The gap junctions permit the diffusion of ions, and thus the spread of electric excitation, from one cell to the next. The mass of interconnected cardiac muscle cells forms a single, functioning unit called a *myocardium*. Electric impulses begin spontaneously in a specific region of the myocardium known as the *pacemaker*. These impulses are *not* initiated by impulses in motor neurons, as they are in skeletal muscle, but rather are produced by the cardiac muscle cells themselves. From the pacemaker, the impulses spread throughout the myocardium via gap junctions, causing contraction.

The heart has two myocardia, one that receives blood from the body and one that ejects blood into the body. Because all of the cells in a myocardium are stimulated as a unit, cardiac muscle cannot produce summated contractions or tetanus. This would interfere with the alternation between contraction and relaxation that is necessary for pumping.

Smooth Muscle

Smooth muscle surrounds hollow internal organs, including the stomach, intestines, bladder, and uterus, as well as all blood vessels except capillaries. Smooth muscle cells are long and spindle-shaped, and each contains a single nucleus. They also contain actin and myosin, but these contractile proteins are not organized into sarcomeres. Parallel arrangements of thick and thin filaments cross diagonally from one side of the cell to the other. The thick filaments are attached either to structures called dense bodies, the functional equivalents of Z lines, or to the plasma membrane. Most smooth muscle cells have 10 to 15 thin filaments per thick filament, compared to 3 per thick filament in striated muscle fibers.

Smooth muscle cells do not have a sarcoplasmic reticulum; during a contraction, Ca^{++} enters from the extracellular fluid. In the cytoplasm, Ca^{++} binds to calmodulin, a protein that is structurally similar to troponin. The Ca^{++}-calmodulin complex activates an enzyme that phosphorylates (adds a phosphate group to) the myosin heads. Unlike the case with striated muscles, this phosphorylation is required for the myosin heads to form cross-bridges with actin.

This mechanism allows gradations in the strength of contraction in a smooth muscle cell, increasing contraction strength as more Ca^{++} enters the cytoplasm. Heart patients sometimes take drugs that block Ca^{++} entry into smooth muscle cells, reducing the cells' ability to contract. This treatment causes vascular smooth muscle to relax, dilating the blood vessels and reducing the amount of work the heart must do to pump blood through them.

In some smooth muscle tissues, the cells contract only when they are stimulated by the nervous system. These muscles line the walls of many blood vessels and make up the iris of the eye. Other smooth muscle tissues, like those in the wall of the gut, contains cells that produce electric impulses spontaneously. These impulses spread to adjoining cells through gap junctions, leading to a slow, steady contraction of the tissue.

Neither skeletal nor cardiac muscle can be greatly stretched because if the thick and thin filaments no longer overlay in the sarcomere, cross-bridges cannot form. Unlike these striated muscles, smooth muscle can contract even when it is greatly stretched. If one considers the degree to which some internal organs may be stretched—a uterus during pregnancy, for example—it is no wonder that these organs contain smooth muscle instead of striated muscle.

Cardiac muscle cells interconnect physically and electrically to form a single, functioning unit called a myocardium, which produces its own impulses at a pacemaker region. Smooth muscles lack the organization of myofilaments into sarcomeres and lack sarcoplasmic reticulum but contraction still occurs as myofilaments slide past one another by use of cross-bridges.

Modes of Animal Locomotion

Animals are unique among multicellular organisms in their ability to actively move from one place to another. Locomotion requires both a propulsive mechanism and a control mechanism. Animals employ a wide variety of propulsive mechanisms, most involving contracting muscles to generate the necessary force. The quantity, quality, and position of contractions are initiated and coordinated by the nervous system. In large animals, active locomotion is almost always produced by appendages that oscillate—*appendicular locomotion*—or by bodies that undulate, pulse, or undergo peristaltic waves—*axial locomotion*.

While animal locomotion occurs in many different forms, the general principles remain much the same in all groups. The physical restraints to movement—gravity and frictional drag—are the same in every environment, differing only in degree. You can conveniently divide the environments through which animals move into three types, each involving its own forms of locomotion: water, land, and air.

Locomotion in Water

Many aquatic and marine invertebrates move along the bottom using the same form of locomotion employed by terrestrial animals moving over the land surface. Flatworms employ ciliary activity to brush themselves along, roundworms a peristaltic slither, leeches a contract-anchor-extend creeping. Crabs walk using limbs to pull themselves along; mollusks use a muscular foot, while starfish use unique tube feet to do the same thing.

Moving directly through the water, or swimming, presents quite a different challenge. Water's buoyancy reduces the influence of gravity. The primary force retarding forward movement is frictional drag, so body shape is important in reducing the friction and turbulence produced by swimming through the water.

Some marine invertebrates swim using hydraulic propulsion. Scallops clap their shells together forcefully, while squids and octopuses squirt water like a marine jet. All aquatic and marine vertebrates, however, swim.

Swimming involves using the body or its appendages to push against the water. An eel swims by sinuous undulations of its whole body (figure 50.20*a*). The undulating body waves of eel-like swimming are created by waves of muscle contraction alternating between the left and right axial musculature. As each body segment in turn pushes against the water, the moving wave forces the eel forward.

Fish, reptiles, and aquatic amphibians swim in a way similar to eels, but only undulate the posterior (back) portion of the body (figure 50.20*b*) and sometimes only the caudal (rear) fin. This allows considerable specialization of the front end of the body, while sacrificing little propulsive force.

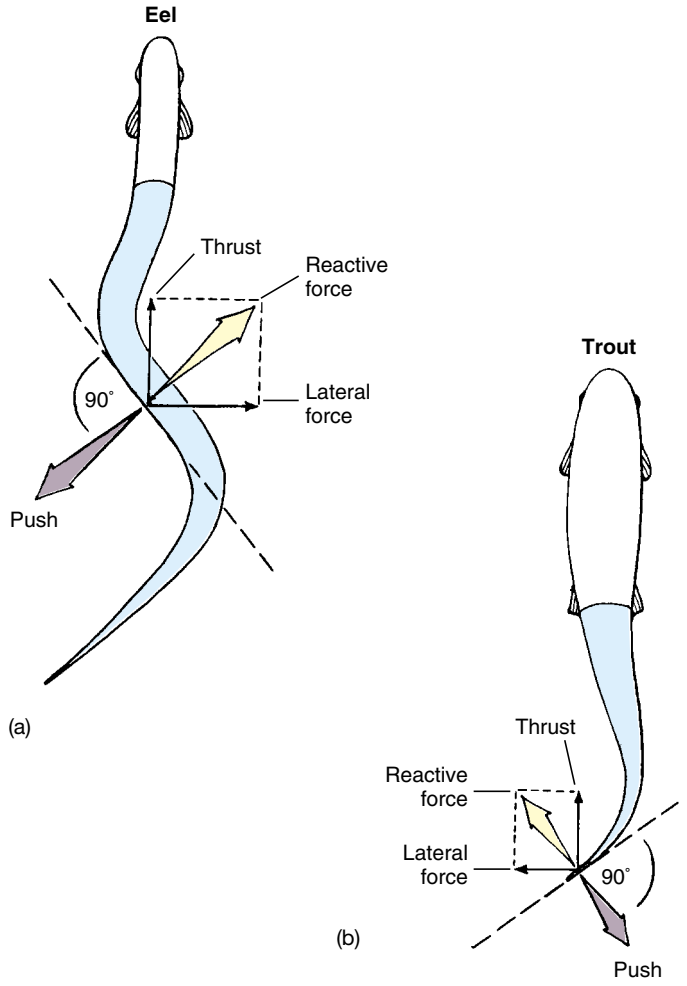


FIGURE 50.20
Movements of swimming fishes. (*a*) An eel pushes against the water with its whole body, (*b*) a trout only with its posterior half.

Whales also swim using undulating body waves, but unlike any of the fishes, the waves pass from top to bottom and not from side to side. The body musculature of eels and fish is highly segmental; that is, a muscle segment alternates with each vertebra. This arrangement permits the smooth passage of undulatory waves along the body. Whales are unable to produce lateral undulations because mammals do not have this arrangement.

Many tetrapod vertebrates swim, usually with appendicular locomotion. Most birds that swim, like ducks and geese, propel themselves through the water by pushing against it with their hind legs, which typically have webbed feet. Frogs, turtles, and most marine mammals also swim with their hind legs and have webbed feet. Tetrapod vertebrates that swim with their forelegs usually have these limbs modified as flippers, and pull themselves through the water. These include sea turtles, penguins, and fur seals. A few principally terrestrial tetrapod vertebrates, like polar bears and platypuses, swim with walking forelimbs not modified for swimming.

FIGURE 50.21
Animals that hop or leap use their rear legs to propel themselves through the air. The powerful leg muscles of this frog allow it to explode from a crouched position to a takeoff in about 100 milliseconds.

Locomotion on Land

The three great groups of terrestrial animals—mollusks, arthropods, and vertebrates—each move over land in different ways.

Mollusk locomotion is far less efficient than that of the other groups. Snails, slugs, and other terrestrial mollusks secrete a path of mucus that they glide along, pushing with a muscular foot.

Only vertebrates and arthropods (insects, spiders, and crustaceans) have developed a means of rapid surface locomotion. In both groups, the body is raised above the ground and moved forward by pushing against the ground with a series of jointed appendages, the legs.

Because legs must provide support as well as propulsion, it is important that the sequence of their movements not shove the body's center of gravity outside of the legs' zone of support. If they do, the animal loses its balance and falls. It is the necessity to maintain stability that determines the sequence of leg movements, which are similar in vertebrates and arthropods.

The apparent differences in the walking gaits of these two groups reflects the differences in leg number. Vertebrates are tetrapods (four limbs), while all arthropods have six or more limbs. Although having many legs increases stability during locomotion, they also appear to reduce the maximum speed that can be attained.

The basic walking pattern of all tetrapod vertebrates is left hind leg (LH), left foreleg (LF), right hindleg (RH), right foreleg (RF), and then the same sequence again and again. Unlike insects, vertebrates can begin to walk with any of the four legs, and not just the posterior pair. Both arthropods and vertebrates achieve faster gaits by overlapping the leg movements of the left and right sides. For example, a horse can convert a walk to a trot, by moving diagonally opposite legs simultaneously.

The highest running speeds of tetrapod vertebrates, such as the gallop of a horse, are obtained with asymmetric gaits. When galloping, a horse is never supported by more than two legs, and occasionally is supported by none. This reduces friction against the ground to an absolute minimum, increasing speed. With their larger number of legs, arthropods cannot have these speedy asymmetric gaits, because the movements of the legs would interfere with each other.

Not all animals walk or run on land. Many insects, like grasshoppers, leap using strong rear legs to propel themselves through the air. Vertebrates such as kangaroos, rabbits, and frogs are also effective leapers (figure 50.21).

Many invertebrates use peristaltic motion to slide over the surface. Among vertebrates, this form of locomotion is exhibited by snakes and caecilians (legless amphibians). Most snakes employ serpentine locomotion, in which the body is thrown into a series of sinuous curves. The movements superficially resemble those of eel-like swimming, but the similarity is more apparent than real. Propulsion is not by a wave of contraction undulating the body, but by a simultaneous lateral thrust in all segments of the body in contact with the ground. To go forward, it is necessary that the strongest muscular thrust push against the ground opposite the direction of movement. Because of this, thrust tends to occur at the anterior (outside) end of the inward-curving side of the loop of the snake's body.

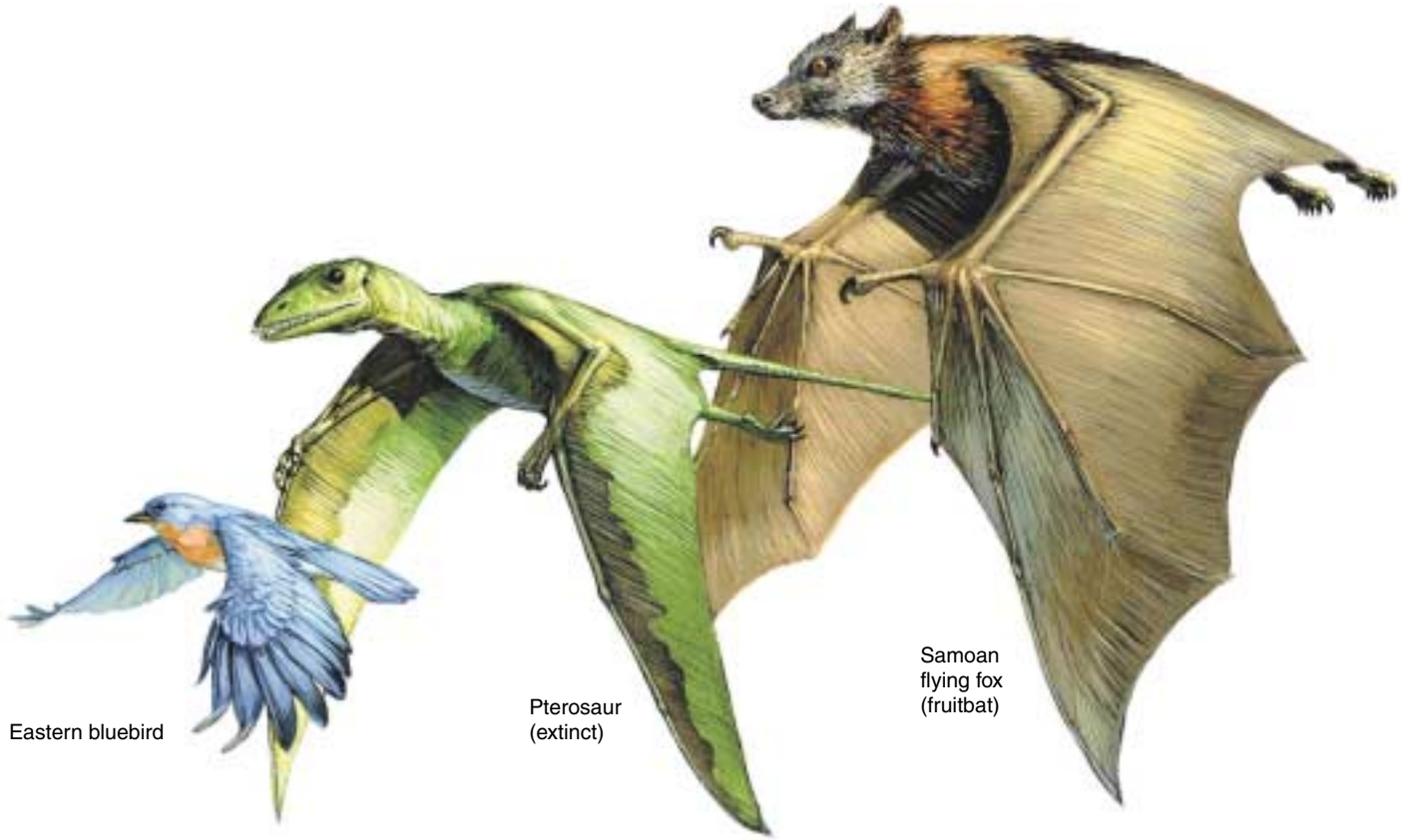


FIGURE 50.22
Flight has evolved three times among the vertebrates. These three very different vertebrates all have lightened bones and forelimbs transformed into wings.

Locomotion in Air

Flight has evolved among the animals four times: insects, pterosaurs (extinct flying reptiles), birds, and bats. In all four groups, active flying takes place in much the same way. Propulsion is achieved by pushing down against the air with wings. This provides enough lift to keep insects in the air. Vertebrates, being larger, need greater lift, obtaining it with wings that are convex in cross section. Because air must travel farther over the top surface, it moves faster, creating lift over the wing.

In birds and most insects, the raising and lowering of the wings is achieved by the alternate contraction of extensor muscles (elevators) and flexor muscles (depressors). Four insect orders (containing flies, mosquitoes, wasps, bees, and beetles), however, beat their wings at frequencies from 100 to more than 1000 times per second, faster than nerves can carry successive impulses! In these insects, the flight muscles are not attached to the wings at all but rather to the stiff wall of the thorax, which is distorted in and out by their contraction. The reason that these muscles can beat so fast is that the contraction of one set stretches the other, triggering its contraction in turn without waiting for the arrival of a nerve impulse.

Among vertebrates (figure 50.22), flight first evolved some 200 million years ago among flying reptiles called pterosaurs. A very successful and diverse group, pterosaurs ranged in size from individuals no bigger than sparrows to pterodons the size of a fighter plane. For much of this time, they shared the skies with birds, which most paleontologists believe evolved from feathered dinosaurs about 150 million years ago. How did they share their ecological world for 100 million years without competition driving one or the other from the skies? No one knows for sure. Perhaps these early birds were night fliers, while pterosaurs flew by day.

Such an arrangement for sharing resources is not as unlikely as it might at first appear. Bats, flying mammals which evolved after the pterosaurs disappeared with the dinosaurs, are night fliers. By flying at night bats are able to shop in a store with few other customers and a wealth of food: night-flying insects. It has proven to be a very successful approach. One-quarter of all mammal species are bats.

Locomotion in larger animals is almost always produced by appendages that push against the surroundings in some fashion, or by shoving the entire body forward by an undulation.

Chapter 50

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Summary

Questions

Media Resources

50.1 A skeletal system supports movement in animals.

- There are three types of skeleton: hydrostatic skeletons, exoskeletons, and endoskeletons.
- Bone is formed by the secretion of an organic matrix by osteoblasts; this organic matrix becomes calcified.

1. What are the two major components of the extracellular matrix in bone? What structural properties does each component have? How do the two components combine to make bone resistant to fracture?

- *On Science* Article: Running improperly

- Walking

50.2 Skeletal muscles contract to produce movements at joints.

- Freely movable joints surround the articulating bones with a synovial capsule filled with a lubricating fluid.
- Skeletal muscles can work together as synergists, or oppose each other as antagonists.

2. What are the three types of joints in a vertebrate skeleton? Give an example of where each type is found in the body.

3. What is the difference between a skeletal muscle's origin and its insertion?

- Bioethics case study: Sports and fitness

50.3 Muscle contraction powers animal locomotion.

- A muscle fiber contains numerous myofibrils, which consist of thick filaments composed of myosin and thin filaments of actin.
- There are small cross-bridges of myosin that extend out toward the actin; the cross-bridges are activated by the hydrolysis of ATP so that it can bind to actin and undergo a power stroke that causes the sliding of the myofilaments.
- When Ca^{++} binds to troponin, the tropomyosin shifts position in the thin filament, allowing the cross-bridges to bind to actin and undergo a power stroke.
- The release of Ca^{++} from the sarcoplasmic reticulum is stimulated by impulses in the muscle fiber produced by neural stimulation.
- Slow-twitch fibers are adapted for aerobic respiration and are resistant to fatigue; fast-twitch fibers can provide power quickly but produce lactic acid and fatigue quickly.
- Cardiac muscle cells have gap junctions that permit the spread of electric impulses from one cell to the next.
- Cardiac and smooth muscles are involuntary and regulated by autonomic nerves; the contractions are automatically produced in cardiac muscle and some smooth muscles.
- Animals have adapted modes of locomotion to three different environments: water, land, and air.

4. Of what proteins are thick and thin filaments composed?

5. Describe the steps involved in the cross-bridge cycle. What functions does ATP perform in the cycle?

6. Describe the steps involved in excitation-contraction coupling. What functions do acetylcholine and Ca++ perform in this process?

7. How does a somatic motor neuron stimulate a muscle fiber to contract?

8. What is the difference between a muscle twitch and tetanus?

9. Why can't a myocardium produce a sustained contraction?

10. How does smooth muscle differ from skeletal muscle in terms of thick and thin filament organization, the role of Ca++ in contraction, and the effect of stretching on the muscle's ability to contract?

11. What do all modes of locomotion have in common?

- *On Science* Article: Climbing the walls

- Straited muscle contraction
- Muscle contraction action potential
- Detailed straited muscle
- Actin-myosin crossbridges

- Activity: Muscle contraction
- Muscle cell function
- Body musculature
- Head and neck muscles
- Trunk muscles
- Upper limb muscles
- Lower limb muscles
- Muscle characteristics