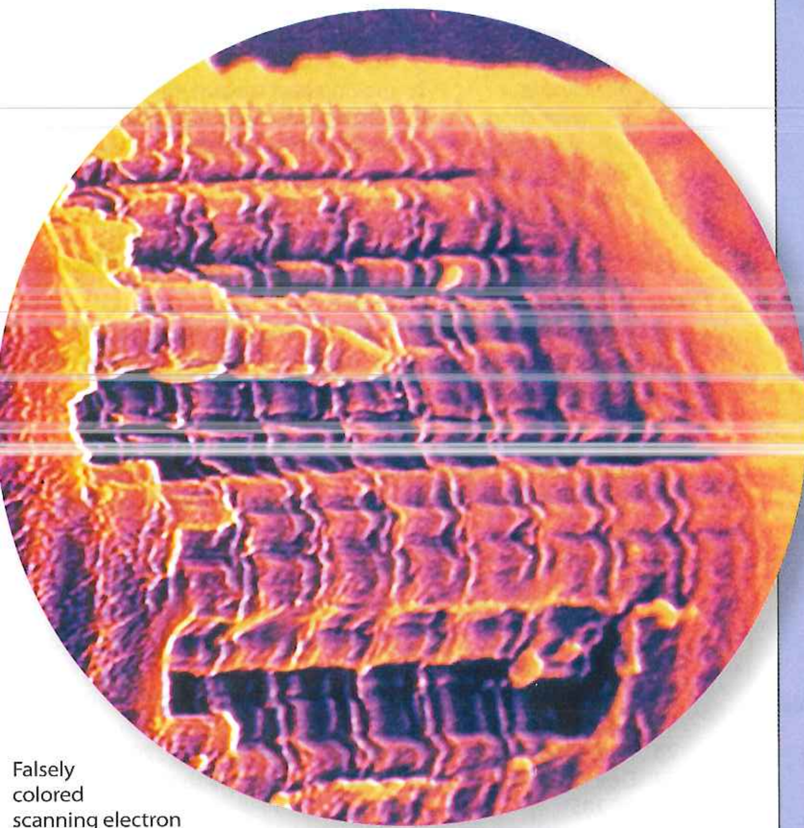
9 Muscular System



Falsely colored scanning electron micrograph (SEM) of a normal human striated muscle fiber reveals the characteristic banding pattern of the myofibrils (3,000×).

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Module 6: Muscular System

Learning Outcomes

After you have studied this chapter, you should be able to:

9.1 Introduction

1 List various outcomes of muscle actions. (p. 293)

9.2 Structure of a Skeletal Muscle

2 Describe the structure of a skeletal muscle. (p. 293)

3 Name the major parts of a skeletal muscle fiber and describe the functions of each. (p. 295)

9.3 Skeletal Muscle Contraction

4 Describe the neural control of skeletal muscle contraction. (p. 297)

5 Identify the major events of skeletal muscle fiber contraction. (p. 298)

6 List the energy sources for skeletal muscle fiber contraction. (p. 302)

7 Describe oxygen debt. (p. 303)

8 Describe how a muscle may become fatigued. (p. 304)

9.4 Muscular Responses

9 Distinguish between a twitch and a sustained contraction. (p. 304)

10 Explain how various types of muscular contractions produce body movements and help maintain posture. (p. 306)

11 Distinguish between fast and slow twitch muscle fibers. (p. 307)

9.5 Smooth Muscles

12 Distinguish between the structures and functions of multiunit smooth muscle and visceral smooth muscle. (p. 308)

13 Compare the contraction mechanisms of skeletal and smooth muscle fibers. (p. 309)

9.6 Cardiac Muscle

14 Compare the contraction mechanisms of skeletal and cardiac muscle fibers. (p. 309)

9.7 Skeletal Muscle Actions

15 Explain how the attachments, locations, and interactions of skeletal muscles make possible certain movements. (p. 310)

9.8 Major Skeletal Muscles

16 Identify and locate the skeletal muscles of each body region and describe the action(s) of each muscle. (p. 314)

9.9 Life-Span Changes

17 Describe aging-related changes in the muscular system. (p. 341)

18 Discuss how exercise can help maintain a healthy muscular system as the body ages. (p. 341)

LEARN PRACTICE ASSESS

Understanding Words

calat-, something inserted: inter*calat*ed disc—membranous band that connects cardiac muscle cells.

erg-, work: syn*erg*ist—muscle that works with a prime mover, producing a movement.

fasc-, bundle: *fasc*iculus—bundle of muscle fibers.

-gram, something written: myo*gram*—recording of a muscular contraction.

hyper-, over, more: muscular *hyper*trophy—enlargement of muscle fibers.

inter-, between: *inter*calated disc—membranous band that connects cardiac muscle cells.

iso-, equal: *iso*tonic contraction—contraction during which the tension in a muscle remains unchanged.

laten-, hidden: *laten*t period—period between a stimulus and the beginning of a muscle contraction.

myo-, muscle: *myo*fibril—contractile fiber of a muscle cell.

reticul-, a net: sarcoplasmic *reticul*um—network of membranous channels within a muscle fiber.

sarco-, flesh: *sarco*plasm—substance (cytoplasm) within a muscle fiber.

syn-, together: *syn*ergist—muscle that works with a prime mover, producing a movement.

tetan-, stiff: *tetan*ic contraction—sustained muscular contraction.

-tonic, stretched: iso*tonic* contraction—contraction during which the tension of a muscle remains unchanged.

-troph, well fed: muscular hyper*trophy*—enlargement of muscle fibers.

voluntar-, of one's free will: *voluntary* muscle—muscle that can be controlled by conscious effort.

The Muscular Movements Behind "Texting"

Our musculoskeletal systems can rapidly adapt to new challenges. Consider texting or other movements that require the fingers to rapidly press precise sequences of very small buttons. Texting is similar to other challenges to dexterity, such as manipulating buttons on clothing or slicing or dicing foods. Loss of this dexterity may be an early sign of a disease that affects the muscles, such as amyotrophic lateral sclerosis (Lou Gehrig's disease).

Fingertip dexterity and hand movements are more complex than it may seem, altogether involving more than 30 muscles. To track the exact movements required for sending a text message, researchers recorded the electrical activity (using a measure called an electromyogram) and fingertip force in seven muscles of the index fingers of volunteers as they pushed their fingers against a surface. The researchers used an algorithm to assess the coordination and movements of the hand as the finger pressed the pad. They saw two clearly different patterns of muscle activation, indicating two different types of movement—light tapping from an angle versus direct downward pressure on one key. The act of texting entails a key-locating "tap" followed by a more direct push (static force). The switch from one type of movement to another is so fast and fluid that we usually are not aware of it.

Understanding the complexity of these dual tasks helps to explain why it takes years for children to master fine-hand coordination, as well as why these skills are often the first to be noticeably lost in neuromuscular disease. Practical applications of the findings include guidance of prosthetic design, suggesting physical therapy techniques, and assisting the design of machines and electronic devices to be compatible with our natural finger and hand movements. ■

9.1 INTRODUCTION

Talking and walking, breathing and sneezing—all movements—require muscles. Muscles are organs composed of specialized cells that use the chemical energy stored in nutrients to exert a pulling force on structures to which they are attached. Muscular actions also provide muscle tone, propel body fluids and food, generate the heartbeat, and distribute heat.

Muscles are of three types—skeletal muscle, smooth muscle, and cardiac muscle, as described in chapter 5 (pp. 171–172). This chapter focuses mostly on skeletal muscle, which attaches to bones and to the skin of the face and is under conscious control. Smooth muscle and cardiac muscle are discussed briefly.

9.2 STRUCTURE OF A SKELETAL MUSCLE

A skeletal muscle is an organ of the muscular system. It is composed primarily of skeletal muscle tissue, nervous tissue, blood and other connective tissues.

Connective Tissue Coverings

An individual skeletal muscle is separated from adjacent muscles and held in position by layers of dense connective tissue called **fascia** (fash'e-ah). This connective tissue surrounds each muscle and may project beyond the ends of its muscle fibers, forming a cordlike **tendon.** Fibers in a tendon may intertwine with those in the periosteum of a bone, attaching the muscle to the bone. Or, the connective tissues associated with a muscle form broad, fibrous sheets called **aponeuroses** (ap″o-nu-ro′sēz), which may attach to bone or the coverings of adjacent muscles (figs. 9.1 and 9.2).

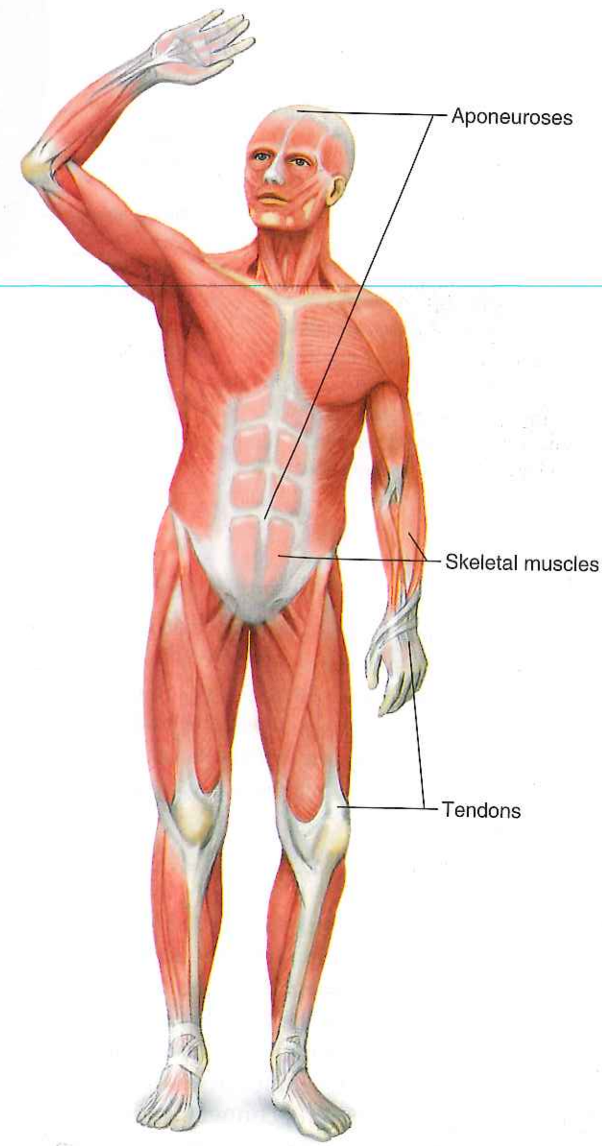


FIGURE 9.1 Tendons attach muscles to bones, whereas aponeuroses attach muscles to other muscles or to bone.

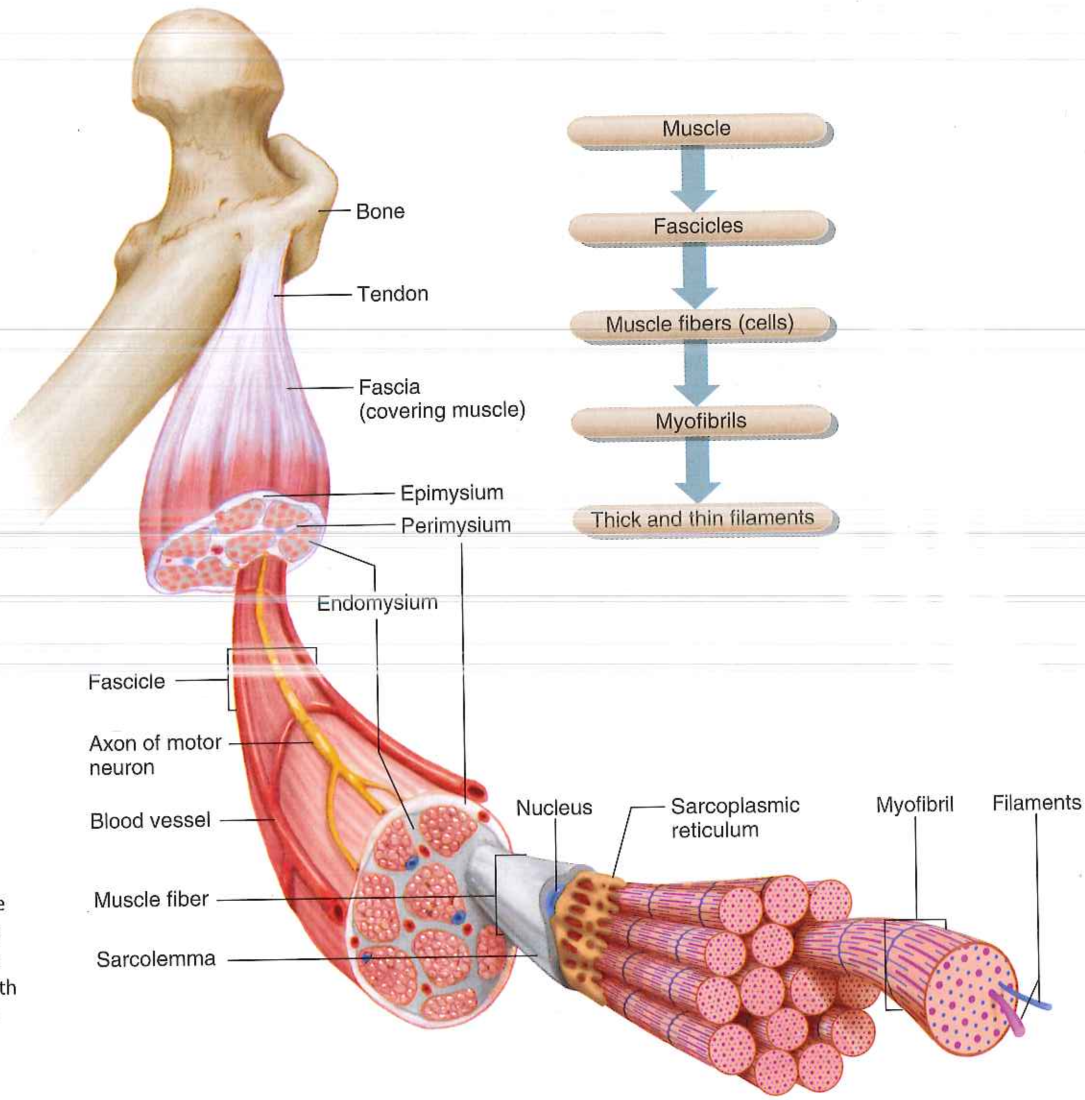


FIGURE 9.2 AP|R A skeletal muscle is composed of a variety of tissues, including layers of connective tissue. Fascia covers the surface of the muscle, epimysium lies beneath the fascia, and perimysium extends into the structure of the muscle where it separates fascicles. Endomysium separates individual muscle fibers.

A tendon or the connective tissue sheath of a tendon (tenosynovium) may become painfully inflamed and swollen following an injury or the repeated stress of athletic activity. These conditions are called *tendinitis* and *tenosynovitis*, respectively. The tendons most commonly affected are those associated with the joint capsules of the shoulder, elbow, hip, and knee and those involved with moving the wrist, hand, thigh, and foot.

The layer of connective tissue that closely surrounds a skeletal muscle is called the *epimysium*. Another layer of connective tissue, called the *perimysium*, extends inward from the epimysium and separates the muscle tissue into small sections. These sections contain bundles of skeletal muscle fibers called *fascicles* (fasciculi). Each muscle fiber within a fascicle (fasciculus) lies within a layer of connective tissue in the form of a thin covering called *endomysium* (fig. 9.2 and fig. 9.3). Layers of connective tissue, therefore, enclose and separate all parts of a skeletal muscle. This organization allows the parts to move somewhat independently. Also, many blood vessels and nerves pass through these layers.

A *compartment* is the space that contains a particular group of muscles, blood vessels, and nerves, all tightly enclosed by fascia. The limbs have many such compartments. If an injury causes fluid, such as blood from an internal hemorrhage, to accumulate in a compartment, the pressure inside will rise. The increased pressure, in turn, may interfere with blood flow into the region, reducing the supply of oxygen and nutrients to the affected tissues. This condition, called compartment syndrome, often produces severe, unrelenting pain. Persistently elevated compartmental pressure may irreversibly damage the enclosed muscles and nerves. Treatment for compartment syndrome may require an immediate surgical incision through the fascia (fasciotomy) to relieve the pressure and restore circulation.

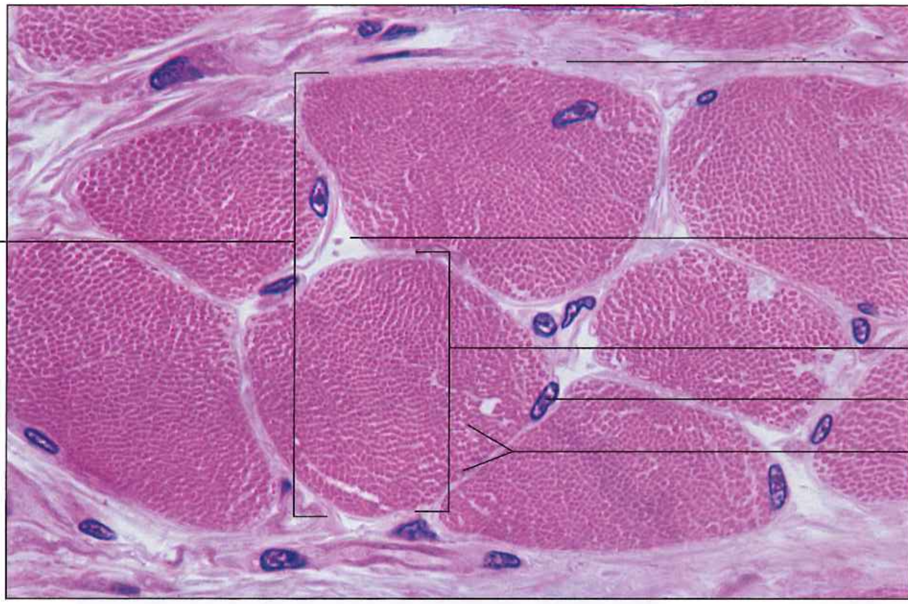


FIGURE 9.3 Scanning electron micrograph of a fascicle (fasciculus) surrounded by its connective tissue sheath, the perimysium. Muscle fibers within the fascicle are surrounded by endomysium (320×).

The fascia associated with each individual organ of the muscular system is part of a complex network of fasciae that extends throughout the body. The portion of the network that surrounds the muscles is called *deep fascia.* It is continuous with the *subcutaneous fascia* that lies just beneath the skin, forming the subcutaneous layer described in chapter 6 (p. 181). The network is also continuous with the *subserous fascia* that forms the connective tissue layer of the serous membranes covering organs in various body cavities and lining those cavities (see chapter 5, p. 171).

Skeletal Muscle Fibers

Recall from chapter 5 (p. 171) that a skeletal muscle fiber is a single muscle cell (see fig. 5.28, p. 172). Each fiber forms from many undifferentiated cells that fuse during development. The resulting multinucleated muscle fiber is a thin, elongated cylinder with rounded ends that attach to the connective tissues associated with a muscle. Just beneath the muscle cell membrane *(sarcolemma),* the cytoplasm *(sarcoplasm)* of the fiber contains many small, oval nuclei and mitochondria. The sarcoplasm also has abundant, parallel, threadlike structures called **myofibrils** (mi″o-fi′-brilz) (fig. 9.4*a*).

The myofibrils play a fundamental role in the muscle contraction mechanism. They consist of two types of protein filaments: thick filaments composed of the protein **myosin** (mi′o-sin), and thin filaments composed primarily of the protein **actin** (ak′tin). (Two other thin filament proteins, troponin and tropomyosin, will be discussed later.) The organization of these filaments produces the alternating light and dark striations characteristic of skeletal muscle (and cardiac muscle) fibers. The striations form a repeating pattern of units called **sarcomeres** (sar′ko-mērz) along each muscle fiber. The myofibrils may be thought of as sarcomeres joined end to end (fig. 9.4*a*). Muscle fibers, and in a way muscles themselves, are basically collections of sarcomeres, discussed later in this chapter as the functional units of muscle contraction.

The striation pattern of skeletal muscle has two main parts. The first, the *I bands* (the light bands), are composed of thin actin filaments held by direct attachments to structures called *Z lines,* which appear in the center of the I bands. The second part of the striation pattern consists of the *A bands* (the dark bands), composed of thick myosin filaments overlapping thin actin filaments (fig. 9.4*b*).

The A band consists not only of a region where thick and thin filaments overlap, but also a slightly lighter central region *(H zone)* consisting only of thick filaments. The A band includes a thickening known as the *M line,* which consists of proteins that help hold the thick filaments in place (fig. 9.4*b*). The myosin filaments are also held in place by the Z lines but are attached to them by a large protein called **titin** (connectin) (fig. 9.5). A sarcomere extends from one Z line to the next.

Thick filaments are composed of many molecules of myosin. Each myosin molecule consists of two twisted protein strands with globular parts called heads that project outward along their lengths. Thin filaments consist of double strands of actin twisted into a helix. Actin molecules are globular, and each has a binding site to which the heads of a myosin molecule can attach (fig. 9.6).

Two other types of protein, **troponin** and **tropomyosin,** associate with actin filaments. Troponin molecules have three protein subunits and are attached to actin. Tropomyosin molecules are rod-shaped and occupy the longitudinal grooves of the actin helix. Each tropomyosin is held in place by a troponin molecule, forming a troponin-tropomyosin complex (see fig. 9.6).

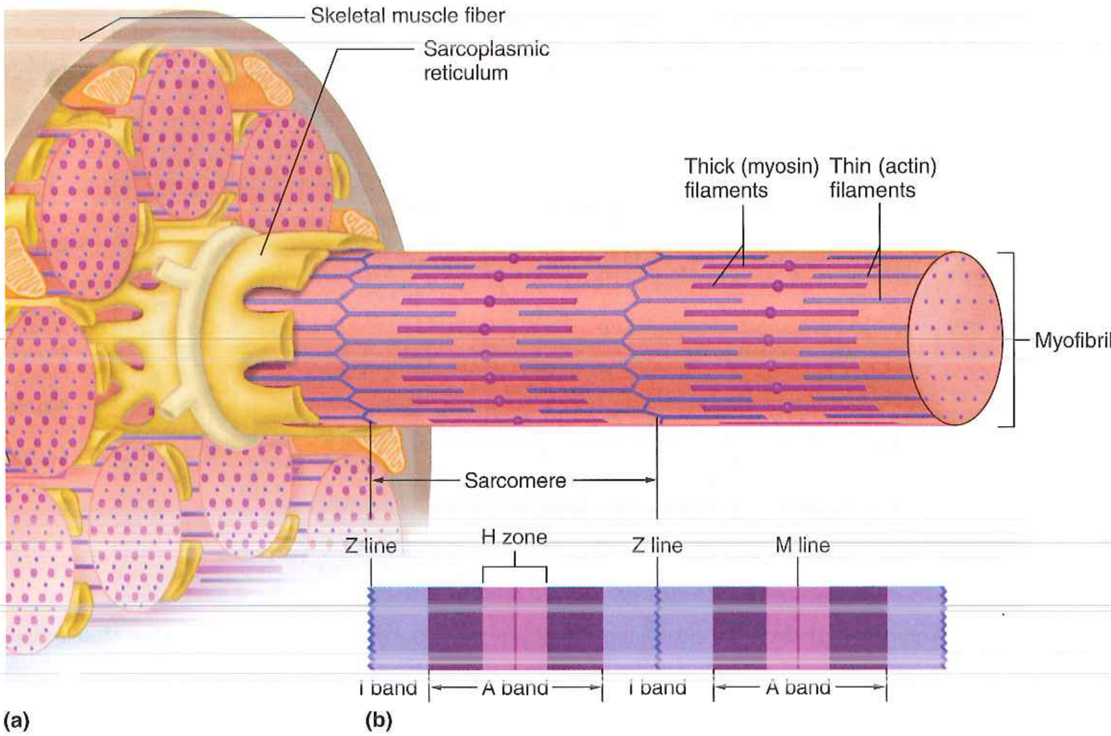


FIGURE 9.4 Skeletal muscle fiber. *(a)* A skeletal muscle fiber contains numerous myofibrils, each consisting of *(b)* repeating units called sarcomeres. The characteristic striations of a sarcomere reflect the organization of actin and myosin filaments.

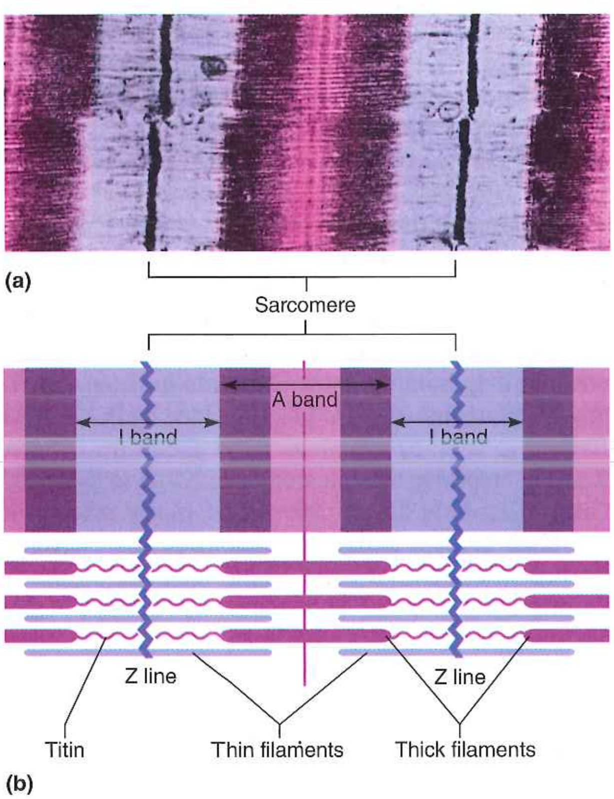


FIGURE 9.5 AP|R A sarcomere. *(a)* Micrograph (16,000×). *(b)* The relationship of thin and thick filaments in a sarcomere.

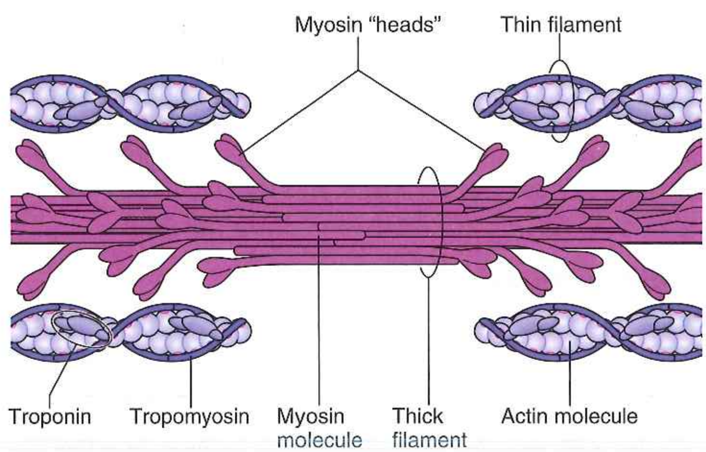


FIGURE 9.6 Thick filaments are composed of the protein myosin, and thin filaments are primarily composed of the protein actin. Myosin molecules have heads that extend toward nearby actin filaments.

Within the sarcoplasm of a muscle fiber is a network of membranous channels that surrounds each myofibril and runs parallel to it. These membranes form the **sarcoplasmic reticulum,** which corresponds to the endoplasmic reticulum of other cells (see figs. 9.2 and 9.4). A set of membranous channels, the **transverse tubules** (T tubules), extends into the sarcoplasm as invaginations continuous with the sarcolemma and contains extracellular fluid. Each transverse tubule lies between two enlarged portions of the sarcoplasmic reticulum called **cisternae.** These three structures form a **triad** near the region where the actin and myosin filaments overlap (fig. 9.7).

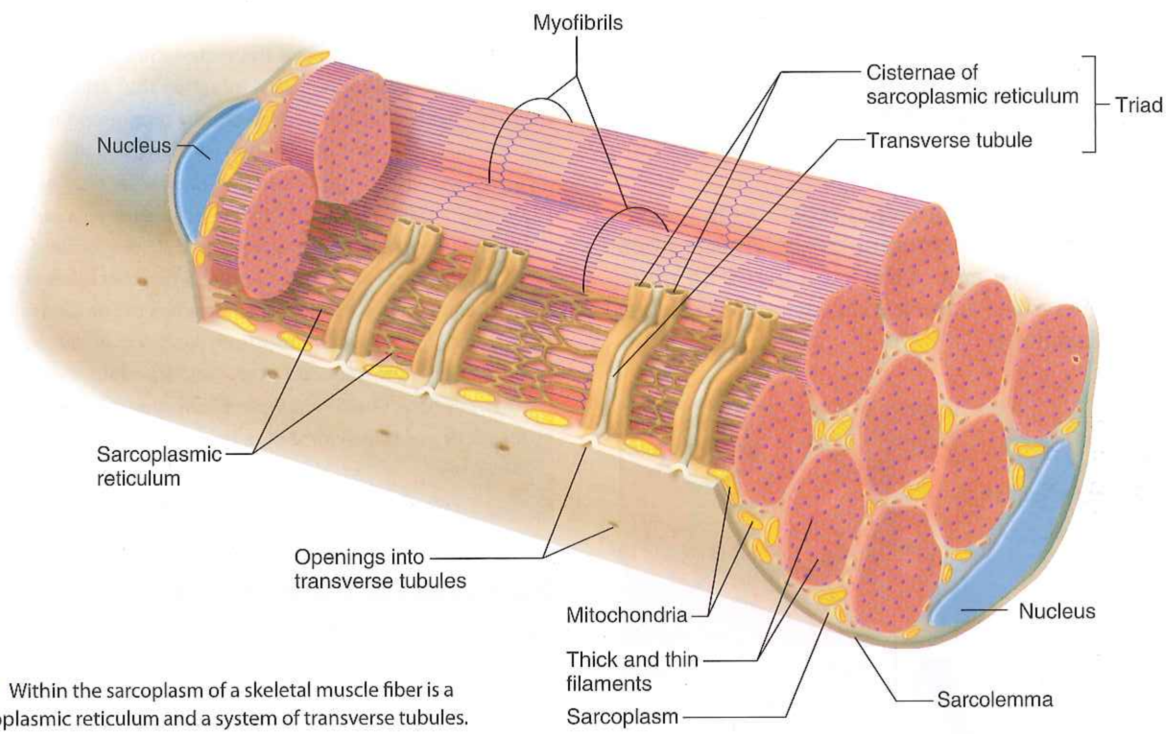


FIGURE 9.7 Within the sarcoplasm of a skeletal muscle fiber is a network of sarcoplasmic reticulum and a system of transverse tubules.

Muscle fibers and the connective tissues associated with them are flexible, but they can tear if overstretched. This type of injury, common in athletes, is called a *muscle strain*. Severity of the injury depends on the degree of damage the tissues sustain. In a mild strain, only a few muscle fibers are injured, the fascia remains intact, and little function is lost. In a severe strain, many muscle fibers as well as fascia tear, and muscle function may be lost completely. A severe strain is very painful and is accompanied by discoloration and swelling of tissues due to torn blood vessels. Surgery may be required to reconnect the separated tissues.

PRACTICE

1. Describe how connective tissue is associated with a skeletal muscle.
2. Describe the general structure of a skeletal muscle fiber.
3. Explain why skeletal muscle fibers appear striated.
4. Explain the physical relationship between the sarcoplasmic reticulum and the transverse tubules.

9.3 SKELETAL MUSCLE CONTRACTION

A muscle fiber contraction is a complex interaction of several cellular and chemical constituents. The result is a movement within the myofibrils in which the filaments of actin and myosin slide past one another, shortening the sarcomeres. When this happens, the muscle fiber shortens and pulls on its attachments.

Actin, myosin, troponin, and tropomyosin are abundant in muscle cells. Scarcer proteins are also vital to muscle function. This is the case for a rod-shaped muscle protein called *dystrophin*. It accounts for only 0.002% of total muscle protein in skeletal muscle, but its absence causes the devastating inherited disorder Duchenne muscular dystrophy, a disease that only affects males. Dystrophin binds to the inside face of muscle cell membranes, supporting them against the powerful force of contraction. Without even these minute amounts of dystrophin, muscle cells lose their normal structure and die.

Neuromuscular Junction

Recall from chapter 5 (p. 173) that neurons establish communication networks throughout the body. This involves a combination of specialized structure and function. Each neuron has a process called an axon, which extends from the cell body and is capable of conducting electrical impulses called *action potentials* (described in chapter 10, pp. 376–377).

Each cell that a neuron controls is connected functionally (but not physically) to the end of an axon, in much the same way that you can talk into a cell phone although your mouth is not in direct physical contact with it. The site of this functional connection is called a **synapse.** Neurons communicate with the cells that they control by releasing chemicals, called **neurotransmitters** (nu″ro-trans-mit-erz), at a synapse. The molecules then diffuse a very short distance to the cell being controlled, where they have a specific effect.

Neurons that control effectors, including skeletal muscle fibers, are called **motor neurons**. Normally a skeletal muscle fiber contracts only upon stimulation by its motor neuron.

The synapse where a motor neuron axon and a skeletal muscle fiber meet is called a **neuromuscular junction** (myoneural junction). There, the muscle fiber membrane is specialized to form a **motor end plate,** where nuclei and mitochondria are abundant and the sarcolemma is extensively folded (fig. 9.8).

A small gap called the **synaptic cleft** separates the membrane of the neuron and the membrane of the muscle fiber. The cytoplasm at the distal end of the axon is rich in mitochondria and contains many tiny vesicles (synaptic vesicles) that store neurotransmitters.

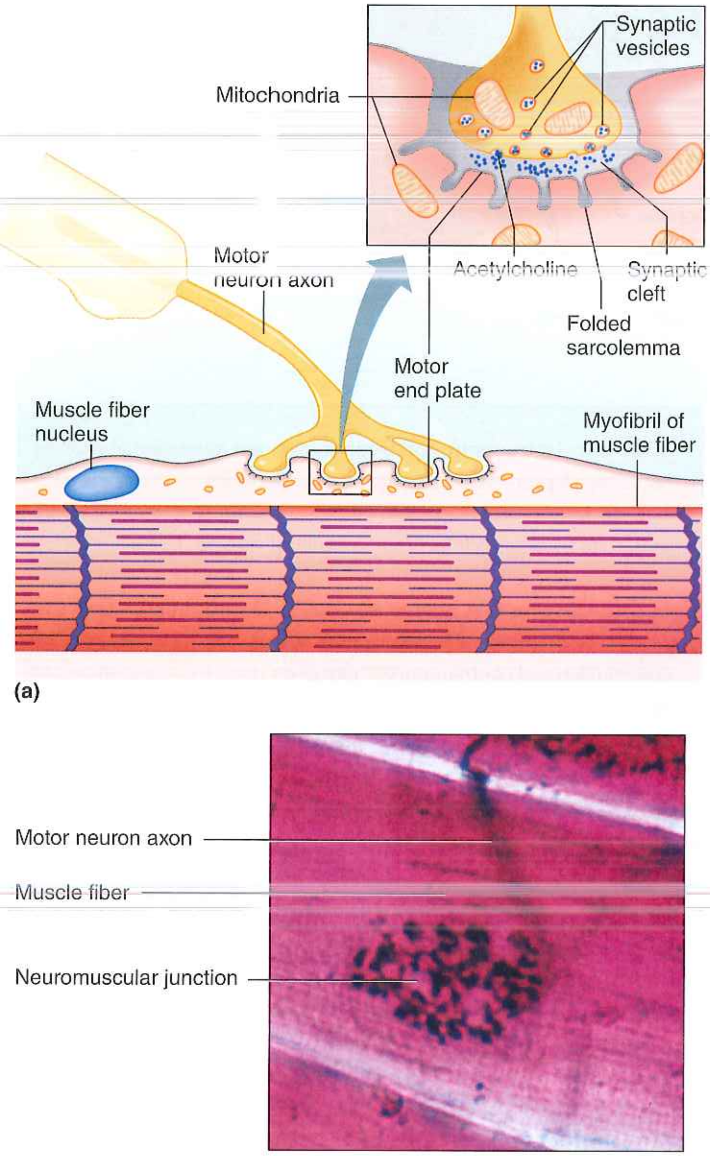


FIGURE 9.8 AP|R Neuromuscular junction. *(a)* A neuromuscular junction includes the end of a motor neuron and the motor end plate of a muscle fiber. *(b)* Micrograph of a neuromuscular junction (500×).

Q: *How does neurotransmitter released into the synaptic cleft reach the muscle fiber membrane?*

Answers can be found in Appendix G on page 938.

In the summer months of the early 1950s, millions of children contracted poliomyelitis, a viral infection that attacks motor neurons. Fever, headache, and nausea rapidly progressed to a stiffened back and neck, drowsiness, and then paralysis, usually of the lower limbs or muscles that control breathing or swallowing. Today in the United States, a third of the 1.6 million polio survivors suffer the fatigue, muscle weakness and atrophy, and difficulty breathing of postpolio syndrome. Researchers think that in this condition, surviving motor neurons that grew extra axon branches to compensate for neurons lost during polio degenerate from years of overuse.

Vaccines introduced in the middle 1950s vanquished polio in many nations. The Global Polio Eradication Initiative has reduced the incidence of polio worldwide by more than 99% since its launch in 1988.

Stimulus for Contraction

Acetylcholine (ACh) is the neurotransmitter that motor neurons use to control skeletal muscle contraction. ACh is synthesized in the cytoplasm of the motor neuron and is stored in synaptic vesicles near the distal end of its axon. When an action potential reaches the end of the axon, some of these vesicles release acetylcholine into the synaptic cleft (fig. 9.8).

Acetylcholine diffuses rapidly across the synaptic cleft and binds to specific protein molecules (receptors) in the muscle fiber membrane, increasing the membrane permeability to sodium ions. Recall from chapter 3 (pp. 103–104) that active transport of sodium and potassium ions across the cell membrane creates a condition in which the sodium ion concentration is higher outside the cell and the potassium ion concentration is higher inside the cell. Also remember that an ion will diffuse across a cell membrane only if two conditions are met: there is a concentration gradient and the membrane is permeable to that ion. The sodium/potassium pump maintains the concentration gradients for these two ions, but membrane permeability is normally very low, so in the non-stimulated state the extent of diffusion of these ions across the membrane is very low.

When a motor neuron stimulates a muscle cell, the situation changes. Membrane permeability to sodium and potassium ions increases temporarily in a pattern that results in positively charged ions first entering (sodium) and then leaving (potassium) the muscle cell. This mechanism, which is similar in muscle cells and nerve cells, is discussed in more detail in chapter 10 (pp. 376–377). The result of these ion movements is a bioelectric current, an action potential. In much the same way that an impulse is conducted down an axon, an impulse now spreads throughout the muscle cell. This electrical impulse is what triggers the release of calcium ions from the sarcoplasmic reticulum, leading to muscle contraction. Clinical Application 9.1 discusses myasthenia gravis, in which the immune system attacks certain neuromuscular junctions.

9.1 CLINICAL APPLICATION

Myasthenia Gravis

In an autoimmune disorder, the immune system attacks part of the body. In myasthenia gravis (MG), that part is the muscular system. The body produces antibodies that target receptors for the neurotransmitter acetylcholine on skeletal muscle cells at neuromuscular junctions. People with MG have one-third the normal number of acetylcholine receptors here. On a whole-body level, this causes weak and easily fatigued muscles.

MG affects hundreds of thousands of people worldwide, mostly women beginning in their twenties or thirties, and men in their sixties and seventies. The specific symptoms depend upon the site of attack. For 85% of patients, the disease causes generalized muscle weakness. Many people develop a characteristic flat smile and nasal voice and have difficulty chewing and swallowing due to affected facial and neck muscles. Many have limb weakness. About 15% of patients experience the illness only in the muscles surrounding their eyes. The disease reaches crisis level when respiratory muscles are affected, requiring a ventilator to support breathing. MG does not affect sensation or reflexes.

Most people with MG live a normal life span, with symptoms that are controlled with a combination of treatments that include the following:

- Drugs may inhibit acetylcholinesterase, the enzyme that normally breaks down acetylcholine, thus increasing levels of the neurotransmitter.
- Immunosuppressant drugs decrease production of antibodies.
- Intravenous antibodies bind and inactivate the ones causing the damage.
- Plasma exchange rapidly removes the damaging antibodies from circulation, helping people in crisis. ■

When the bacterium *Clostridium botulinum* grows in an anaerobic (oxygen-poor) environment, such as in a can of unrefrigerated food, it produces a toxin that prevents the release of acetylcholine from axon terminals if ingested by a person. Symptoms of such food poisoning include nausea, vomiting, and diarrhea; headache, dizziness, and blurred or double vision; and finally, weakness, hoarseness, and difficulty swallowing and, eventually, inability to breathe. Physicians can administer an antitoxin substance that binds to and inactivates botulinum toxin in the bloodstream, stemming further symptoms, although not correcting damage already done. Small amounts of botulinum toxin are used to treat migraine headaches and to temporarily paralyze selected facial muscles, smoothing wrinkles (Botox).

Excitation Contraction Coupling APIR

The sarcoplasmic reticulum has a high concentration of calcium ions compared to the cytosol. This is due to active transport of calcium ions (calcium pump) in the membrane of the sarcoplasmic reticulum. In response to a muscle impulse, the membranes of the cisternae become more permeable to these ions, and the calcium ions diffuse out of the cisternae into the cytosol of the muscle fiber (see fig. 9.7).

RECONNECT

To Chapter 3, Active Transport, pages 103-104.

When a muscle fiber is at rest, the troponin-tropomyosin complexes block the binding sites on the actin molecules and thus prevent the formation of linkages with myosin cross-bridges (fig. 9.9 ①). As the concentration of calcium ions in the cytosol rises, however, the calcium ions bind to the troponin, changing its shape (conformation) and altering the position of the tropomyosin. The movement of the tropomyosin molecules exposes the binding sites on the actin filaments, allowing linkages to form between myosin heads and actin, forming cross-bridges (fig. 9.9 ②).

RECONNECT

To Chapter 2, Proteins, pages 74–76.

The Sliding Filament Model of Muscle Contraction

The sarcomere is considered the functional unit of skeletal muscles because contraction of an entire skeletal muscle can be described in terms of the shortening of the sarcomeres of its muscle fibers. According to the **sliding filament model,** when sarcomeres shorten, the thick and thin filaments do not change length. Rather, they slide past one another, with the thin filaments moving toward the center of the sarcomere from both ends. As this occurs, the H zones and the I bands narrow; the regions of overlap widen; and the Z lines move closer together, shortening the sarcomere (fig. 9.10).

Cross-Bridge Cycling

The force that shortens the sarcomeres comes from cross-bridges pulling on the thin filaments. A myosin head can attach to an actin binding site forming a cross-bridge, and bend slightly, pulling on the actin filament. Then the head can release, straighten, combine with another binding site further down the actin filament, and pull again (see fig. 9.9 ②–⑥).

Myosin heads contain the enzyme **ATPase,** which catalyzes the breakdown of ATP to ADP and phosphate. This reaction releases energy (see chapter 4, p. 127) that provides the force for muscle contraction. Breakdown of ATP puts

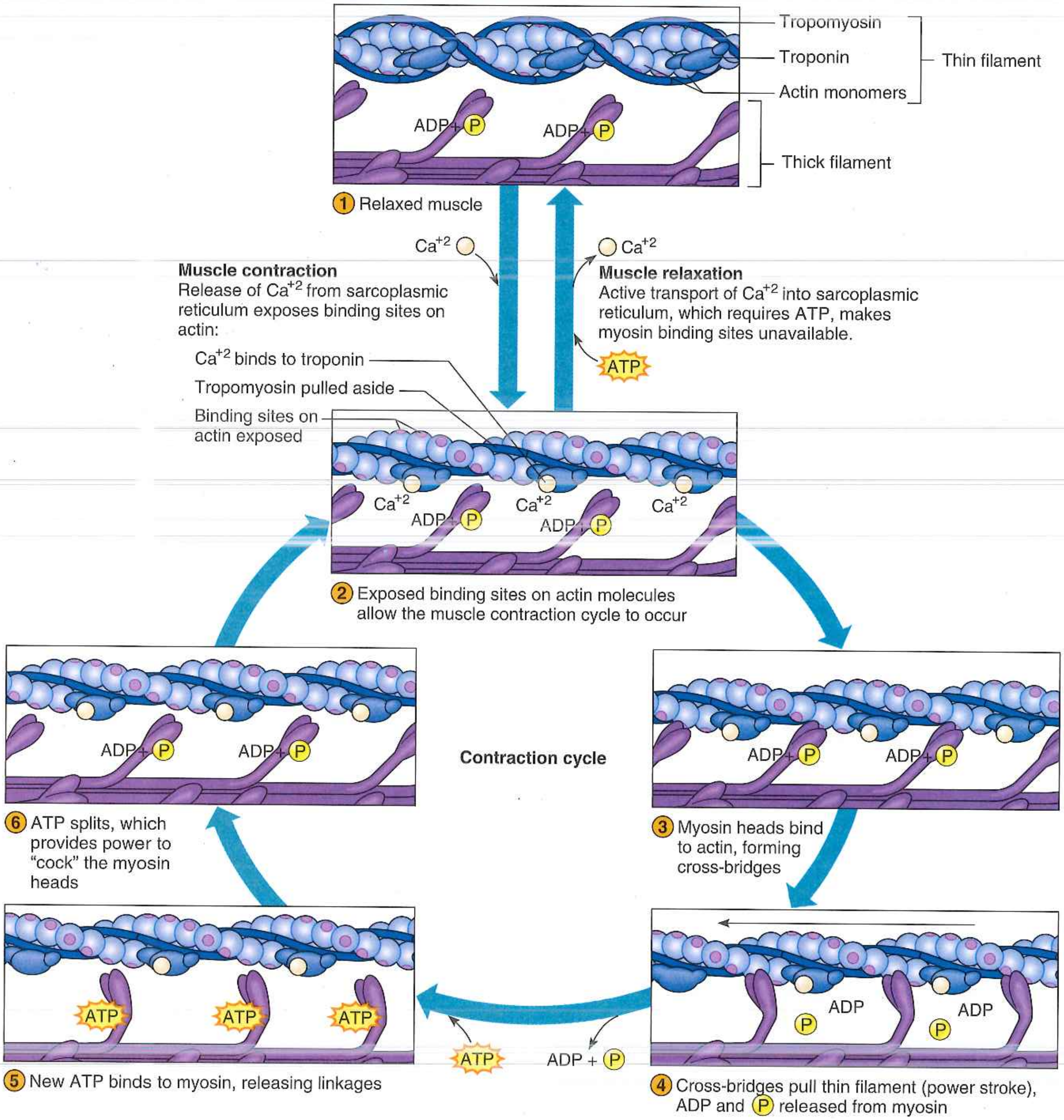


FIGURE 9.9 APR According to the sliding filament theory (*1–3*), when calcium ion concentration rises, binding sites on actin filaments open, and myosin heads attach, forming cross-bridges. (*4*) Upon forming, cross-bridges spring from the cocked position and pull on actin filaments. (*5*) ATP binds to the cross-bridge (but the ATP is not yet broken down), releasing it from the actin filament. (*6*) ATP breakdown provides energy to "cock" the unattached myosin head. As long as ATP and calcium ions are present, the cycle continues. When calcium ion concentration is low in the cytosol, the muscle cell remains relaxed. Not all cross-bridges form and release simultaneously.

the myosin head in a "cocked" position (see fig. 9.9 ⑥). When a muscle is stimulated to contract, a cocked myosin head attaches to actin (see fig. 9.9 ③), forming a cross-bridge that pulls the actin filament toward the center of the sarcomere (see fig. 9.9 ④). This causes a greater overlap of the actin and myosin filaments, shortens the sarcomere and thus shortens the muscle (fig. 9.10). When another ATP binds, the myosin head first detaches from the actin binding site (see fig. 9.9 ⑤), then breaks down the ATP to return to the cocked position (see fig. 9.9 ⑥). This cross-bridge cycle may repeat as long as ATP is present and action potentials release ACh at that neuromuscular junction.

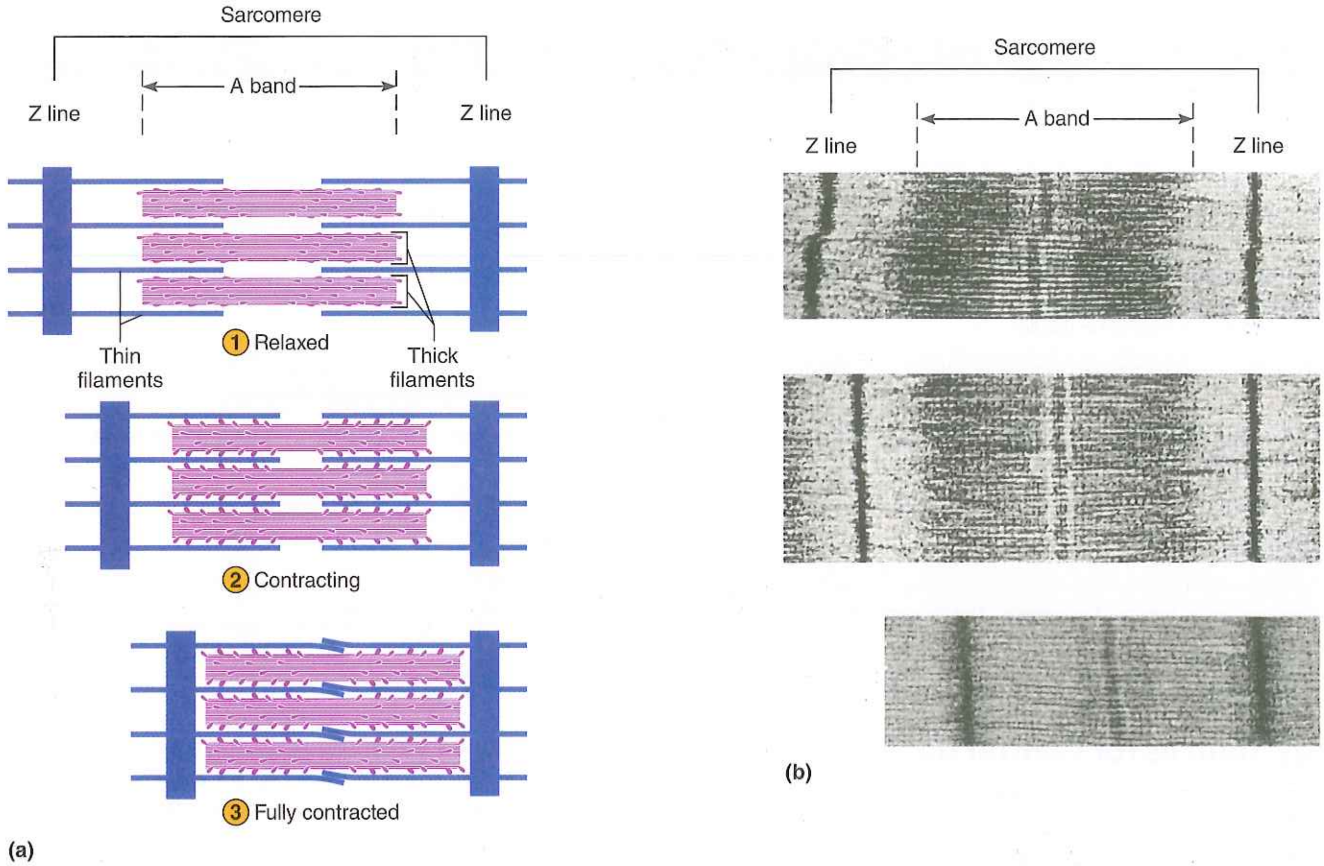


FIGURE 9.10 AP|R When a skeletal muscle contracts (*a*), individual sarcomeres shorten as thick and thin filaments slide past one another. (*b*) Transmission electron micrograph showing a sarcomere shortening during muscle contraction (23,000×).

Q: *What happens to the length of the thick and thin filaments during contraction?*

Answer can be found in Appendix G on page 938.

Relaxation

When nervous stimulation of the muscle fiber ceases (when action potentials no longer reach the axon terminal), two events relax the muscle fiber. First, an enzyme called **acetylcholinesterase** rapidly decomposes acetylcholine remaining in the synapse. This enzyme, also on the membranes of the motor end plate, prevents a single action potential from continuously stimulating a muscle fiber. Second, when ACh breaks down, the stimulus to the sarcolemma and the membranes of the muscle fiber ceases. The calcium pump (which requires ATP) quickly moves calcium ions back into the sarcoplasmic reticulum, decreasing the calcium ion concentration of the cytosol. The cross-bridge linkages break (see fig. 9.9 ⑥—this also requires ATP, although it is not broken down in this step), and tropomyosin rolls back into its groove, preventing cross-bridge attachment (see fig. 9.9 ①). Consequently, the muscle fiber relaxes. Table 9.1 summarizes the major events leading to muscle contraction and relaxation.

It is important to remember that ATP is necessary for both muscle contraction and for muscle relaxation. The trigger for contraction is the increase in cytosolic calcium in response to stimulation by ACh from a motor neuron.

A few hours after death, the skeletal muscles partially contract, fixing the joints. This condition, called *rigor mortis,* may continue for seventy-two hours or more. It results from an increase in membrane permeability to calcium ions, which promotes cross-bridge formation, and a decrease in availability of ATP in the muscle fibers, which prevents myosin release from actin. Thus, the actin and myosin filaments of the muscle fibers remain linked until the muscles begin to decompose.

PRACTICE

5 Describe a neuromuscular junction.

6 List four proteins associated with myofibrils, and explain their structural and functional relationships.

7 Explain how the filaments of a myofibril interact during muscle contraction.

8 Explain how a motor neuron action potential can trigger a skeletal muscle fiber contraction.

TABLE 9.1 | Major Events of Muscle Contraction and Relaxation

Muscle Fiber Contraction	Muscle Fiber Relaxation
1. An action potential is conducted down a motor neuron axon.	1. Acetylcholinesterase decomposes acetylcholine, and the muscle fiber membrane is no longer stimulated.
2. The motor neuron terminal releases the neurotransmitter acetylcholine (ACh).	2. Calcium ions are actively transported into the sarcoplasmic reticulum.
3. ACh binds to ACh receptors on the muscle fiber.	3. ATP breaks linkages between actin and myosin filaments without breakdown of the ATP itself.
4. The sarcolemma is stimulated, an action potential is generated, and the impulse is conducted over the surface of the muscle fiber and deep into the fiber through the transverse tubules.	4. Breakdown of ATP "cocks" the myosin heads.
5. The impulse reaches the sarcoplasmic reticulum, and calcium channels open.	5. Troponin and tropomyosin molecules inhibit the interaction between myosin and actin filaments.
6. Calcium ions diffuse from the sarcoplasmic reticulum into the sarcoplasm and bind to troponin molecules.	6. Muscle fiber remains relaxed, yet ready until stimulated again.
7. Tropomyosin molecules move and expose specific sites on actin.	
8. Actin and myosin link, forming cross-bridges.	
9. Thin (actin) filaments are pulled toward the center of the sarcomere by myosin cross-bridges increasing the overlap of the thin and thick filaments.	
10. The muscle fiber contracts.	

Energy Sources for Contraction

The energy that powers the interaction between actin and myosin filaments as muscle fibers contract comes from ATP molecules. However, a muscle fiber has only enough ATP to contract briefly, and must regenerate ATP.

The initial source of energy available to regenerate ATP from ADP and phosphate is **creatine phosphate.** Like ATP, creatine phosphate includes a high-energy phosphate bond. Creatine phosphate is four to six times more abundant in muscle fibers than is ATP, but it cannot directly supply energy to a cell. Instead, it stores energy released from mitochondria. Whenever sufficient ATP is present, an enzyme in the mitochondria (creatine phosphokinase) promotes the synthesis of creatine phosphate, which stores excess energy in its phosphate bond (fig. 9.11).

As ATP is decomposed to ADP, the energy from creatine phosphate molecules is transferred to these ADP molecules, quickly phosphorylating them back into ATP. The amount of ATP and creatine phosphate in a skeletal muscle, however, is usually not sufficient to support maximal muscle activity for more than about ten seconds during an intense contraction. As a result, the muscle fibers in an active muscle soon use cellular respiration of glucose to synthesize ATP. Typically, a muscle stores glucose in the form of glycogen.

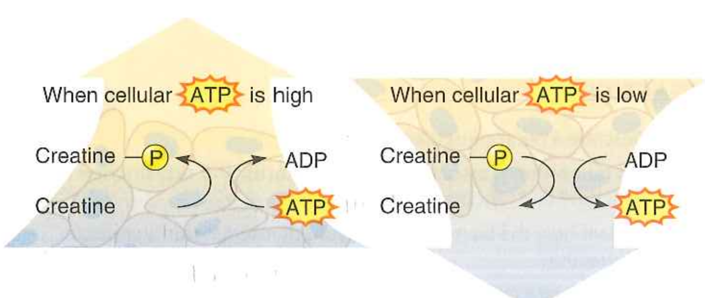


FIGURE 9.11 Creatine phosphate may be used to replenish ATP stores when ATP levels in a muscle cell are low.

Oxygen Supply and Cellular Respiration

Recall from chapter 4 (p. 128) that glycolysis, the early phase of cellular respiration, occurs in the cytosol and is *anaerobic*, not requiring oxygen. This phase only partially breaks down energy-supplying glucose and yields only two ATP molecules for each molecule of glucose. The complete breakdown of glucose occurs in the mitochondria and is *aerobic*, requiring oxygen. This process, which includes the complex series of reactions of the *citric acid cycle* and *electron transport chain*, produces many ATP molecules (see chapter 4, pp. 130–132).

Blood carries the oxygen necessary to support the aerobic reactions of cellular respiration from the lungs to body cells. Oxygen is transported in red blood cells, where it is loosely bound to molecules of hemoglobin, the pigment responsible for the red color of blood. In regions of the body where the oxygen concentration is low, oxygen is released from hemoglobin and becomes available for the aerobic reactions of cellular respiration.

Another pigment, **myoglobin,** is synthesized in muscle cells and imparts the reddish brown color of skeletal muscle tissue. Like hemoglobin, myoglobin can loosely bind oxygen and, in fact, has a greater attraction for oxygen than does hemoglobin. Myoglobin can temporarily store oxygen in muscle tissue, which reduces a muscle's requirement for a continuous blood supply during contraction (fig. 9.12). This oxygen storage is important because blood flow may decrease during muscular contraction when contracting muscle fibers compress blood vessels.

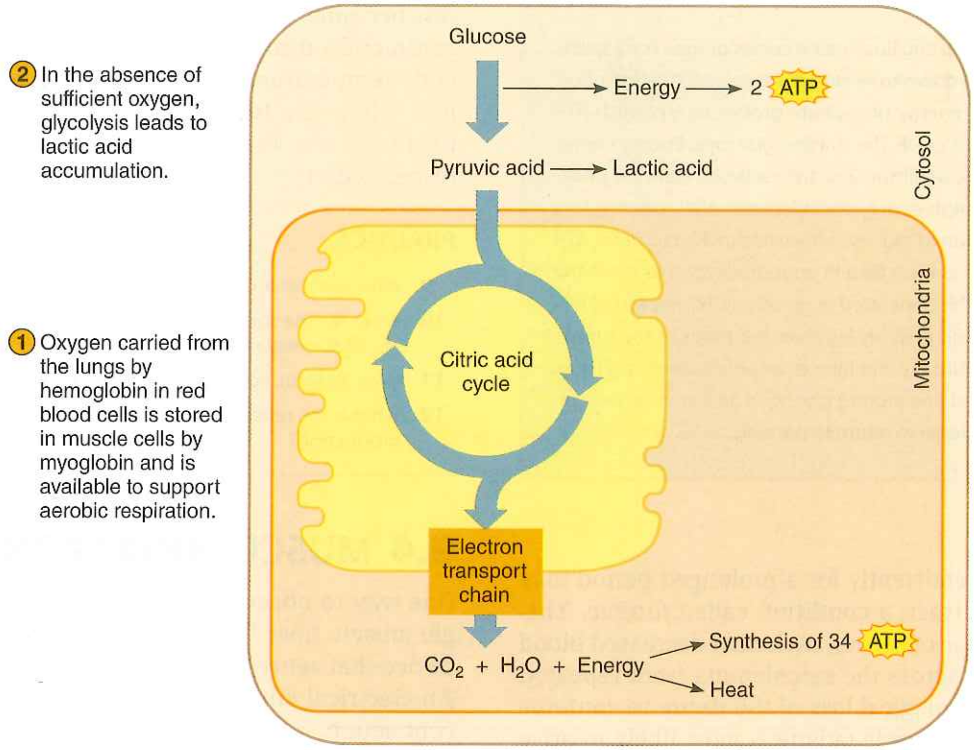


FIGURE 9.12 The oxygen required to support the aerobic reactions of cellular respiration is carried in the blood and stored in myoglobin. The maximum number of ATPs generated per glucose molecule varies with cell type; in skeletal muscle, it is 36 (2 + 34). In the absence of sufficient oxygen, anaerobic reactions use pyruvic acid to produce lactic acid.

Oxygen Debt

When a person is resting or moderately active, the respiratory and cardiovascular systems can usually supply sufficient oxygen to the skeletal muscles to support the aerobic reactions of cellular respiration. However, when skeletal muscles are used more strenuously, these systems may not be able to supply enough oxygen to sustain the aerobic reactions of cellular respiration.

Chapter 4 (pp. 128–129) discussed how the anaerobic reactions break down glucose into pyruvic acid, which then reacts to produce lactic acid. This shift in metabolism is referred to as the anaerobic threshold, or the **lactic acid threshold.** The lactic acid diffuses out of the muscle fibers and is carried in the bloodstream to the liver. Liver cells can react the lactic acid to form *glucose,* but this requires energy from ATP (fig. 9.13). During strenuous exercise, available oxygen is primarily used to synthesize ATP for muscle contraction rather than to make ATP for reacting lactic acid to yield glucose. Consequently, as lactic acid accumulates, a person develops an **oxygen debt** that must be repaid at a later time. The amount of oxygen debt includes the amount of oxygen that liver cells require to use the accumulated lactic acid to produce glucose, as well as the amount that the muscle cells require to resynthesize sufficient ATP and creatine phosphate to restore their original concentrations. The degree of oxygen debt also reflects the oxygen required to restore blood and tissue oxygen levels to preexercise levels.

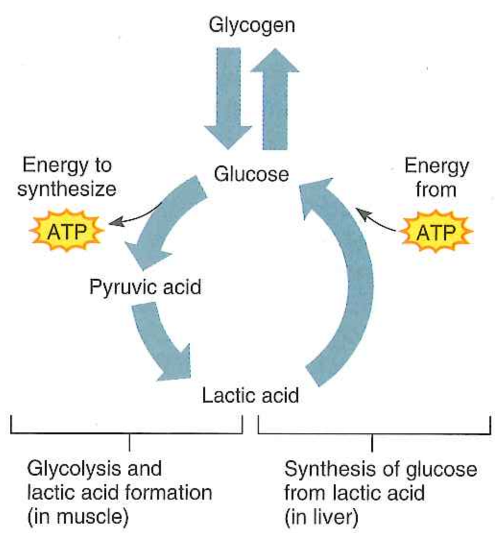


FIGURE 9.13 Liver cells can react lactic acid generated by muscles anaerobically to produce glucose.

The metabolic capacity of a muscle may change with athletic training. With high-intensity exercise, which depends more on glycolysis for ATP, a muscle will synthesize more glycolytic enzymes, and its capacity for glycolysis will increase. With aerobic exercise, more capillaries and mitochondria develop, and the muscles' capacity for the aerobic reactions of cellular respiration increases.

The runners are on the starting line, their muscles primed for a sprint. Glycogen will be broken down to release glucose, and creatine phosphate will supply high-energy phosphate groups to replenish ATP stores by phosphorylating ADP. The starting gun fires. Energy comes first from residual ATP, but almost instantaneously, creatine phosphate begins donating high-energy phosphates to ADP, regenerating ATP. Meanwhile, oxidation of glucose ultimately produces more ATP. But because the runner cannot take in enough oxygen to meet the high demand, most ATP is generated in glycolysis. Formation of lactic acid causes fatigue and possibly leg muscle cramps as the runner crosses the finish line. Already, her liver is actively converting lactic acid back to pyruvic acid and storing glycogen. In her muscles, creatine phosphate levels begin to return to normal.

Muscle Fatigue

A muscle exercised persistently for a prolonged period may lose its ability to contract, a condition called *fatigue*. This condition has a number of causes, including decreased blood flow, ion imbalances across the sarcolemma from repeated stimulation, and psychological loss of the desire to continue the exercise. However, muscle fatigue is most likely to arise at least in part from accumulation of hydrogen ions due to lactic acid formation in the muscle from anaerobic ATP production. The lowered pH from the lactic acid prevents muscle fibers from responding to stimulation.

As muscle metabolism shifts from aerobic to anaerobic ATP production, lactic acid begins to accumulate in muscles and to appear in the bloodstream (lactic acid threshold). This leads to muscle fatigue. How quickly this happens varies among individuals, although people who regularly exercise aerobically produce less lactic acid than those who do not. The strenuous exercise of aerobic training stimulates new capillaries to extend into muscles, supplying more oxygen and nutrients to the muscle fibers. Such physical training also adds mitochondria, increasing the ability of muscle fibers to produce ATP aerobically. Some muscle fibers may be more likely to accumulate lactic acid than others, as described in a later section entitled "Fast- and Slow-Twitch Muscle Fibers."

Occasionally a muscle fatigues and cramps at the same time. A cramp is a sustained, painful, involuntary muscle contraction. The cause of muscle cramps is not fully understood. One hypothesis suggests that cramps may result from changes in electrolyte concentration in the extracellular fluid surrounding the muscle fibers and their motor neurons, triggering uncontrolled stimulation of the muscle.

Heat Production

All active cells generate heat, which is a by-product of cellular respiration. Muscle tissue constitutes such a large proportion of total body mass that it is a major source of heat.

Less than half of the energy released in cellular respiration is available for use in metabolic processes. The rest becomes heat. Blood transports the heat from muscle contraction throughout the body, which helps to maintain body temperature. Homeostatic mechanisms promote heat loss when the temperature of the internal environment begins to rise (see chapters 1 and 6, p. 19 and 190–191, respectively).

PRACTICE

9 What are the sources of energy used to regenerate ATP?

10 What are the sources of oxygen required for the aerobic reactions of cellular respiration?

11 How do lactic acid and oxygen debt relate to muscle fatigue?

12 What is the relationship between cellular respiration and heat production?

9.4 MUSCULAR RESPONSES

One way to observe muscle contraction is to remove a single muscle fiber from a skeletal muscle and connect it to a device that senses and records changes in the fiber's length. An electrical stimulator is usually used to promote muscle contraction.

Threshold Stimulus

When an isolated muscle fiber is exposed to a series of stimuli of increasing strength, the fiber remains unresponsive until a certain strength of stimulation called the **threshold stimulus** (thresh'old stim'u-lus) is applied. Once threshold is reached, an action potential is generated, resulting in an impulse that spreads throughout the muscle fiber, releasing enough calcium ions from the sarcoplasmic reticulum to activate cross-bridge formation and contract the fiber. A single action potential conducted down a motor neuron normally releases enough ACh to bring the muscle fibers to threshold, generating an impulse in the muscle fiber.

Recording of a Muscle Contraction

The contractile response of a single muscle fiber to a muscle impulse is called a **twitch.** A twitch consists of a period of contraction, during which the fiber pulls at its attachments, followed by a period of relaxation, during which the pulling force declines. These events can be recorded in a pattern called a myogram (fig. 9.14). A twitch has a brief delay between the time of stimulation and the beginning of contraction. This is the **latent period,** which in human muscle may be less than 2 milliseconds.

The length to which a muscle fiber is stretched before stimulation affects the force it will develop. If a skeletal muscle fiber is stretched well beyond its normal resting length, the force will decrease. This is because sarcomeres of that fiber become so extended that some myosin heads cannot reach binding sites on the thin filaments and cannot contribute to contraction. Conversely, at very short fiber lengths, the sarcomeres become compressed, and further shortening

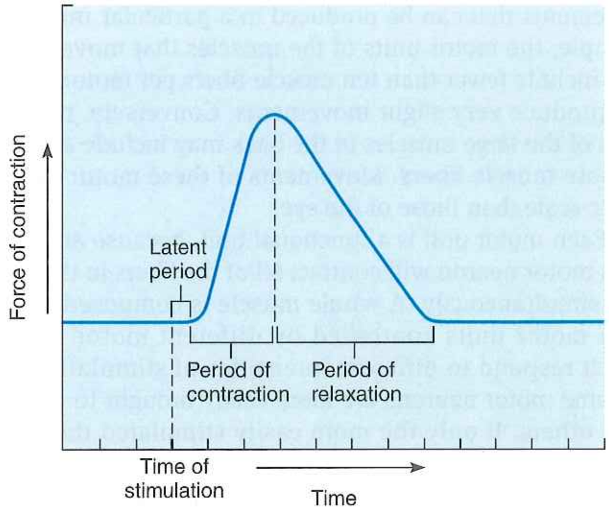


FIGURE 9.14 A myogram of a single muscle twitch.

is not possible (fig. 9.15). During normal activities, muscle fibers contract at their optimal lengths. Some activities, such as walking up stairs two at a time or lifting something from an awkward position, put fibers at a disadvantageous length and compromise muscle performance.

A GLIMPSE AHEAD | To Chapter 15

Cardiac muscle does not normally decrease its force of contraction when stretched. This allows the heart to respond to conditions of greater demand, such as exercise.

A muscle fiber brought to threshold under a given set of conditions contracts completely, and each twitch generates equal force. This is an *all-or-none* response. However, "all-or-none" is misleading, because in normal use of muscles, the force generated by muscle fibers and by whole muscles must vary.

Understanding how individual muscle fibers contract is important for understanding how muscles work, but such contractions by themselves are of little significance in day-to-day activities. Rather, the actions we need to perform usually require the contribution of multiple muscle fibers simultaneously. To record how a whole muscle responds to stimulation, a skeletal muscle can be removed from a frog or other small animal and mounted on a special device. The muscle is then electrically stimulated, and when it contracts, it pulls on a lever. The lever's movement is recorded as a myogram, which reflects the combined twitches of muscle fibers contracting, so it looks like the twitch contraction depicted in figure 9.14.

Sustained contractions of whole muscles enable us to perform everyday activities, but the force generated by those contractions must be controlled. For example, holding a styrofoam cup of coffee firmly enough to keep it from slipping through our fingers, but not so forcefully as to crush it, requires precise control of contractile force. In the whole muscle, the force developed reflects (1) the frequency at which individual muscle fibers are stimulated and (2) how many fibers take part in the overall contraction of the muscle.

Summation

The force that a muscle fiber can generate is not limited to the maximum force of a single twitch (fig. 9.16*a*). A muscle fiber exposed to a series of stimuli of increasing frequency reaches a point when it is unable to completely relax before the next stimulus in the series arrives. When this happens, the individual twitches begin to combine, and the contraction becomes sustained. In such a *sustained contraction*, the force of individual twitches combines by the process of **summation** (fig. 9.16*b*). At higher frequencies of stimulation, as the time spent in relaxation becomes very brief, a condition called *partial tetany* results. When the resulting forceful, sustained contraction lacks even partial relaxation, it is called a **complete** (fused) **tetanic** (tĕ-tan′ik) **contraction** (tetanus) (fig. 9.16*c*).

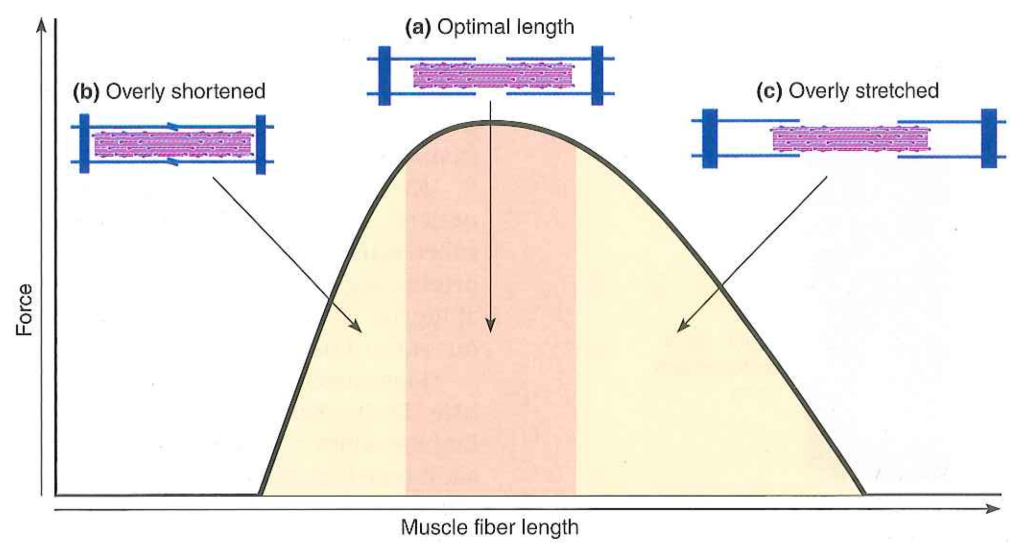


FIGURE 9.15 The force a muscle fiber can generate depends on the length to which it is stretched when stimulated.

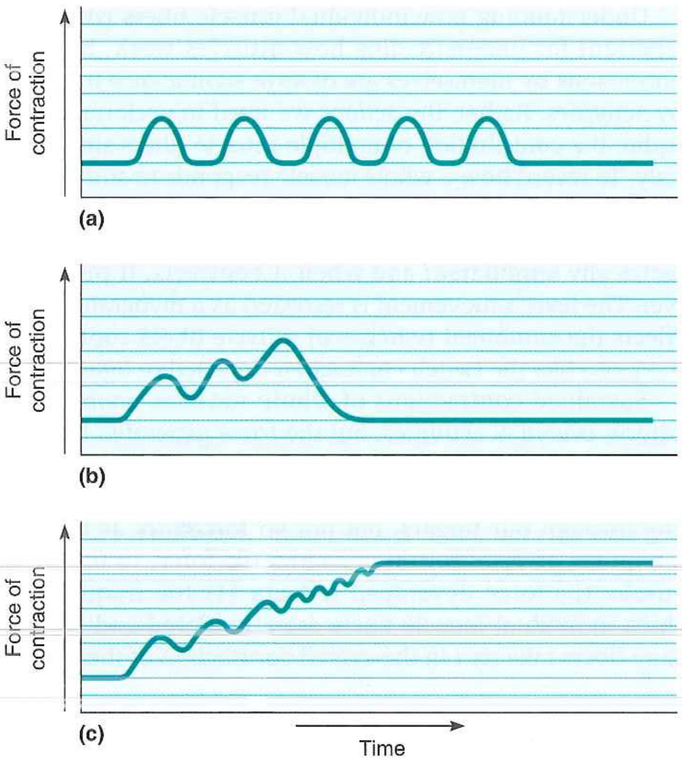


FIGURE 9.16 Myograms of (*a*) a series of twitches, (*b*) summation, and (*c*) a tetanic contraction. Stimulation frequency increases from one myogram to the next.

Recruitment of Motor Units

Most muscle fibers have only one motor end plate. Motor neuron axons, however, are densely branched, which enables one such axon to connect to many muscle fibers. Together, a motor neuron and the muscle fibers it controls constitute a *motor unit* (mo′tor u′nit) (fig. 9.17). The number of muscle fibers in a motor unit varies considerably. The fewer muscle fibers in the motor units, however, the more precise the movements that can be produced in a particular muscle. For example, the motor units of the muscles that move the eyes may include fewer than ten muscle fibers per motor unit and can produce very slight movements. Conversely, the motor units of the large muscles in the back may include a hundred or more muscle fibers. Movements of these motor units are larger-scale than those of the eye.

Each motor unit is a functional unit, because an impulse in its motor neuron will contract all of the fibers in that motor unit simultaneously. A whole muscle is composed of many such motor units controlled by different motor neurons, which respond to different intensities of stimulation. That is, some motor neurons are more easily brought to threshold than others. If only the more easily stimulated motor neurons are involved, few motor units contract. At higher intensities of stimulation, other motor neurons respond, and more motor units are activated. Such an increase in the number of activated motor units is called *multiple motor unit summation,* or **recruitment** (re-kro͞o-t′ment). As the intensity of stimulation increases, recruitment of motor units continues until finally all possible motor units are activated in that muscle.

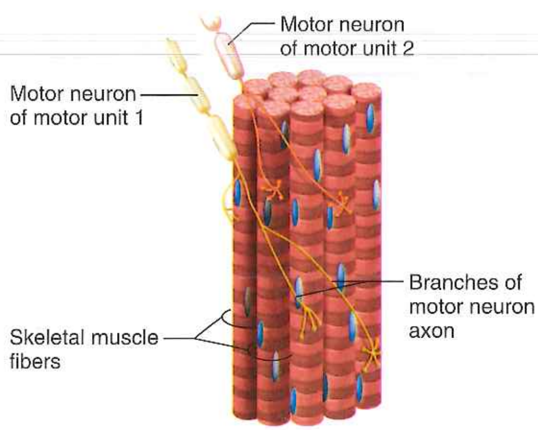


FIGURE 9.17 Two motor units. The muscle fibers of a motor unit are innervated by a single motor neuron and may be distributed throughout the muscle.

Sustained Contractions

During sustained contractions, smaller motor units, whose neurons have smaller-diameter axons, are more easily stimulated and are recruited earlier. The larger motor units, whose neurons have larger-diameter axons, respond later and with greater force. Summation and recruitment together can produce a sustained contraction of increasing strength.

Typically, many action potentials are triggered in a motor neuron, and so individual twitches do not normally occur. Partial tetanic contractions of muscle fibers are common. On the whole-muscle level, contractions are smooth rather than irregular or jerky because the spinal cord stimulates contractions in different sets of motor units at different moments.

Partial tetanic contractions occur frequently in skeletal muscles during everyday activities, often in only a portion of a muscle. For example, when a person lifts a weight or walks, sustained contractions are maintained in the upper limb or lower limb muscles for varying lengths of time. These contractions are responses to a rapid series of action potentials from the brain and spinal cord on motor neurons.

Even when a muscle appears to be at rest, its fibers undergo a certain degree of sustained contraction. This is called **muscle tone** (tonus), and it is a response to impulses originating repeatedly in the spinal cord and conducted along axons to a few muscle fibers. The result is a continuous state of partial contraction.

Muscle tone is particularly important in maintaining posture. Tautness in the muscles of the neck, trunk, and lower limbs enables a person to hold the head upright, stand, or sit. If tone is suddenly lost, such as when a person loses consciousness, the body collapses. Muscle tone is maintained in health but is lost if motor nerve axons are cut or if diseases interfere with impulse conduction.

When skeletal muscles contract forcefully, they may generate up to 50 pounds of pull for each square inch of muscle cross section. Consequently, large muscles such as those in the thigh can pull with several hundred pounds of force. Occasionally, this force is so great that the tendons of muscles tear away from their attachments to the bones.

Types of Contractions

Sometimes muscles shorten when they contract. For example, if a person lifts an object, the muscles remain taut, their attached ends pull closer together, and the object is moved. This type of contraction is termed **isotonic** (equal force—change in length), and because shortening occurs, it is called **concentric.**

Another type of isotonic contraction, called a lengthening or an **eccentric contraction,** occurs when the force a muscle generates is less than that required to move or lift an object, as in laying a book down on a table. Even in such a contraction, cross-bridges are working but not generating enough force to shorten the muscle.

At other times, a skeletal muscle contracts, but the parts to which it is attached do not move. This happens, for instance, when a person pushes against a wall or holds a yoga pose but does not move. Tension within the muscles increases, but the wall does not move, and the muscles remain the same length. Contractions of this type are called **isometric** (equal length—change in force). Isometric contractions occur continuously in postural muscles that stabilize skeletal parts and hold the body upright. Figure 9.18 illustrates isotonic and isometric contractions.

Most body actions require both isotonic and isometric contractions. In walking, for instance, certain leg and thigh muscles contract isometrically and keep the limb stiff as it touches the ground, while other muscles contract isotonically, bending and lifting the opposite limb. Similarly, walking down stairs requires eccentric contraction of certain thigh muscles. Isometric contractions of muscles around a joint can maintain a fixed position, such as holding out a printed page to read.

Fast- and Slow-Twitch Muscle Fibers

Muscle fibers vary in contraction speed (slow-twitch or fast-twitch) and in whether they produce ATP oxidatively or glycolytically. At least three combinations of these characteristics are found in humans. Slow-twitch fibers (type I) are always oxidative and are therefore resistant to fatigue. Fast-twitch fibers (type II) may be primarily glycolytic (fatigable) or primarily oxidative (fatigue resistant).

Slow-twitch (type I) fibers, such as those in the long muscles of the back, are often called *red fibers* because they contain the red, oxygen-storing pigment myoglobin. These fibers are well supplied with oxygen-carrying blood. In addition, red fibers contain many mitochondria, which is an adaptation for the aerobic reactions of cellular respiration. These fibers have a high respiratory capacity and can generate ATP fast enough to keep up with the ATP breakdown that occurs when they contract. For this reason, these fibers can contract for long periods without fatiguing.

Fast-twitch glycolytic fibers (type IIb) are also called *white fibers* because they have less myoglobin and have a poorer blood supply than red fibers. They include fibers in certain hand muscles as well as in muscles that move the eye. These fibers have fewer mitochondria and thus have a reduced respiratory capacity. However, they have a more extensive sarcoplasmic reticulum to store and reabsorb calcium ions, and their ATPase is faster than that of red fibers. White muscle fibers can contract rapidly because of these factors, although they fatigue as lactic acid accumulates and as the ATP and the biochemicals to regenerate ATP are depleted.

A type of white fiber, the fast-twitch fatigue-resistant fibers (type IIa), are also called *intermediate fibers.* These

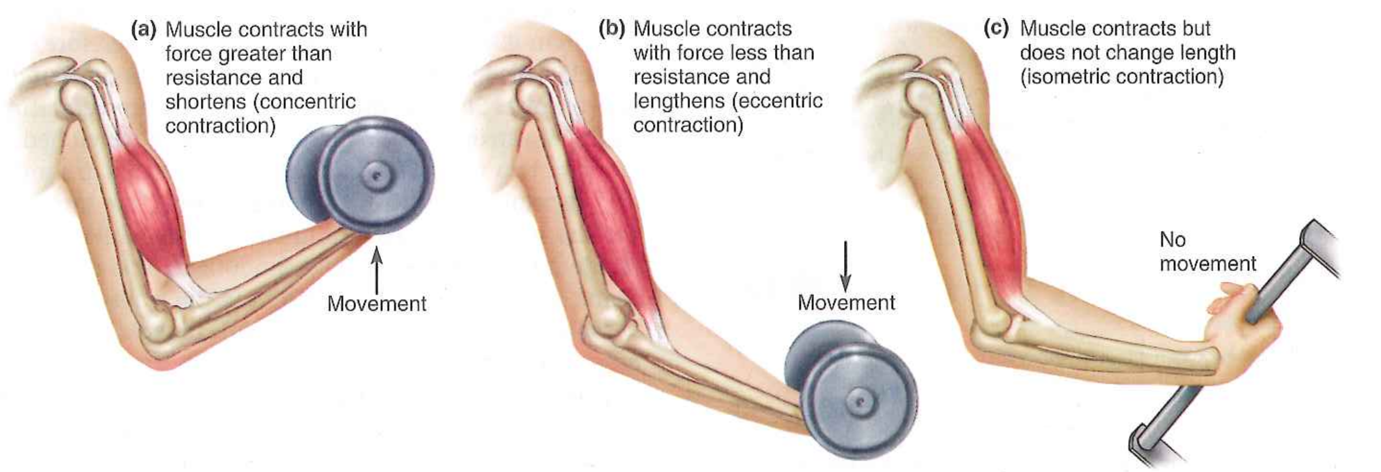


FIGURE 9.18 Types of muscle contractions. (*a* and *b*) Isotonic contractions include concentric and eccentric contractions. (*c*) Isometric contractions occur when a muscle contracts but does not shorten or lengthen.

9.2 CLINICAL APPLICATION

Use and Disuse of Skeletal Muscles

Skeletal muscles respond to use and disuse. Forcefully exercised muscles enlarge, or *hypertrophy*. Unused muscles *atrophy*, decreasing in size and strength.

The way a muscle responds to use also depends on the type of exercise. Weak contractions, such as in swimming and running, activate slow, fatigue-resistant red fibers. In response, these fibers develop more mitochondria and more extensive capillary networks, which increase fatigue-resistance during prolonged exercise, although sizes and strengths of the muscle fibers may not change.

In forceful exercise, such as weightlifting, a muscle exerts more than 75% of its maximum tension, using predominantly the muscle's fast, fatigable white fibers. In response, existing muscle fibers synthesize new filaments of actin and myosin, and as their diameters increase, the entire muscle enlarges. However, no new muscle fibers are produced during hypertrophy.

The strength of a contraction is directly proportional to the diameter of the muscle fibers. Therefore, an enlarged muscle can contract more strongly than before. However, such a change does not increase the muscle's ability to resist fatigue during activities such as running or swimming.

Microscopic muscle damage can occur with too-frequent weightlifting (strength training). This is why trainers advise lifting weights every other day, rather than daily.

If regular exercise stops, capillary networks shrink, and muscle fibers lose some mitochondria. Actin and myosin filaments diminish, and the entire muscle atrophies. Injured limbs immobilized in casts, or accidents or diseases that interfere with nervous stimulation, also cause muscle atrophy. An unexercised muscle may shrink to less than one-half its usual size in a few months.

In functional electrical stimulation, physical therapists apply electrodes to the skin over an injured muscle. The electrical current triggers action potentials in motor neurons controlling nearby muscle fibers, contracting those muscle fibers. This technique can prevent tissue atrophy, increase muscle strength, reduce pain, and promote healing by increasing blood supply.

Muscle fibers whose motor neurons are severed not only shrink but also may fragment, and in time fat or fibrous tissue replaces them. However, reinnervation of such a muscle within the first few months following an injury can restore function.

New technologies can compensate for some muscle loss. "Targeted muscle reinnervation," for example, can tap into the neuromuscular system to assist a person who has lost an upper limb. A surgeon reattaches muscles from a severed arm to the patient's chest wall, then uses electromyography to detect the electrical activity that still reaches those muscles. The information is sent to a microprocessor built into an attached prosthetic arm, where a "neural-machine interface" enables the patient to move the replacement arm at will, just as he or she would consciously direct the movement of the missing part. ■

fibers have the fast-twitch speed associated with white fibers with a substantial oxidative capacity more characteristic of red fibers.

All muscles include a combination of fiber types, although some muscles may have mostly one fiber type. The speed of contraction and aerobic capacities of the fibers reflect the specialized functions of the muscle. For example, muscles that move the eyes contract about ten times faster than those that maintain posture, and the muscles that move the limbs contract at intermediate rates. Slowing of eye movements is an early sign of certain neurological diseases. Clinical Application 9.2 discusses noticeable effects of muscle use and disuse.

Birds that migrate long distances have abundant dark, slow-twitch muscles—this is why their flesh is dark. In contrast, chickens that can only flap around the barnyard have abundant fast-twitch muscles and mostly white flesh. World-class distance runners are the human equivalent of the migrating bird. Their muscles may have more than 90% slow-twitch fibers!

PRACTICE

13 Define *threshold stimulus*.

14 Distinguish between a twitch and a sustained contraction.

15 Define *motor unit*.

16 Define *muscle tone*.

17 Explain the differences between isometric and isotonic contractions.

18 Distinguish between fast-twitch and slow-twitch muscle fibers.

9.5 SMOOTH MUSCLES

The contractile mechanisms of smooth and cardiac muscles are essentially the same as those of skeletal muscles. However, the cells of these tissues have important structural and functional distinctions.

Smooth Muscle Fibers

Recall from chapter 5 (p. 172) that smooth muscle cells are shorter than the fibers of skeletal muscle, and they have single, centrally located nuclei. Smooth muscle cells are elongated with tapering ends and contain filaments of actin and myosin in myofibrils that extend throughout their lengths, but these filaments are thin and more randomly distributed than those in skeletal muscle fibers. Therefore, smooth muscle cells lack striations and appear "smooth" under the microscope. Smooth muscle cells lack transverse tubules, and their sarcoplasmic reticula are not well developed.

The two major types of smooth muscles are multiunit and visceral. In **multiunit smooth muscle,** the muscle fibers are less well organized and function as separate units, independent of neighboring cells. Smooth muscle of this type is found in the irises of the eyes and in the walls of large blood vessels. Typically, multiunit smooth muscle contracts only after stimulation by neurons or certain hormones.

Visceral smooth muscle (single-unit smooth muscle) is composed of sheets of spindle-shaped cells held in close contact by gap junctions. The thick portion of each cell lies next to the thin parts of adjacent cells. Fibers of visceral smooth muscle respond as a single unit. When one fiber is stimulated, the impulse conducted over its surface may excite adjacent fibers that, in turn, stimulate others. Some visceral smooth muscle cells also display *rhythmicity*—a pattern of spontaneous repeated contractions.

These two features of visceral smooth muscle—conduction of impulses from cell to cell and rhythmicity—are largely responsible for the wavelike motion called **peristalsis** of certain tubular organs (see chapter 17, p. 651). Peristalsis consists of alternate contractions and relaxations of the longitudinal and circular muscles. These movements help force the contents of a tube along its length. In the intestines, for example, peristaltic waves move masses of partially digested food and help to mix them with digestive fluids. Peristalsis in the ureters moves urine from the kidneys to the urinary bladder.

Visceral smooth muscle is the more common type of smooth muscle. It is found in the walls of hollow organs, such as the stomach, intestines, urinary bladder, and uterus. Most of the smooth muscle in the walls of these organs is of two thicknesses. The fibers of the outer coats are longitudinal, whereas those of the inner coats are circular. The muscular layers change the sizes and shapes of the organs as they contract and relax.

Vascular smooth muscle, a form of visceral smooth muscle, is found in the walls of many of the smaller blood vessels, where it plays a role in controlling blood flow and blood pressure. The function of vascular smooth muscle will be discussed further in chapter 15 (pp. 580 and 585).

Smooth Muscle Contraction

Smooth muscle contraction resembles skeletal muscle contraction in a number of ways. Both mechanisms reflect reactions of actin and myosin. Both are triggered by membrane impulses and release of calcium ions. Finally, both use energy from ATP molecules. However, smooth and skeletal muscles also differ in their action. Smooth muscle fibers do not have troponin, the protein that binds to calcium ions in skeletal muscle. Instead, smooth muscle uses a protein called *calmodulin,* which binds to calcium ions released when its fibers are stimulated, activating contraction. In addition, much of the calcium necessary for smooth muscle contraction diffuses into the cell from the extracellular fluid.

Acetylcholine, the neurotransmitter in skeletal muscle, as well as *norepinephrine,* affect smooth muscle. Each of these neurotransmitters stimulates contractions in some smooth muscles and inhibits contractions in others. The discussion of the autonomic nervous system in chapter 11 (pp. 432–435) describes these actions in greater detail.

Hormones affect smooth muscles by stimulating or inhibiting contraction in some cases and altering the degree of response to neurotransmitters in others. For example, during the later stages of childbirth, the hormone oxytocin stimulates smooth muscles in the wall of the uterus to contract (see chapter 23, p. 890).

Stretching of smooth muscle fibers can also trigger contractions. This response is particularly important to the function of visceral smooth muscle in the walls of certain hollow organs, such as the urinary bladder and the intestines. For example, when partially digested food stretches the wall of the intestine, contractions move the contents further along the intestine.

Smooth muscle is slower to contract and relax than skeletal muscle, yet smooth muscle can forcefully contract longer with the same amount of ATP. Unlike skeletal muscle, smooth muscle fibers can change length without changing tautness. This ability enables smooth muscles in the stomach and intestinal walls to stretch as these organs fill, holding the pressure inside the organs constant.

PRACTICE

19 Describe the two major types of smooth muscle.

20 What special characteristics of visceral smooth muscle make peristalsis possible?

21 How is smooth muscle contraction similar to skeletal muscle contraction?

22 How do the contraction mechanisms of smooth and skeletal muscles differ?

9.6 CARDIAC MUSCLE

Cardiac muscle is only in the heart. It is composed of striated cells joined end to end, forming fibers interconnected in branching, three-dimensional networks. Each cell contains a single nucleus and many filaments of actin and myosin similar to those in skeletal muscle. A cardiac muscle cell also has a well-developed sarcoplasmic reticulum, a system of transverse tubules, and many mitochondria. However, the cisternae of the sarcoplasmic reticulum of a cardiac muscle fiber are less developed and store less calcium than those of a skeletal muscle fiber. On the other hand, the transverse tubules of cardiac muscle fibers are larger than those in skeletal muscle, and they release many calcium ions into the sarcoplasm in response to a single muscle impulse.

The calcium ions in transverse tubules come from the fluid outside the muscle fiber. In this way, extracellular calcium partially controls the strength of cardiac muscle contraction and enables cardiac muscle fibers to contract longer than skeletal muscle fibers can.

> Drugs called calcium channel blockers are used to treat irregular heart rhythms. They do this by blocking ion channels that admit extracellular calcium into cardiac muscle cells.

The opposing ends of cardiac muscle cells are connected by cross-bands called *intercalated discs.* These bands are complex membrane junctions that include components of desmosomes and gap junctions.

Not only do they help join cells and transmit the force of contraction from cell to cell, but the intercellular junctions of the fused membranes of intercalated discs allow ions to diffuse between the cells. This allows muscle impulses

FIGURE 9.19 APR The intercalated discs of cardiac muscle, shown in this transmission electron micrograph, bind adjacent cells and allow ions to move between cells (12,500×).

TABLE 9.2 | Characteristics of Muscle Tissues

	Skeletal	Smooth	Cardiac
Dimensions			
Length	Up to 30 cm	30–200 μm	50–100 μm
Diameter	10–100 μm	3–6 μm	14 μm
Major location	Skeletal muscles	Walls of hollow organs	Wall of the heart
Major function	Movement of bones at joints; maintenance of posture	Movement of walls of hollow organs; peristalsis; vasoconstriction	Pumping action of the heart
Cellular characteristics			
Striations	Present	Absent	Present
Nucleus	Multiple nuclei	Single nucleus	Single nucleus
Special features	Transverse tubule system is well developed	Lacks transverse tubules	Transverse tubule system is well developed; intercalated discs connect cells
Mode of control	Voluntary	Involuntary	Involuntary
Contraction characteristics	Contracts and relaxes relatively rapidly	Contracts and relaxes relatively slowly; some types self-exciting; rhythmic	Network of fibers contracts as a unit; self-exciting; rhythmic; remains refractory until contraction ends

to travel rapidly from cell to cell (see fig. 5.30, p. 173 and fig. 9.19). Thus, when one portion of the cardiac muscle network is stimulated, the impulse passes to other fibers of the network, and the whole structure contracts as a unit or *syncytium* (sin-sish′e-um); that is, the network responds to stimulation in an all-or-none manner. Cardiac muscle is also self-exciting and rhythmic. Consequently, a pattern of contraction and relaxation repeats, generating the rhythmic contraction of the heart. Also, cardiac muscle becomes non-responsive (refractory) after stimulation until the contraction ends. Therefore, sustained or tetanic contractions do not occur in the heart muscle. Table 9.2 summarizes characteristics of the three types of muscles.

RECONNECT

To Chapter 5, Figure 5.1, Intercellular Junctions, page 153.

PRACTICE

23 How is cardiac muscle similar to skeletal muscle?

24 How does cardiac muscle differ from skeletal muscle?

25 What is the function of intercalated discs?

26 What characteristic of cardiac muscle causes the heart to contract as a unit?

9.7 SKELETAL MUSCLE ACTIONS

Skeletal muscles generate a great variety of body movements. The action of each muscle mostly depends upon the type of joint it is associated with and the way the muscle is attached on either side of that joint.

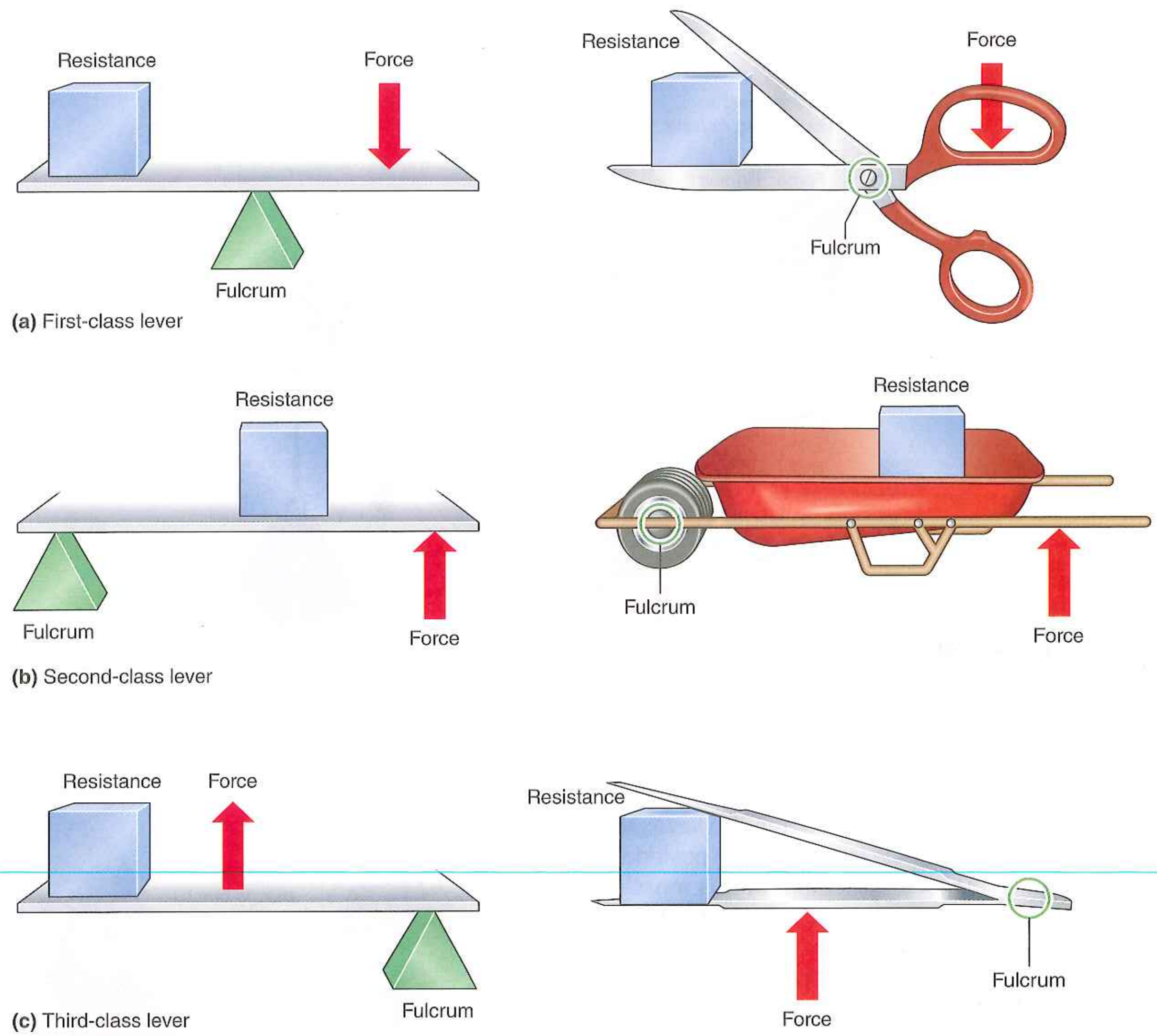


FIGURE 9.20 Three types of levers. (*a*) A first-class lever is used in a pair of scissors, (*b*) a second-class lever is used in a wheelbarrow, and (*c*) a third-class lever is used in a pair of forceps.

Body Movement

Whenever limbs or other body parts move, bones and muscles interact as simple mechanical devices called **levers** (lev′erz). A lever has four basic components: (1) a rigid bar or rod, (2) a fulcrum or pivot on which the bar turns, (3) an object moved against resistance, and (4) a force that supplies energy to move the bar.

A pair of scissors is a lever. The handle and blade form a rigid bar that rocks on a fulcrum near the center (the screw). The material the blades cut represents the resistance, while the person on the handle end supplies the force to cut the material.

Figure 9.20 shows the three types of levers, which differ in their arrangements. A first-class lever's parts are like those of a pair of scissors. Its fulcrum is located between the resistance and the force, making the sequence of components resistance–fulcrum–force. Other examples of first-class levers are seesaws and hemostats (devices used to clamp blood vessels).

The parts of a second-class lever are in the sequence fulcrum–resistance–force, as in a wheelbarrow. The parts of a third-class lever are in the sequence resistance–force–fulcrum. Eyebrow tweezers or forceps used to grasp an object illustrate this type of lever.

The actions of bending and straightening the upper limb at the elbow illustrate bones and muscles functioning as levers. When the upper limb bends, the forearm bones represent the rigid bar, the elbow joint is the fulcrum, the hand is moved against the resistance provided by the weight, and the force is supplied by muscles on the anterior side of the arm (fig. 9.21*a*). One of these muscles, the *biceps brachii*, is attached by a tendon to a projection (radial tuberosity) on the *radius* bone in the forearm, a short distance below the elbow. Because the parts of this lever are arranged in the sequence resistance–force–fulcrum, it is a third-class lever.

When the upper limb straightens at the elbow, the forearm bones again serve as the rigid bar, the hand moves against

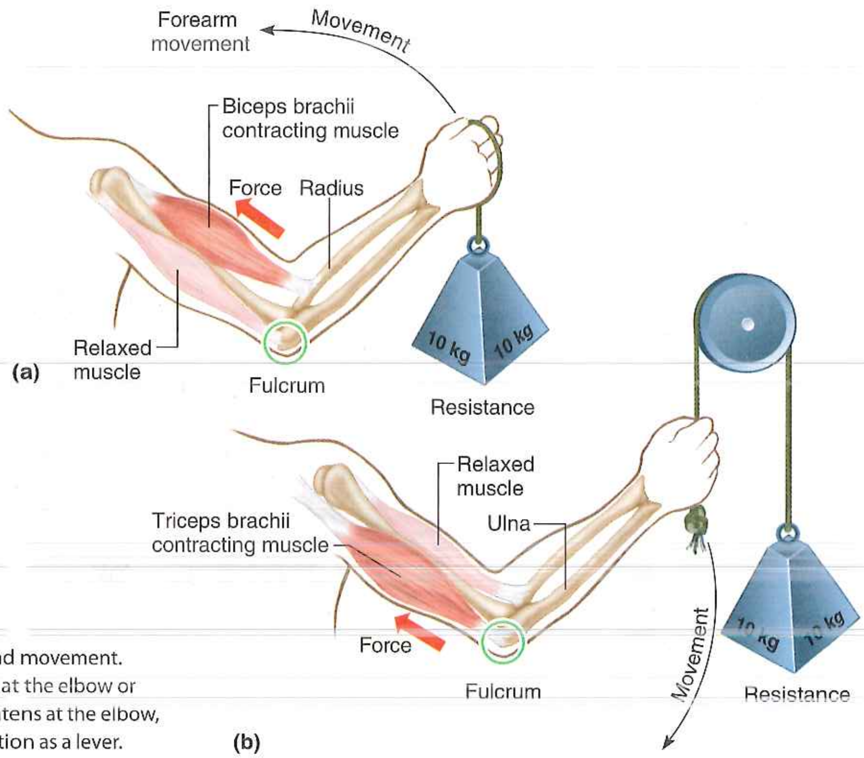


FIGURE 9.21 Levers and movement. (*a*) When the forearm bends at the elbow or (*b*) when the forearm straightens at the elbow, the bones and muscles function as a lever.

the resistance by pulling on the rope to raise the weight (fig. 9.21*b*), and the elbow joint serves as the fulcrum. However, in this case the *triceps brachii,* a muscle located on the posterior side of the arm, supplies the force. A tendon of this muscle attaches to a projection (olecranon process) of the ulna bone at the point of the elbow. Because the parts of the lever are arranged resistance–fulcrum–force, it is a first-class lever.

The human body also has a second-class lever (fulcrum–resistance–force). The fulcrum is the temporomandibular joint. Muscles supply the resistance, attaching to a projection (coronoid process) and body of the mandible. These muscles resist or oppose opening the mouth. The muscles attached to the chin area of the mandible provide the force that opens the mouth.

Levers provide a range of movements. Levers that move limbs, for example, produce rapid motions, whereas others, such as those that move the head, help maintain posture with minimal effort.

Origin and Insertion

Recall from chapter 8 (p. 276) that one end of a skeletal muscle is usually fastened to a relatively immovable or fixed part on one side of a joint, and the other end is connected to a movable part on the other side of that joint. The less movable end is called the **origin** of the muscle, and the more movable end is called its **insertion.** When a muscle contracts, its insertion is pulled toward its origin (fig. 9.22). The head of a muscle is the part nearest its origin.

Some muscles have more than one origin or insertion. The *biceps brachii* in the arm, for example, has two origins.

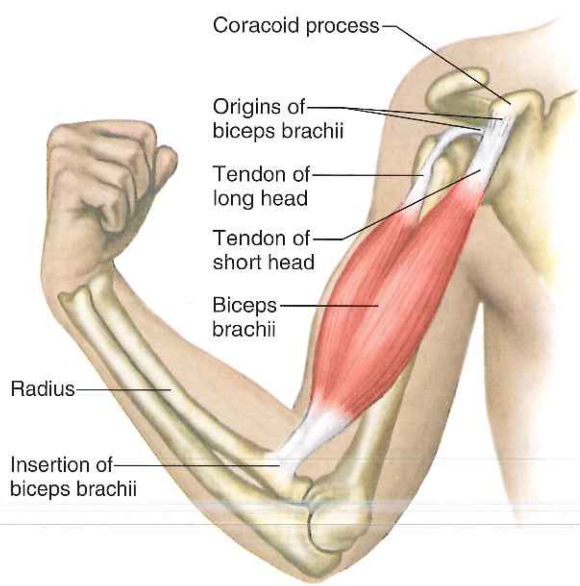


FIGURE 9.22 The biceps brachii has two heads that originate on the scapula. A tendon inserts this muscle on the radius.

This is reflected in its name *biceps,* meaning "two heads." As figure 9.22 shows, one head of the muscle is attached to the coracoid process of the scapula, and the other head arises from a tubercle above the glenoid cavity of the scapula. The muscle extends along the anterior surface of the humerus and is inserted by a single tendon on the radial tuberosity of the radius. When the biceps brachii contracts, its insertion is pulled toward its origin, and the elbow bends.

Interaction of Skeletal Muscles

Most skeletal muscles function in groups. Consequently, a particular body movement requires more than contracting a single muscle. Instead, after learning to make a particular movement, the person initiates the movement consciously, and the nervous system stimulates the appropriate group of muscles.

It is possible to determine the roles of particular muscles by carefully observing body movements. For instance, contracting the *deltoid* muscle causes abduction of the arm. A muscle that causes an action is called an **agonist** for that action. Thus the deltoid is an agonist for abduction of the arm.

While an agonist is acting, other nearby muscles may also contract and help with the action. For example, when the deltoid muscle abducts the arm, the supraspinatus, a muscle that originates on the scapula helps with the abduction. Muscles that work together like this are called **synergists** (sin′er-jists).

In some cases, and abduction of the arm by the deltoid is an example, one of the agonists is doing most of the work. In such a case, the agonist may also be called a **prime mover.**

Still other muscles act as **antagonists** (an-tag′o-nists), working to oppose an action. These muscles can cause movement in the opposite direction. The antagonist of the muscles that raise the upper limb can lower the upper limb, or the antagonist of the muscles that bend the upper limb can straighten it. If both an agonist and an antagonist for a particular movement contract simultaneously, the structure they act upon remains rigid. Similarly, smooth body movements depend upon the antagonists' relaxing to a degree and giving way to the agonists' action. Once again, the nervous system coordinates these complex actions, as chapter 11 describes (p. 417).

The relationship between two muscles can differ depending on circumstance. For example, the pectoralis major and latissimus dorsi are antagonistic for flexion and extension of the shoulder. However, they are synergistic for medial rotation of the shoulder. Thus, the relationship between muscles must be learned in the context of a particular movement.

The movements termed "flexion" and "extension" describe changes in the angle between bones that meet at a joint. For example, flexion of the elbow joint refers to a movement of the forearm that decreases the angle at the elbow joint. Alternatively, one could say that flexion at the elbow results from the action of the biceps brachii on the radius of the forearm.

Students find it helpful to think of movements in terms of the specific actions of the muscles involved, so we may also describe flexion and extension in these terms. Thus, the action of the biceps brachii may be described as "flexion of the forearm at the elbow" and the action of the quadriceps group as "extension of the leg at the knee." We believe that this occasional departure from strict anatomical terminology eases understanding and learning.

PRACTICE

27 Explain how parts of the upper limb form a first-class lever and a third-class lever.

28 Distinguish between the origin and the insertion of a muscle.

29 Define *prime mover.*

30 What is the function of a synergist? an antagonist?

9.8 MAJOR SKELETAL MUSCLES

This section discusses the locations, actions, origins, and insertions of some of the major skeletal muscles. The tables that summarize the information concerning groups of these muscles also include the names of nerves that supply (innervate) the individual muscles in each group. Chapter 11 (pp. 420–429) presents the origins and pathways of these nerves.

Figures 9.23 and 9.24 show the locations of superficial skeletal muscles—that is, those near the surface. The names of muscles often describe them. A name may indicate a muscle's size, shape, location, action, number of attachments, or the direction of its fibers, as in the following examples:

pectoralis major A muscle of large size (major) in the pectoral region (chest).
deltoid Shaped like a delta or triangle.
extensor digitorum Extends the digits (fingers or toes).
biceps brachii A muscle with two heads (biceps), or points of origin, in the brachium (arm).
sternocleidomastoid Attached to the sternum, clavicle, and mastoid process.
external oblique Located near the outside, with fibers that run obliquely or in a slanting direction.

Muscles of Facial Expression

A number of small muscles beneath the skin of the face and scalp enable us to communicate feelings through facial expression. Many of these muscles are located around the eyes and mouth, and they make possible such expressions as surprise, sadness, anger, fear, disgust, and pain. As a group, the muscles of facial expression connect the bones of the skull to connective tissue in regions of the overlying skin. Figure 9.25 and reference plate 66 (p. 353) show these muscles, and table 9.3 lists them. The muscles of facial expression include the following:

Epicranius	Zygomaticus major
Orbicularis oculi	Zygomaticus minor
Orbicularis oris	Platysma
Buccinator	

The **epicranius** (ep″ĭ-kra′ne-us) covers the upper part of the cranium and consists of two muscular parts—the *frontalis* (frun-ta′lis), which lies over the frontal bone, and the *occipitalis* (ok-sip″ĭ-ta′lis), which lies over the occipital bone. These muscles are united by a broad, tendinous membrane called the *epicranial aponeurosis,* which covers the

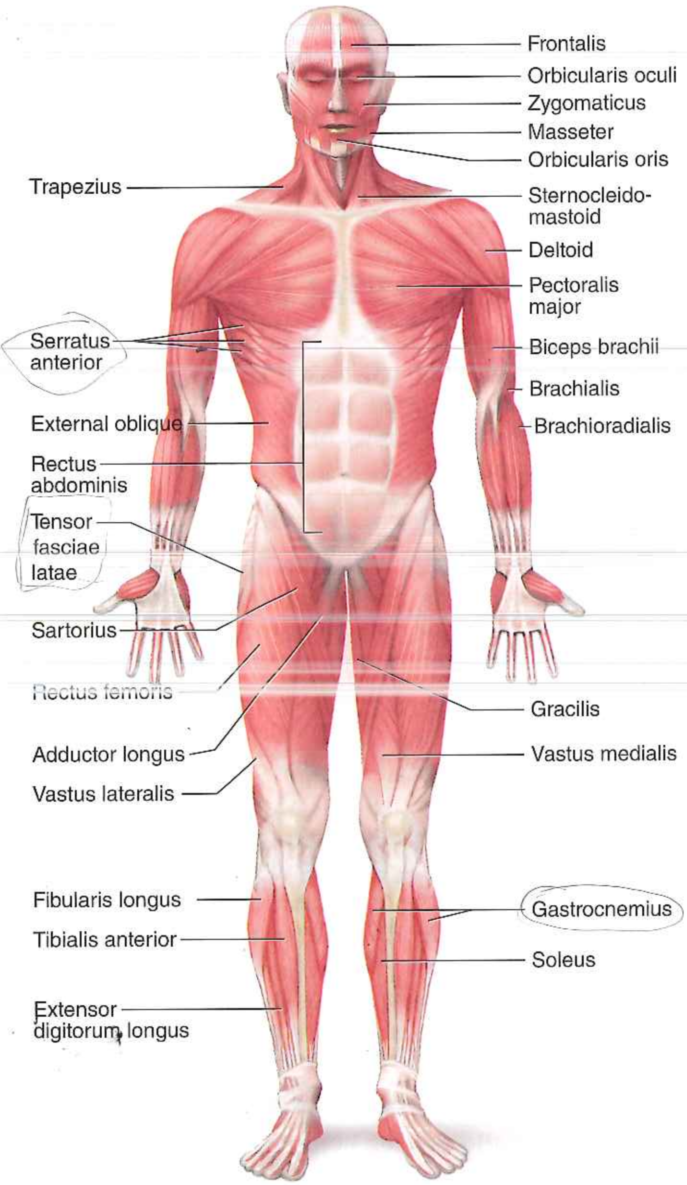


FIGURE 9.23 Anterior view of superficial skeletal muscles.

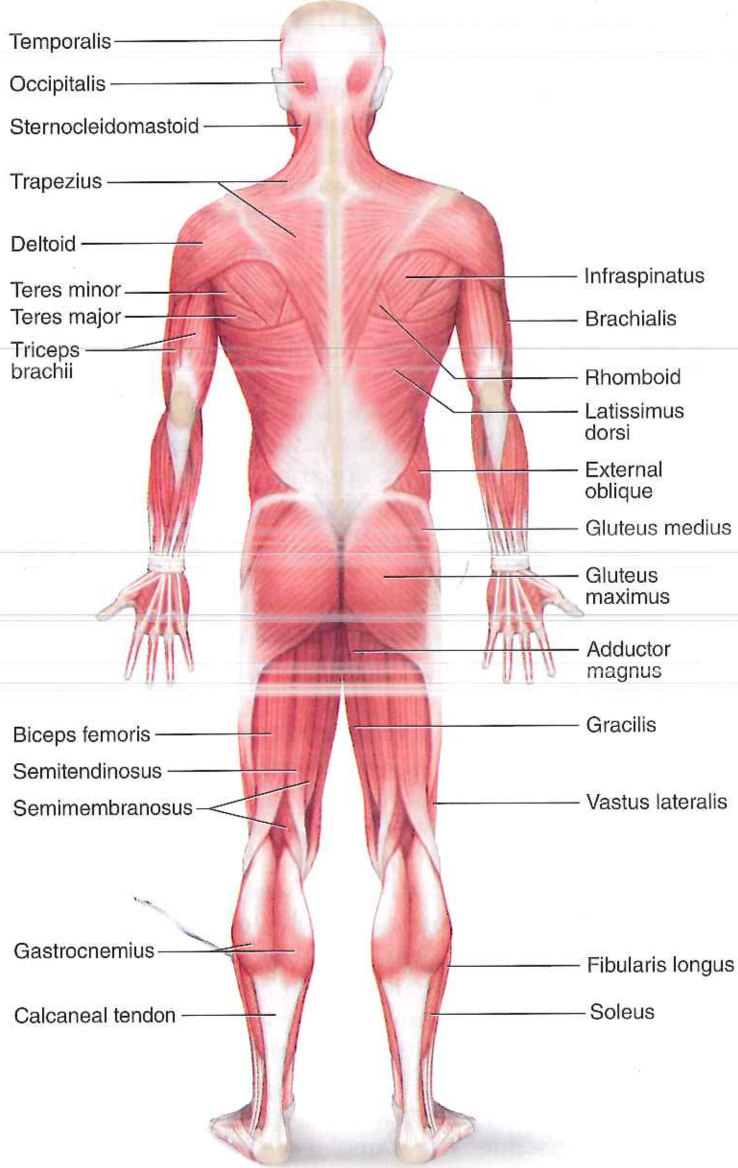


FIGURE 9.24 Posterior view of superficial skeletal muscles.

cranium like a cap. Contraction of the epicranius raises the eyebrows and horizontally wrinkles the skin of the forehead, as when a person expresses surprise. Headaches often result from sustained contraction of this muscle.

The **orbicularis oculi** (or-bik′u-la-rus ok′u-li) is a ringlike band of muscle, called a *sphincter muscle,* that surrounds the eye. It lies in the subcutaneous tissue of the eyelid and closes or blinks the eye. At the same time, it compresses the nearby tear gland, or *lacrimal gland,* aiding the flow of tears over the surface of the eye. Contraction of the orbicularis oculi also causes the folds, or crow's feet, that radiate laterally from the corner of the eye. Chapter 12 (pp. 469–470) describes the muscles that move the eye.

The **orbicularis oris** (or-bik′u-la-rus o′ris) is a sphincter muscle that encircles the mouth. It lies between the skin and the mucous membranes of the lips, extending upward to the nose and downward to the region between the lower lip and chin. The orbicularis oris is also called the kissing muscle because it closes and puckers the lips.

The **buccinator** (buk′sĭ-na″tor) is located in the wall of the cheek. Its fibers are directed forward from the bones of the jaws to the angle of the mouth, and when they contract, the cheek is compressed inward. This action helps hold food in contact with the teeth when a person is chewing. The buccinator also aids in blowing air out of the mouth, and for this reason, it is also called the trumpeter muscle.

The **zygomaticus** (zi″go-mat′ik-us) **major** and **minor** extend from the zygomatic arch downward to the corner of the mouth. When they contract, the corner of the mouth is drawn upward, such as in smiling or laughing.

The **platysma** (plah-tiz′mah) is a thin, sheetlike muscle whose fibers extend from the chest upward over the neck to

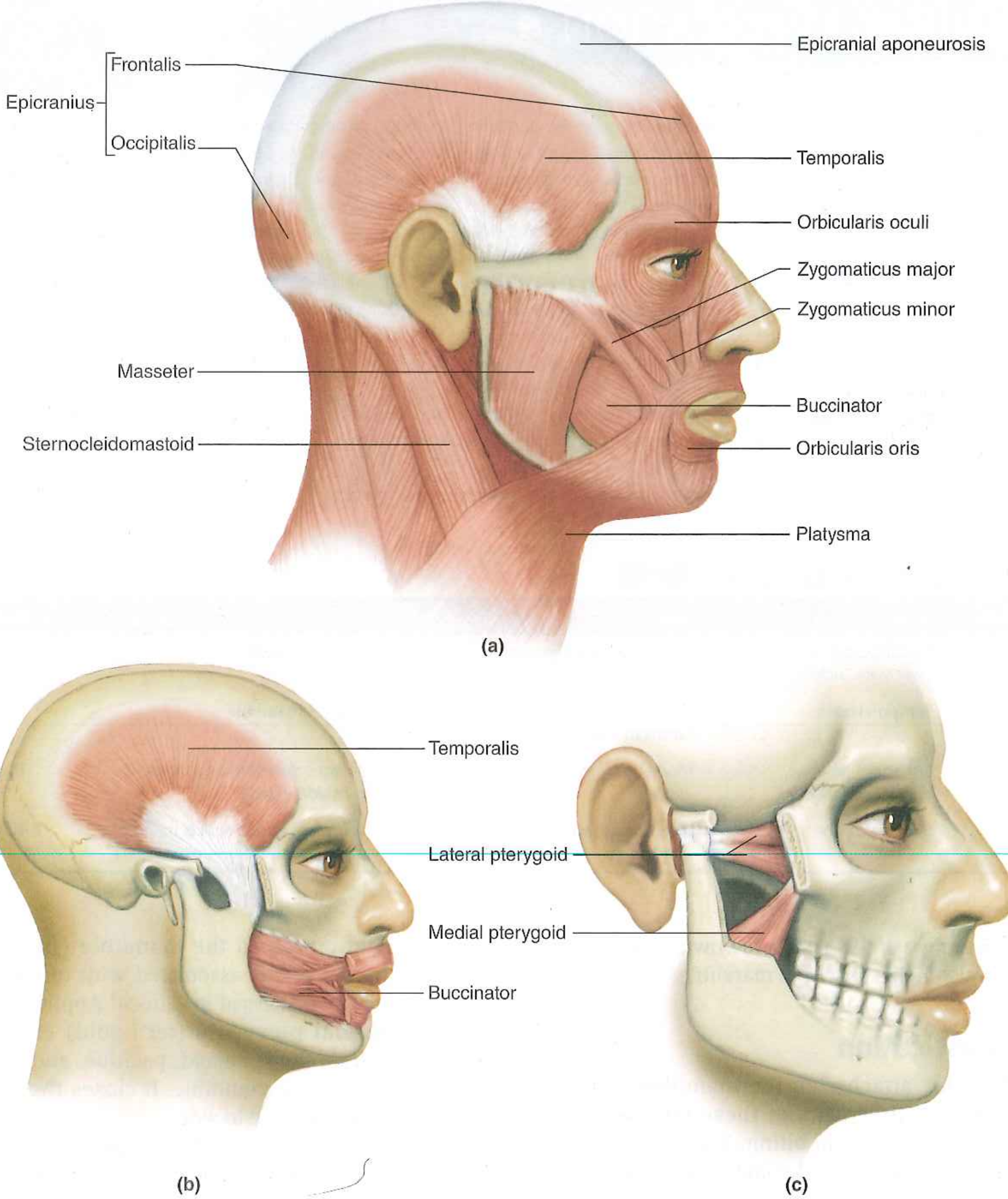


FIGURE 9.25 APR Muscles of the head and face. (*a*) Muscles of facial expression and mastication; isolated views of (*b*) the temporalis and buccinator muscles and (*c*) the lateral and medial pterygoid muscles.

TABLE 9.3 | Muscles of Facial Expression APR

Muscle	Origin	Insertion	Action	Nerve Supply
Epicranius	Occipital bone	Skin and muscles around eye	Raises eyebrow as when surprised	Facial nerve
Orbicularis oculi	Maxillary and frontal bones	Skin around eye	Closes eye as in blinking	Facial nerve
Orbicularis oris	Muscles near the mouth	Skin of central lip	Closes lips, protrudes lips as for kissing	Facial nerve
Buccinator	Outer surfaces of maxilla and mandible	Orbicularis oris	Compresses cheeks inward as when blowing air	Facial nerve
Zygomaticus major	Zygomatic bone	Corner of mouth	Raises corner of mouth as when smiling	Facial nerve
Zygomaticus minor	Zygomatic bone	Corner of mouth	Raises corner of mouth as when smiling	Facial nerve
Platysma	Fascia in upper chest	Lower border of mandible	Draws angle of mouth downward as when pouting	Facial nerve

9.3 CLINICAL APPLICATION

TMJ Syndrome

Temporomandibular joint (TMJ) syndrome causes facial pain, headache, ringing in the ears, a clicking jaw, insomnia, teeth sensitive to heat or cold, backache, dizziness, and pain in front of the ears. A misaligned jaw or grinding or clenching the teeth can cause TMJ by stressing the temporomandibular joint, which is the articulation between the mandibular condyle of the mandible and the mandibular fossa of the temporal bone. Loss of coordination of these structures affects the nerves that pass through the neck and jaw region, causing the symptoms. Tensing a muscle in the forehead can cause a headache, or a spasm in the muscle that normally opens the auditory tubes during swallowing can impair ability to clear the ears.

Getting enough sleep and drinking enough water can help prevent symptoms of TMJ, and eating soft foods, applying hot compresses, using relaxation techniques, and massaging affected muscles can alleviate symptoms. Sitting for long hours in one position can cause or worsen TMJ.

Doctors diagnose TMJ syndrome using an electromyograph, in which electrodes record muscle activity in four pairs of head and neck muscle groups. Several treatments are available. The National Institute of Dental and Craniofacial Research recommends that treatments not permanently alter the teeth or jaw. Low doses of certain antidepressants, or injections of botulinum toxin or corticosteroids, may help. Using a procedure called arthrocentesis, a physician might remove fluid accumulating in the affected joint. Another treatment is an orthotic device fitted by a dentist that fine-tunes the action of jaw muscles to form a more comfortable bite. Very rarely, surgery may be required to repair or replace a joint. ■

TABLE 9.4 | Muscles of Mastication AP|R

Muscle	Origin	Insertion	Action	Nerve Supply
Masseter	Lower border of zygomatic arch	Lateral surface of mandible	Elevates mandible	Trigeminal nerve
Temporalis	Temporal bone	Coronoid process and anterior ramus of mandible	Elevates mandible	Trigeminal nerve
Medial pterygoid	Sphenoid, palatine, and maxillary bones	Medial surface of mandible	Elevates mandible and moves it from side to side	Trigeminal nerve
Lateral pterygoid	Sphenoid bone	Anterior surface of mandibular condyle	Depresses and protracts mandible and moves it from side to side	Trigeminal nerve

the face. It pulls the angle of the mouth downward, as in pouting. The platysma also helps lower the mandible.

Muscles of Mastication

Four pairs of muscles attached to the mandible produce chewing movements. Three pairs of these muscles close the lower jaw, which happens in biting. The fourth pair of muscles of mastication can lower the jaw, cause side-to-side grinding motions of the mandible, and pull the mandible forward so that it protrudes. Figure 9.25 and reference plate 66 (p. 353) show the muscles of mastication, and table 9.4 lists them. They include the following:

Masseter	Medial pterygoid
Temporalis	Lateral pterygoid

The **masseter** (mas-se′ter) is a thick, flattened muscle that can be felt just in front of the ear when the teeth are clenched. Its fibers extend downward from the zygomatic arch to the mandible. The masseter raises the jaw, but it can also control the rate at which the jaw falls open in response to gravity (fig. 9.25*a*).

The **temporalis** (tem-po-ra′lis) is a fan-shaped muscle located on the side of the skull above and in front of the ear. Its fibers, which also raise the jaw, pass downward beneath the zygomatic arch to the mandible (fig. 9.25*a* and *b*). Tensing this muscle is associated with temporomandibular joint syndrome, discussed in Clinical Application 9.3.

The **medial pterygoid** (ter′ĭ-goid) extends back and downward from the sphenoid, palatine, and maxillary bones to the ramus of the mandible. It closes the jaw (fig. 9.25*c*) and moves it from side to side.

The fibers of the **lateral pterygoid** extend forward from the region just below the mandibular condyle to the sphenoid bone. This muscle can open the mouth, pull the mandible forward to make it protrude, and move the mandible from side to side (fig. 9.25*c*).

Muscles That Move the Head and Vertebral Column

Paired muscles in the neck and back flex, extend, and rotate the head and hold the torso erect (figs. 9.26 and 9.28 and table 9.5). They include the following:

Sternocleidomastoid	Quadratus lumborum
Splenius capitis	Erector spinae
Semispinalis capitis	

The **sternocleidomastoid** (ster″no-kli″do-mas′toid) is a long muscle in the side of the neck that extends upward

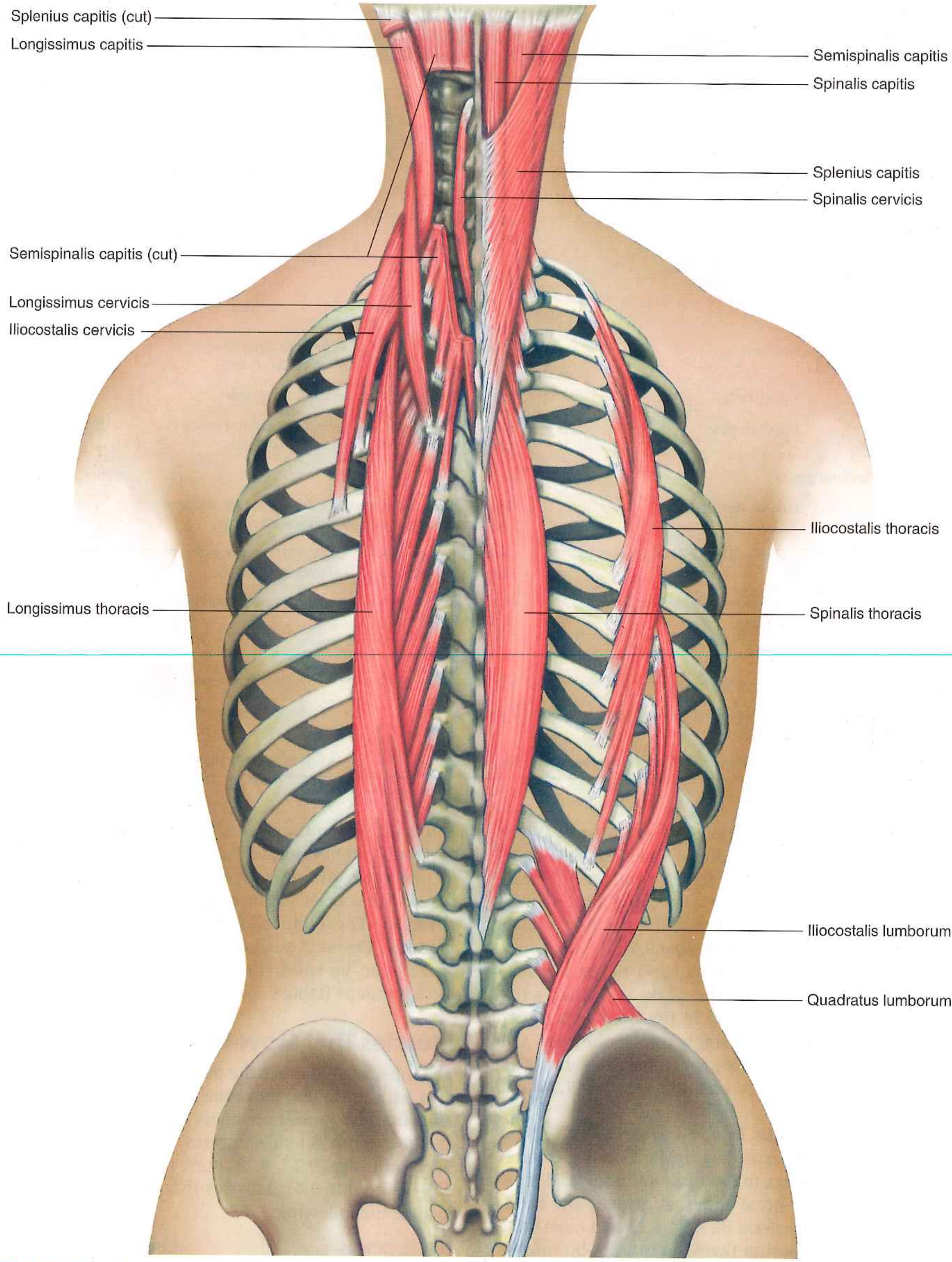


FIGURE 9.26 APIR Deep muscles of the back and the neck help move the head (posterior view) and hold the torso erect. The splenius capitis and semispinalis capitis are removed on the left to show underlying muscles.

TABLE 9.5 | Muscles That Move the Head and Vertebral Column APR

Muscle	Origin	Insertion	Action	Nerve Supply
Sternocleidomastoid	Anterior surface of sternum and upper surface of clavicle	Mastoid process of temporal bone	Pulls head to one side, flexes neck or elevates sternum	Accessory, C2 and C3 cervical nerves
Splenius capitis	Spinous processes of lower cervical and upper thoracic vertebrae	Occipital bone	Rotates head, bends head to one side, or extends neck	Cervical nerves
Semispinalis capitis	Processes of lower cervical and upper thoracic vertebrae	Occipital bone	Extends head, bends head to one side, or rotates head	Cervical and thoracic spinal nerves
Quadratus lumborum	Iliac crest	Upper lumbar vertebrae and twelfth rib	Aids in breathing, extends lumbar region of vertebral column	Thoracic and lumbar spinal nerves
Erector spinae (divides into three columns)				
Iliocostalis (lateral) group				
Iliocostalis lumborum	Iliac crest	Lower six ribs	Extends lumbar region of vertebral column	Lumbar spinal nerves
Iliocostalis thoracis	Lower six ribs	Upper six ribs	Holds spine erect	Thoracic spinal nerves
Iliocostalis cervicis	Upper six ribs	Fourth through sixth cervical vertebrae	Extends cervical region of vertebral column	Cervical spinal nerves
Longissimus (intermediate) group				
Longissimus thoracis	Lumbar vertebrae	Thoracic and upper lumbar vertebrae and ribs 9 and 10	Extends thoracic region of vertebral column	Spinal nerves
Longissimus cervicis	Fourth and fifth thoracic vertebrae	Second through sixth cervical vertebrae	Extends cervical region of vertebral column	Spinal nerves
Longissimus capitis	Upper thoracic and lower cervical vertebrae	Mastoid process of temporal bone	Extends and rotates head	Cervical spinal nerves
Spinalis (medial) group				
Spinalis thoracis	Upper lumbar and lower thoracic vertebrae	Upper thoracic vertebrae	Extends vertebral column	Spinal nerves
Spinalis cervicis	Ligamentum nuchae and seventh cervical vertebra	Axis	Extends vertebral column	Spinal nerves
Spinalis capitis	Upper thoracic and lower cervical vertebrae	Occipital bone	Extends vertebral column	Spinal nerves

from the thorax to the base of the skull behind the ear. When the sternocleidomastoid on one side contracts, the face turns to the opposite side. When both muscles contract, the head bends toward the chest. If other muscles fix the head in position, the sternocleidomastoids can raise the sternum, aiding forceful inhalation (see fig. 9.28 and table 9.5).

The **splenius capitis** (sple′ne-us kap′ĭ-tis) is a broad, straplike muscle in the back of the neck. It connects the base of the skull to the vertebrae in the neck and upper thorax. A splenius capitis acting singly rotates the head and bends it toward one side. Acting together, these muscles bring the head into an upright position (see fig. 9.26 and table 9.5).

The **semispinalis capitis** (sem″e-spi-na′lis kap′ĭ-tis) is a broad, sheetlike muscle extending upward from the vertebrae in the neck and thorax to the occipital bone and mastoid processes of the temporal bones. It extends the head, bends it to one side, or rotates it (see fig. 9.26 and table 9.5).

The **quadratus lumborum** (kwod-ra′tus lum-bo′rum) is located in the lumbar region. When the quadratus lumborum muscles on both sides contract, the vertebral column is extended. When the muscle on only one side contracts, the vertebral column is flexed laterally.

Erector spinae muscles run longitudinally along the back, with origins and insertions at many places on the axial skeleton. These muscles extend and rotate the head and maintain the erect position of the vertebral column. Erector spinae can be subdivided into lateral, intermediate, and medial groups (table 9.5).

Muscles That Move the Pectoral Girdle

The muscles that move the pectoral girdle are closely associated with those that move the arm. A number of these chest and shoulder muscles connect the scapula to nearby bones and move the scapula upward, downward, forward, and backward (figs. 9.27, 9.28, 9.29; reference plates 68, 69, pp. 355–356; table 9.6). Muscles that move the pectoral girdle include the following:

Trapezius	Levator scapulae
Rhomboid major	Serratus anterior
Rhomboid minor	Pectoralis minor

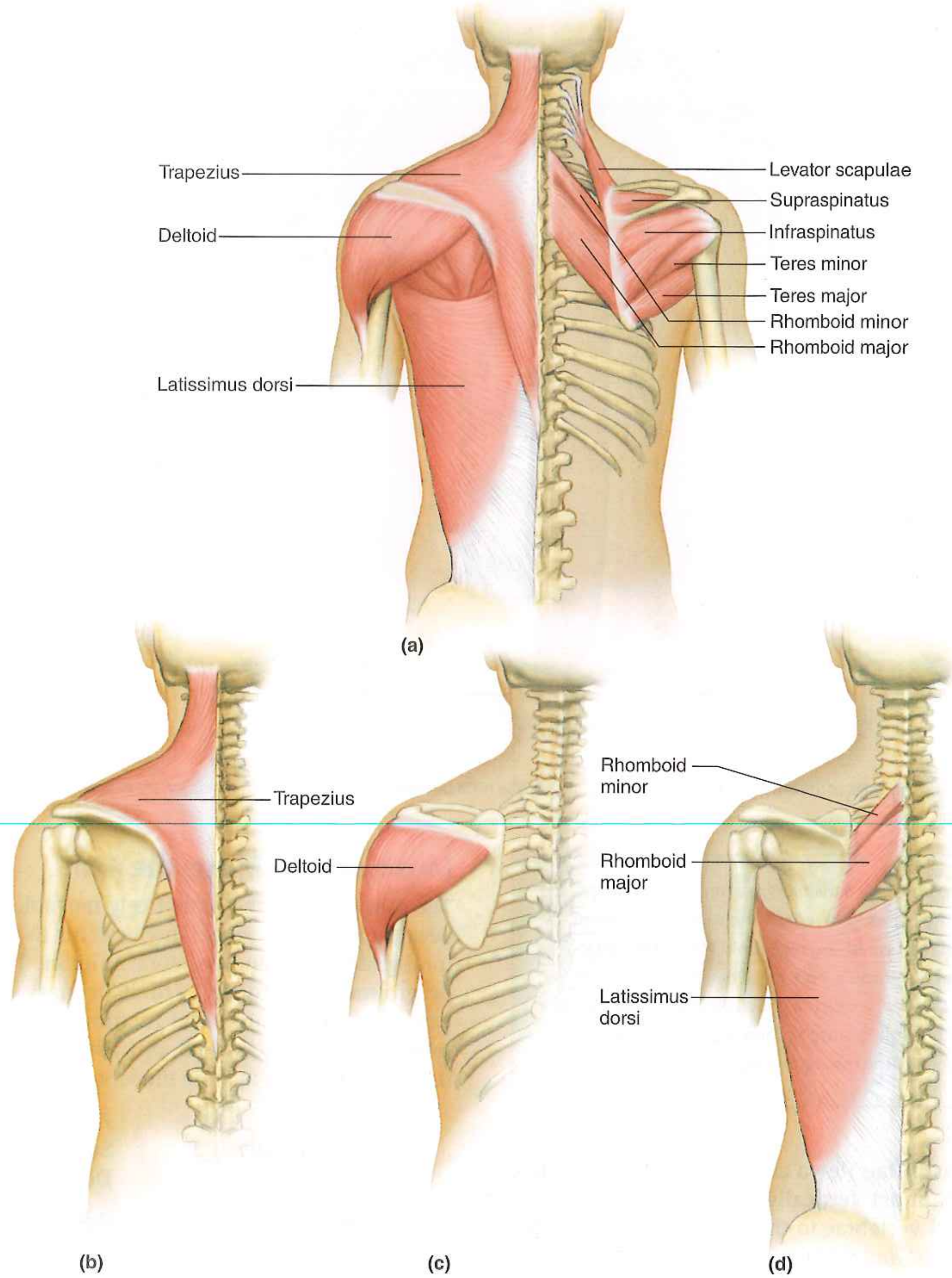


FIGURE 9.27 APR Muscles of the shoulder and back. (*a*) Muscles of the posterior shoulder. The right trapezius is removed to show underlying muscles. Isolated views of (*b*) trapezius, (*c*) deltoid, and (*d*) rhomboid and latissimus dorsi muscles.

The **trapezius** (trah-pe′ze-us) is a large, triangular muscle in the upper back that extends horizontally from the base of the skull and the cervical and thoracic vertebrae to the shoulder. Its fibers are organized into three groups—upper, middle, and lower. Together these fibers rotate the scapula. The upper fibers acting alone raise the scapula and shoulder, such as when shrugging the shoulders to express a feeling of indifference. The middle fibers pull the scapula toward the vertebral column, and the lower fibers draw the scapula and shoulder downward. When other muscles fix the shoulder in position, the trapezius can pull the head backward or to one side (see fig. 9.24).

Rhomboid (rom-boid′) **major** and **minor** connect the vertebral column to the scapula. Both retract and elevate the scapula. Rhomboid major can also rotate the scapula downward (see fig. 9.27).

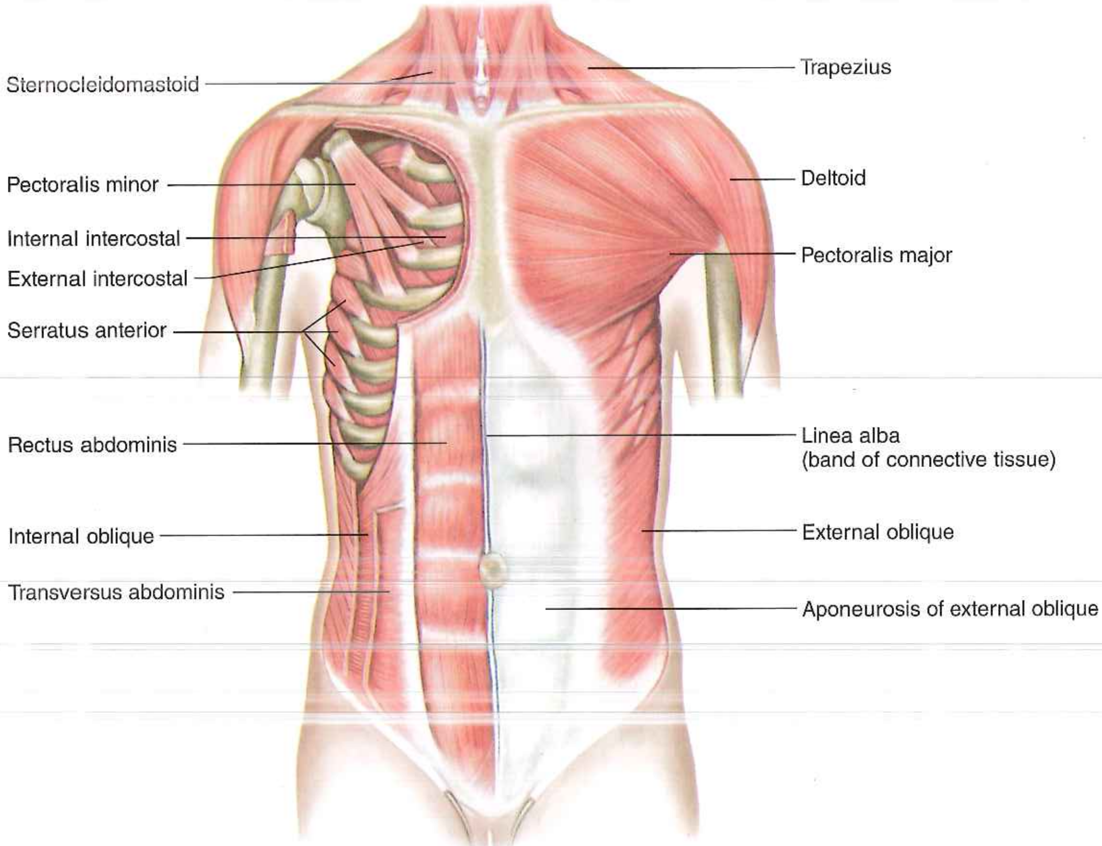


FIGURE 9.28 APR Muscles of the anterior chest and abdominal wall. The right pectoralis major and external oblique are removed to show underlying muscles.

> A small, triangular region, called the *triangle of auscultation*, is located in the back where the trapezius overlaps the superior border of the latissimus dorsi and the underlying rhomboid major. This area, near the medial border of the scapula, enlarges when a person bends forward with the arms folded across the chest. By placing the bell of a stethoscope in the triangle of auscultation, a physician can usually clearly hear the sounds of the respiratory organs.

The **levator scapulae** (le-va'tor scap'u-le) is a straplike muscle that runs almost vertically through the neck, connecting the cervical vertebrae to the scapula. It elevates the scapula (see figs. 9.27 and 9.29).

The **serratus anterior** (ser-ra'tus an-te're-or) is a broad, curved muscle located on the side of the chest. It arises as fleshy, narrow strips on the upper ribs and extends along the medial wall of the axilla to the ventral surface of the scapula. It pulls the scapula downward and anteriorly and is used to thrust the shoulder forward, as when pushing something (see fig. 9.28).

The **pectoralis** (pek'tor-a'lis) **minor** is a thin, flat muscle that lies beneath the larger pectoralis major. It extends laterally and upward from the ribs to the scapula and pulls the scapula forward and downward. When other muscles fix the scapula in position, the pectoralis minor can raise the ribs and thus aid forceful inhalation (see fig. 9.28).

Muscles That Move the Arm

The arm is one of the more freely movable parts of the body because muscles connect the humerus to regions of the pectoral girdle, ribs, and vertebral column. These muscles can be grouped according to their primary actions—flexion, extension, abduction, and rotation (figs. 9.29, 9.30, 9.31; reference plates 67, 68, 69, pp. 354-356; table 9.7). Muscles that move the arm include the following:

Flexors	**Abductors**
Coracobrachialis	Supraspinatus
Pectoralis major	Deltoid
Extensors	**Rotators**
Teres major	Subscapularis
Latissimus dorsi	Infraspinatus
	Teres minor

Flexors

The **coracobrachialis** (kor"ah-ko-bra'ke-al-is) extends from the scapula to the middle of the humerus along its medial surface. It flexes and adducts the arm (see figs. 9.30 and 9.31).

The **pectoralis major** is a thick, fan-shaped muscle in the upper chest. Its fibers extend from the center of the thorax through the armpit to the humerus. This muscle primarily pulls the arm forward and across the chest. It can also rotate the humerus medially and adduct the arm from a raised position (see fig. 9.28).

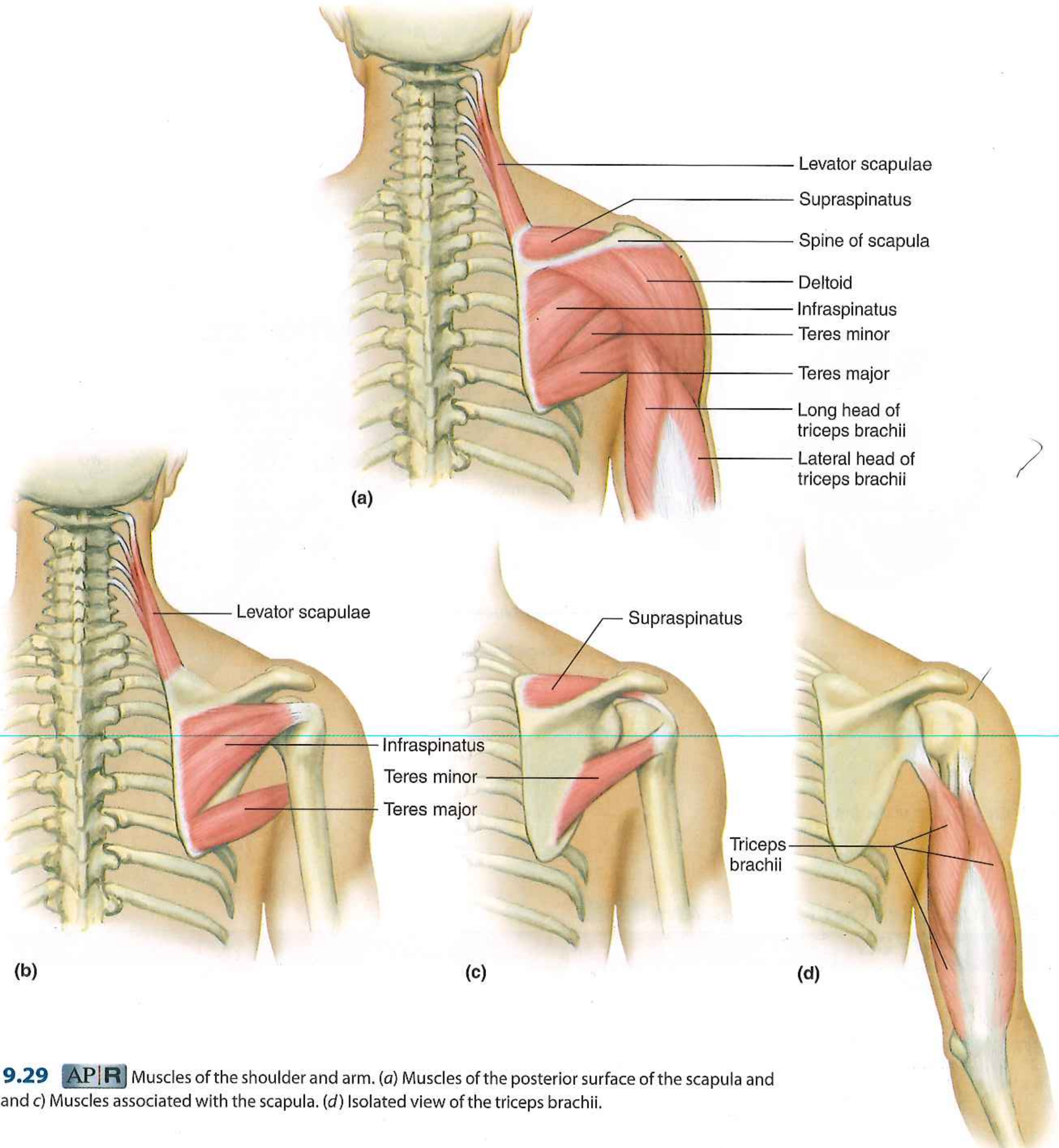


FIGURE 9.29 APR Muscles of the shoulder and arm. (*a*) Muscles of the posterior surface of the scapula and the arm. (*b* and *c*) Muscles associated with the scapula. (*d*) Isolated view of the triceps brachii.

TABLE 9.6 | Muscles That Move the Pectoral Girdle APR

Muscle	Origin	Insertion	Action	Nerve Supply
Trapezius	Occipital bone and spines of cervical and thoracic vertebrae	Clavicle, spine, and acromion process of scapula	Rotates scapula; various fibers raise scapula, pull scapula medially, or pull scapula and shoulder downward	Accessory nerve
Rhomboid major	Spines of upper thoracic vertebrae	Medial border of scapula	Retracts, elevates, and rotates scapula	Dorsal scapular nerve
Rhomboid minor	Spines of lower cervical vertebrae	Medial border of scapula	Retracts and elevates scapula	Dorsal scapular nerve
Levator scapulae	Transverse processes of cervical vertebrae	Medial margin of scapula	Elevates scapula	Dorsal scapular and cervical nerves
Serratus anterior	Outer surfaces of upper ribs	Ventral surface of scapula	Pulls scapula anteriorly and downward	Long thoracic nerve
Pectoralis minor	Sternal ends of upper ribs	Coracoid process of scapula	Pulls scapula forward and downward or raises ribs	Pectoral nerve

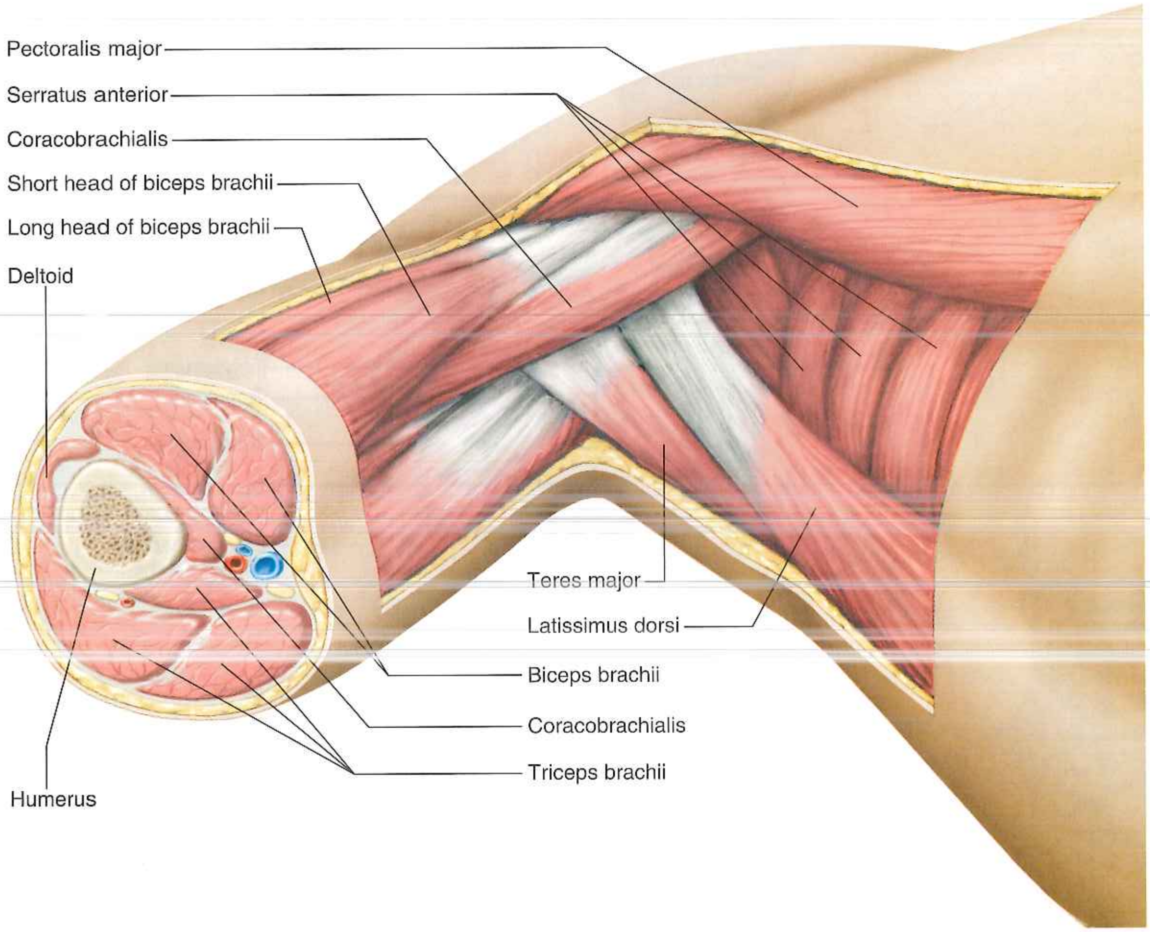


FIGURE 9.30 Cross section of the arm.

TABLE 9.7 | Muscles That Move the Arm APIR

Muscle	Origin	Insertion	Action	Nerve Supply
Coracobrachialis	Coracoid process of scapula	Shaft of humerus	Flexes and adducts the arm	Musculocutaneus nerve
Pectoralis major	Clavicle, sternum, and costal cartilages of upper ribs	Intertubercular groove of humerus	Flexes, adducts, and rotates arm medially	Pectoral nerve
Teres major	Lateral border of scapula	Intertubercular groove of humerus	Extends, adducts, and rotates arm medially	Lower subscapular nerve
Latissimus dorsi	Spines of sacral, lumbar, and lower thoracic vertebrae, iliac crest, and lower ribs	Intertubercular groove of humerus	Extends, adducts, and rotates the arm medially, or pulls the shoulder downward and back	Thoracodorsal nerve
Supraspinatus	Posterior surface of scapula above spine	Greater tubercle of humerus	Abducts the arm	Suprascapular nerve
Deltoid	Acromion process, spine of the s capula, and the clavicle	Deltoid tuberosity of humerus	Abducts, extends, and flexes arm	Axillary nerve
Subscapularis	Anterior surface of scapula	Lesser tubercle of humerus	Rotates arm medially	Subscapular nerve
Infraspinatus	Posterior surface of scapula below spine	Greater tubercle of humerus	Rotates arm laterally	Suprascapular nerve
Teres minor	Lateral border of scapula	Greater tubercle of humerus	Rotates arm laterally	Axillary nerve

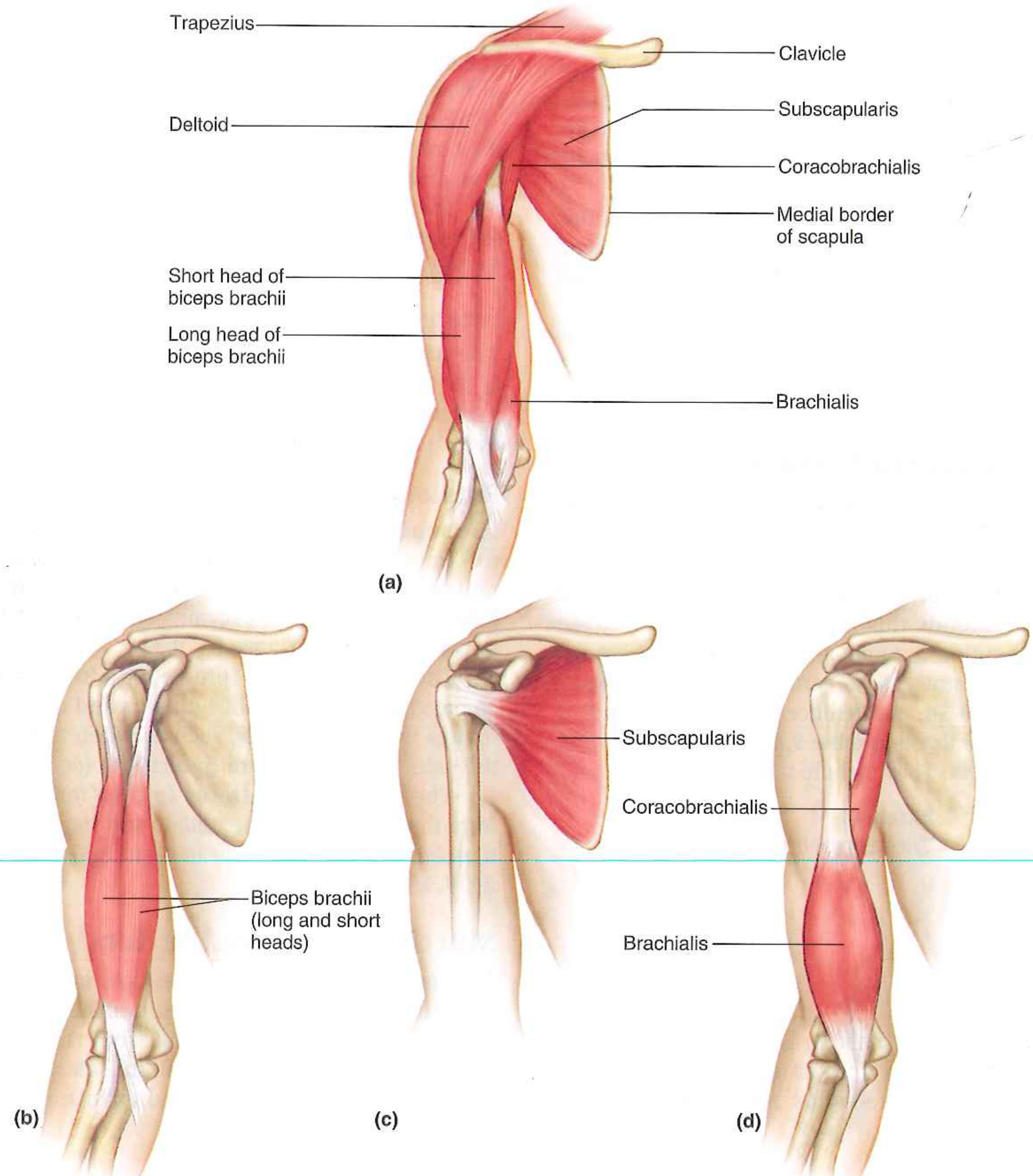


FIGURE 9.31 AP|R Muscles of the shoulder and arm. (*a*) Muscles of the anterior shoulder and the arm, with the rib cage removed. (*b, c,* and *d*) Isolated views of muscles associated with the arm.

Extensors

The **teres** (te′rēz) **major** connects the scapula to the humerus. It extends the humerus and can also adduct and rotate the arm medially (see figs. 9.27 and 9.29).

The **latissimus dorsi** (lah-tis′ĭ-mus dor′si) is a wide, triangular muscle that curves upward from the lower back, around the side, and to the armpit. It can extend and adduct the arm and rotate the humerus medially. It also pulls the shoulder downward and back. The actions of pulling the arm back in swimming, climbing, and rowing use this muscle (see figs. 9.27 and 9.30).

Abductors

The **supraspinatus** (su″prah-spi′na-tus) is located in the depression above the spine of the scapula on its posterior surface. It connects the scapula to the greater tubercle of the humerus and abducts the arm (see figs. 9.27 and 9.29).

The **deltoid** (del′toid) is a thick, triangular muscle that covers the shoulder joint. It connects the clavicle and scapula to the lateral side of the humerus and abducts the arm. The deltoid's posterior fibers can extend the humerus, and its anterior fibers can flex the humerus (see fig. 9.27).

A humerus fractured at its surgical neck may damage the axillary nerve that supplies the deltoid muscle (see fig. 7.43, p. 237). If this occurs, the muscle is likely to shrink and weaken. To test the deltoid for such weakness, a physician may ask a patient to abduct the arm against some resistance and maintain that position for a time.

Rotators

The **subscapularis** (sub-scap′u-lar-is) is a large, triangular muscle that covers the anterior surface of the scapula. It connects the scapula to the humerus and rotates the arm medially (see fig. 9.31).

The **infraspinatus** (in″frah-spi′na-tus) occupies the depression below the spine of the scapula on its posterior surface. The fibers of this muscle attach the scapula to the humerus and rotate the arm laterally (see fig. 9.29).

The **teres minor** is a small muscle connecting the scapula to the humerus. It rotates the arm laterally (see figs. 9.27 and 9.29).

Muscles That Move the Forearm

Most forearm movements are produced by muscles that connect the radius or ulna to the humerus or pectoral girdle. A group of muscles located along the anterior surface of the humerus flexes the forearm at the elbow, whereas a single posterior muscle extends this joint. Other muscles cause movements at the radioulnar joint and rotate the forearm.

The muscles that move the forearm are shown in figures 9.31, 9.32, 9.33, and 9.34, in reference plates 68, 69, and 70 (pp. 355–357, and are listed in table 9.8, grouped according to their primary actions. They include the following:

Flexors	Extensor	Rotators
Biceps brachii	Triceps brachii	Supinator
Brachialis		Pronator teres
Brachioradialis		Pronator quadratus

Flexors

The **biceps brachii** (bi′seps bra′ke-i) is a fleshy muscle that forms a long, rounded mass on the anterior side of the arm. It connects the scapula to the radius and flexes the elbow and rotates the hand laterally (supination), as when a person turns a doorknob or screwdriver (see fig. 9.31).

The **brachialis** (bra′ke-al-is) is a large muscle beneath the biceps brachii. It connects the shaft of the humerus to the ulna and is the strongest flexor of the elbow (see fig. 9.31).

The **brachioradialis** (bra″ke-o-ra″de-a′lis) connects the humerus to the radius. It aids in flexing the elbow (see fig. 9.32).

Extensor

The **triceps brachii** (tri′seps bra′ke-i) has three heads and is the only muscle on the back of the arm. It connects the humerus and scapula to the ulna and is the primary extensor of the elbow (see figs. 9.29 and 9.30).

Rotators

The **supinator** (su′pĭ-na-tor) is a short muscle whose fibers run from the ulna and the lateral end of the humerus to the radius. It assists the biceps brachii in rotating the forearm laterally, such as when turning the hand so the palm faces upward (supination) (see fig. 9.32).

The **pronator teres** (pro-na′tor te′rēz) is a short muscle connecting the ends of the humerus and ulna to the radius. It rotates the arm medially, such as when turning the hand so the palm faces downward (pronation) (see fig. 9.32).

The **pronator quadratus** (pro-na′tor kwod-ra′tus) runs from the distal end of the ulna to the distal end of the radius. It assists the pronator teres in rotating the arm medially (see fig. 9.32).

Muscles That Move the Hand

Movements of the hand include movements of the wrist and fingers. Many of the implicated muscles originate from the distal end of the humerus and from the radius and ulna. The two major groups of these muscles are flexors on the anterior side of the forearm and extensors on the posterior

TABLE 9.8 | Muscles That Move the Forearm APIR

Muscle	Origin	Insertion	Action	Nerve Supply
Biceps brachii	Coracoid process and tubercle above glenoid cavity of scapula	Radial tuberosity of radius	Flexes elbow and rotates hand laterally	Musculocutaneous nerve
Brachialis	Anterior shaft of humerus	Coronoid process of ulna	Flexes elbow	Musculocutaneous, median, and radial nerves
Brachioradialis	Distal lateral end of humerus	Lateral surface of radius above styloid process	Flexes elbow	Radial nerve
Triceps brachii	Tubercle below glenoid cavity and lateral and medial surfaces of humerus	Olecranon process of ulna	Extends elbow	Radial nerve
Supinator	Lateral epicondyle of humerus and crest of ulna	Lateral surface of radius	Rotates forearm laterally and supinates hand	Radial nerve
Pronator teres	Medial epicondyle of humerus and coronoid process of ulna	Lateral surface of radius	Rotates forearm medially and pronates hand	Median nerve
Pronator quadratus	Anterior distal end of ulna	Anterior distal end of radius	Rotates forearm medially and pronates hand	Median nerve

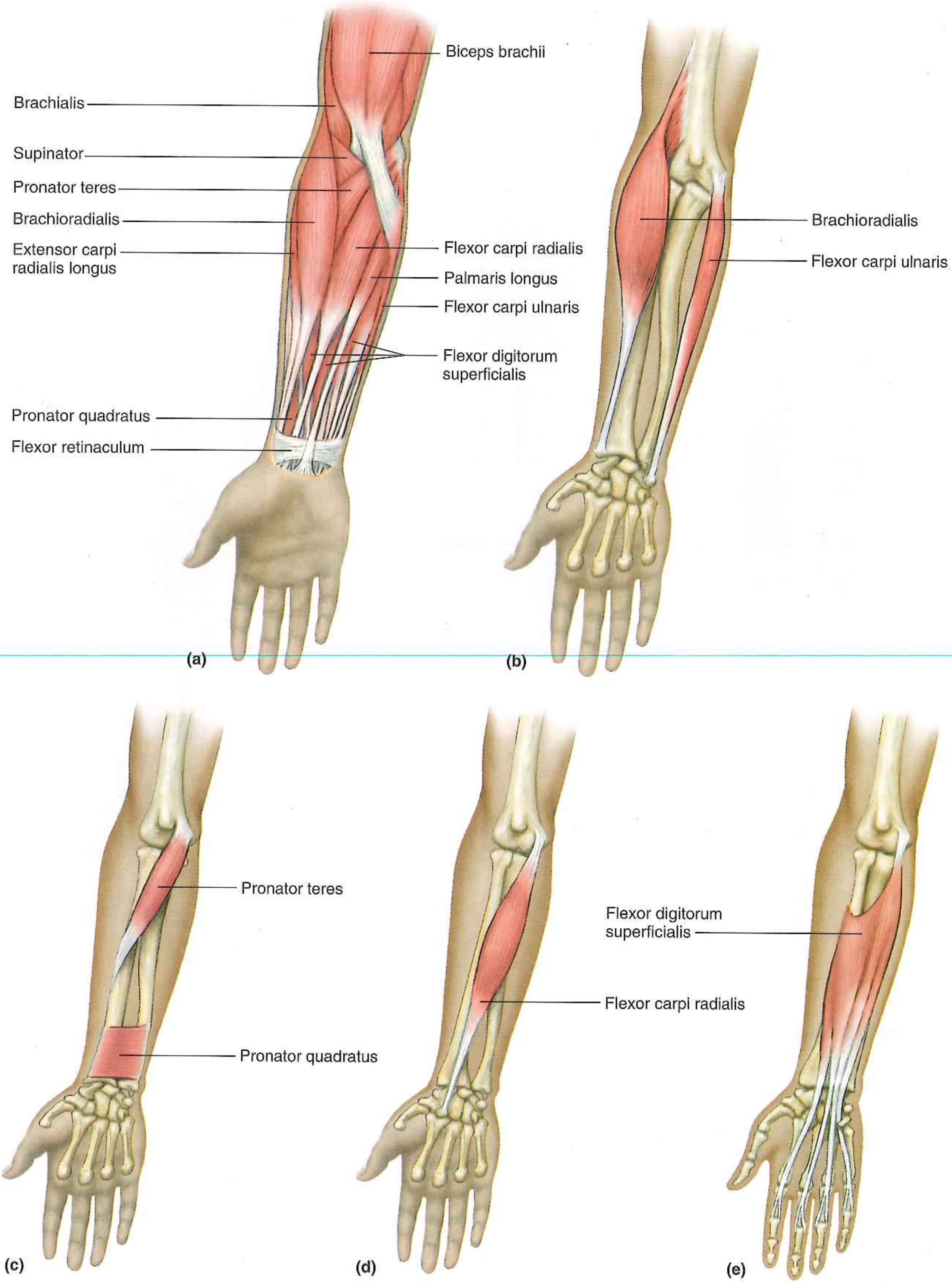


FIGURE 9.32 APR Muscles of the arm and forearm. (*a*) Muscles of the anterior forearm. (*b–e*) Isolated views of muscles associated with the anterior forearm.

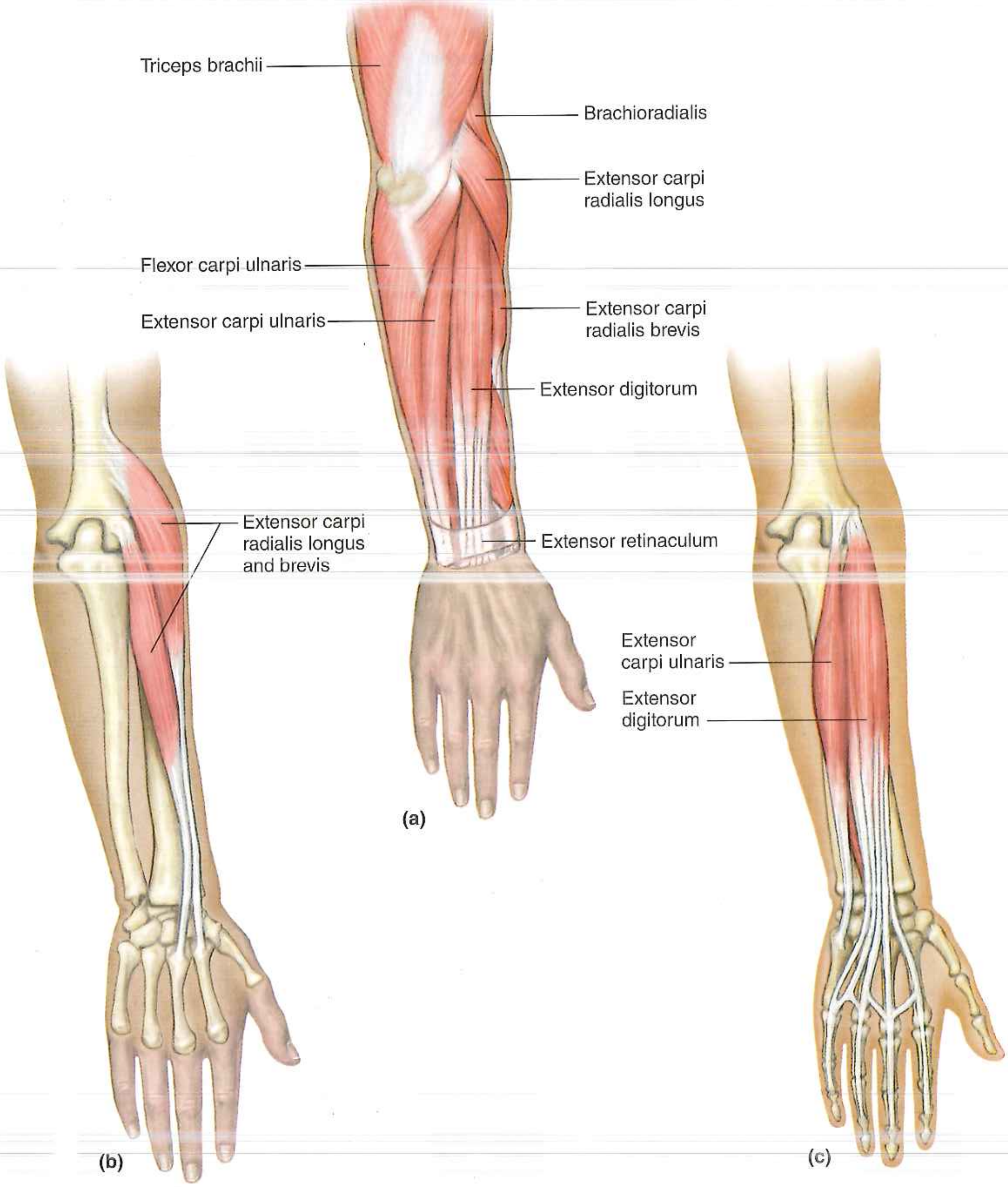


FIGURE 9.33 AP|R Muscles of the arm and forearm. (*a*) Muscles of the posterior forearm. (*b* and *c*) Isolated views of muscles associated with the posterior forearm.

side. Figures 9.32, 9.33, 9.34, reference plate 70 (p. 357), and table 9.9 concern these muscles. The muscles that move the hand include the following:

Flexors	Extensors
Flexor carpi radialis	Extensor carpi radialis longus
Flexor carpi ulnaris	Extensor carpi radialis brevis
Palmaris longus	Extensor carpi ulnaris
Flexor digitorum profundus	Extensor digitorum
Flexor digitorum superficialis	

Flexors

The **flexor carpi radialis** (flek′sor kar-pi′ ra″de-a′lis) is a fleshy muscle that runs medially on the anterior side of the forearm. It extends from the distal end of the humerus into the hand, where it is attached to metacarpal bones. The flexor carpi radialis flexes the wrist and abducts the hand (see fig. 9.32).

The **flexor carpi ulnaris** (flek′sor kar-pi′ ul-na′ris) is located along the medial border of the forearm. It connects the distal end of the humerus and the proximal end of the

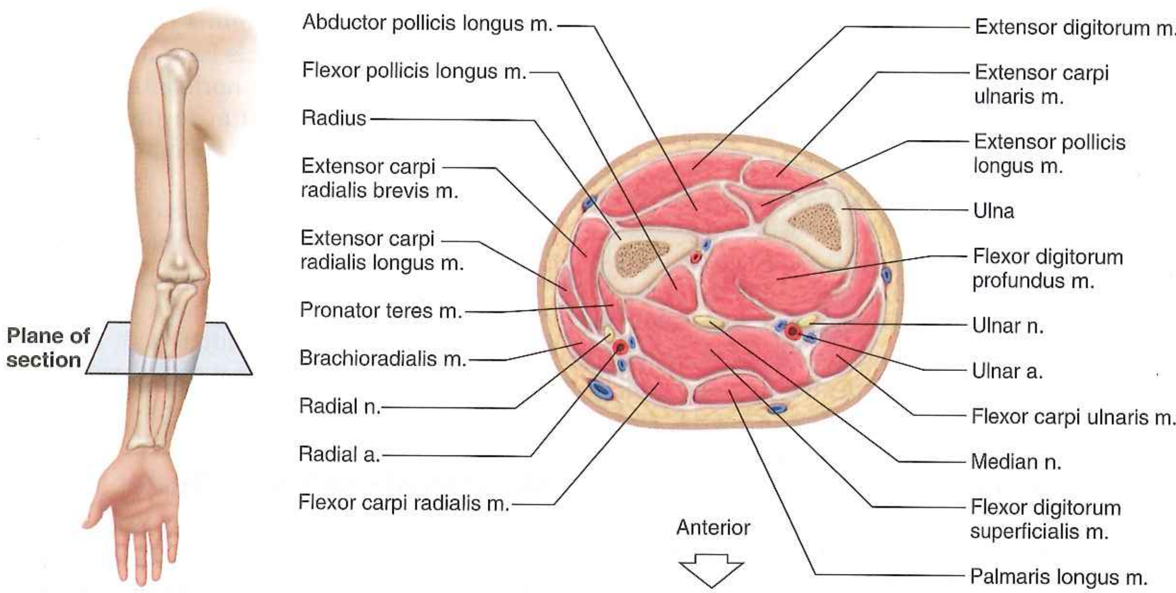


FIGURE 9.34 A cross section of the forearm (superior view). (*a.* stands for artery, *m.* stands for muscle, and *n.* stands for nerve.)

TABLE 9.9 | Muscles That Move the Hand

Muscle	Origin	Insertion	Action	Nerve Supply
Flexor carpi radialis	Medial epicondyle of humerus	Base of second and third metacarpals	Flexes wrist and abducts hand	Median nerve
Flexor carpi ulnaris	Medial epicondyle of humerus and olecranon process	Carpal and metacarpal bones	Flexes wrist and adducts hand	Ulnar nerve
Palmaris longus	Medial epicondyle of humerus	Fascia of palm	Flexes wrist	Median nerve
Flexor digitorum profundus	Anterior surface of ulna	Bases of distal phalanges in fingers 2–5	Flexes distal joints of fingers	Median and ulnar nerves
Flexor digitorum superficialis	Medial epicondyle of humerus, coronoid process of ulna, and radius	Tendons of fingers	Flexes fingers and wrist	Median nerve
Extensor carpi radialis longus	Distal end of humerus	Base of second metacarpal	Extends wrist and abducts hand	Radial nerve
Extensor carpi radialis brevis	Lateral epicondyle of humerus	Base of second and third metacarpals	Extends wrist and abducts hand	Radial nerve
Extensor carpi ulnaris	Lateral epicondyle of humerus	Base of fifth metacarpal	Extends wrist and adducts hand	Radial nerve
Extensor digitorum	Lateral epicondyle of humerus	Posterior surface of phalanges in fingers 2–5	Extends fingers	Radial nerve

ulna to carpal and metacarpal bones. It flexes the wrist and adducts the hand (see fig. 9.32).

The **palmaris longus** (pal-ma′ris long′gus) is a slender muscle located on the medial side of the forearm between the flexor carpi radialis and the flexor carpi ulnaris. It connects the distal end of the humerus to fascia of the palm and flexes the wrist (see fig. 9.32).

The **flexor digitorum profundus** (flek′sor dij″ĭ-to′rum pro-fun′dus) is a large muscle that connects the ulna to the distal phalanges. It flexes the distal joints of the fingers, such as when making a fist (see fig. 9.34).

The **flexor digitorum superficialis** (flek′sor dij″ĭ-to′rum su″per-fish″e-a′lis) is a large muscle located beneath the flexor carpi ulnaris. It arises by three heads—one from the medial epicondyle of the humerus, one from the medial side of the ulna, and one from the radius. It is inserted in the tendons of the fingers and flexes the fingers and, by a combined action, flexes the wrist (see fig. 9.32).

Some of the first signs of Parkinson disease appear in the hands. In this disorder, certain brain cells degenerate, altering the function of nerve cells that control muscles. Once called "shaking palsy," the disease often begins with a hand tremor that resembles the motion of rolling a marble between the thumb and forefinger. Another sign is called "cog-wheel rigidity." When a doctor rotates the patient's hand in an arc, the hand resists the movement and then jerks, like the cogs in a gear.

Extensors

The **extensor carpi radialis longus** (eks-ten'sor kar-pi'ra"de-a'lis long'gus) runs along the lateral side of the forearm, connecting the humerus to the hand. It extends the wrist and assists in abducting the hand (see figs. 9.33 and 9.34).

The **extensor carpi radialis brevis** (eks-ten'sor kar-pi' ra"de-a'lis brev'ĭs) is a companion of the extensor carpi radialis longus and is located medially to it. This muscle runs from the humerus to the metacarpal bones and extends the wrist. It also assists in abducting the hand (see figs. 9.33 and 9.34).

The **extensor carpi ulnaris** (eks-ten'sor kar-pi' ul-na'ris) is located along the posterior surface of the ulna and connects the humerus to the hand. It extends the wrist and assists in adducting the hand (see figs. 9.33 and 9.34).

The **extensor digitorum** (eks-ten'sor dij"ĭ-to'rum) runs medially along the back of the forearm. It connects the humerus to the posterior surface of the phalanges and extends the fingers (see figs. 9.33 and 9.34).

A structure called the *extensor retinaculum* consists of a group of heavy connective tissue fibers in the fascia of the wrist (see fig. 9.33). It connects the lateral margin of the radius with the medial border of the styloid process of the ulna and certain bones of the wrist. The retinaculum gives off branches of connective tissue to the underlying wrist bones, creating a series of sheathlike compartments through which the tendons of the extensor muscles pass to the wrist and fingers.

Muscles of the Abdominal Wall

The walls of the chest and pelvic regions are supported directly by bone, but those of the abdomen are not. Instead, the anterior and lateral walls of the abdomen are composed of layers of broad, flattened muscles. These muscles connect the rib cage and vertebral column to the pelvic girdle. A band of tough connective tissue, called the **linea alba** (lin'e-ah al'bah), extends from the xiphoid process of the sternum to the pubic symphysis. It is an attachment for some of the abdominal wall muscles.

Contraction of the abdominal muscles decreases the volume of the abdominal cavity and increases the pressure inside. This action helps move air out of the lungs during forceful exhalation and also aids in defecation, urination, vomiting, and childbirth.

The abdominal wall muscles are shown in figure 9.35, reference plate 67 (p. 354), and are listed in table 9.10. They include the following:

External oblique	Transversus abdominis
Internal oblique	Rectus abdominis

The **external oblique** (eks-ter'nal ŏ-blēk) is a broad, thin sheet of muscle whose fibers slant downward from the lower ribs to the pelvic girdle and the linea alba. When this muscle contracts, it tenses the abdominal wall and compresses the contents of the abdominal cavity.

Similarly, the **internal oblique** (in-ter'nal ŏ-blēk) is a broad, thin sheet of muscle located beneath the external oblique. Its fibers run up and forward from the pelvic girdle to the lower ribs. Its function is similar to that of the external oblique.

The **transversus abdominis** (trans-ver'sus ab-dom'ĭ-nis) forms a third layer of muscle beneath the external and internal obliques. Its fibers run horizontally from the lower ribs, lumbar vertebrae, and ilium to the linea alba and pubic bones. It functions in the same manner as the external and internal obliques.

The **rectus abdominis** (rek'tus ab-dom'ĭ-nis) is a long, straplike muscle that connects the pubic bones to the ribs and sternum. Three or more fibrous bands cross the muscle transversely, giving it a segmented appearance. The muscle functions with other abdominal wall muscles to compress the contents of the abdominal cavity, and it also helps to flex the vertebral column.

Muscles of the Pelvic Outlet

Two muscular sheets span the outlet of the pelvis—a deeper **pelvic diaphragm** and a more superficial **urogenital diaphragm**. The pelvic diaphragm forms the floor of the pelvic cavity, and the urogenital diaphragm fills the space within the pubic arch. Figure 9.36 and table 9.11 show the muscles of the male and female pelvic outlets. They include the following:

Pelvic Diaphragm	**Urogenital Diaphragm**
Levator ani	Superficial transversus perinei
Coccygeus	Bulbospongiosus
	Ischiocavernosus
	Sphincter urethrae

Pelvic Diaphragm

The **levator ani** (le-va'tor ah-ni') muscles form a thin sheet across the pelvic outlet. They are connected at the midline posteriorly by a ligament that extends from the tip of the coccyx to the anal canal. Anteriorly, they are separated in the male by the urethra and the anal canal, and in the female by the urethra, vagina, and anal canal. These muscles help support the pelvic viscera and provide sphincterlike action in the anal canal and vagina.

An *external anal sphincter* under voluntary control and an *internal anal sphincter* formed of involuntary muscle fibers of the intestine encircle the anal canal and keep it closed.

The **coccygeus** (kok-sij'e-us) is a fan-shaped muscle that extends from the ischial spine to the coccyx and sacrum. It aids the levator ani.

Urogenital Diaphragm

The **superficial transversus perinei** (soo'per-fish'al trans-ver'sus per"ĭ-ne'i) consists of a small bundle of muscle fibers that passes medially from the ischial tuberosity along the posterior border of the urogenital diaphragm. It assists other muscles in supporting the pelvic viscera.

In the male, the **bulbospongiosus** (bul"bo-spon"je-o'sus) muscles are united surrounding the base of the penis and assist in emptying the urethra. In the female, these muscles are separated by the vagina medially, and constrict the vaginal opening. These muscles can also retard the flow of

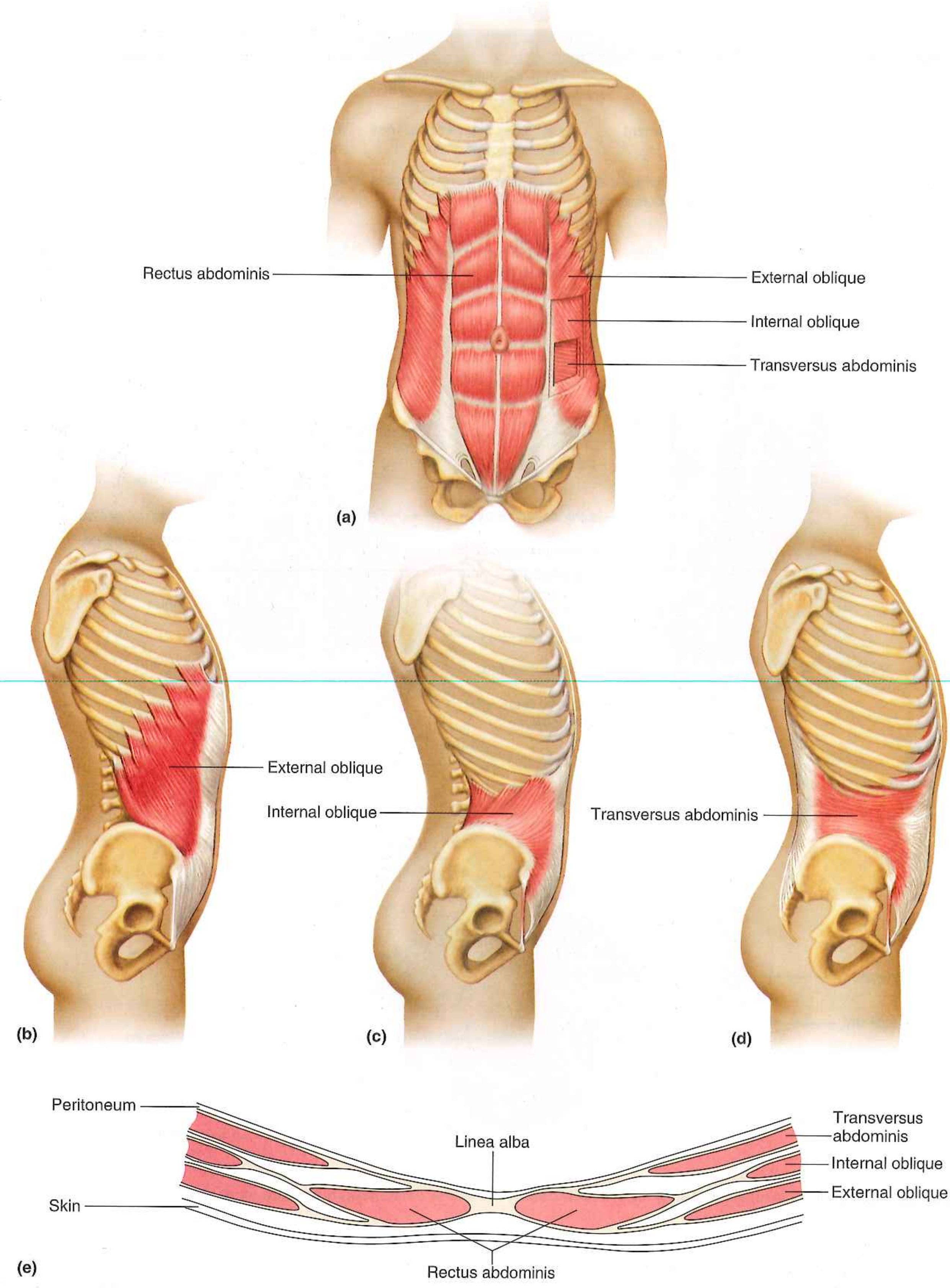


FIGURE 9.35 APR Muscles of the abdominal wall. (*a–d*) Isolated muscles of the abdominal wall. (*e*) Transverse section through the abdominal wall.

TABLE 9.10 | Muscles of the Abdominal Wall APR

Muscle	Origin	Insertion	Action	Nerve Supply
External oblique	Outer surfaces of lower ribs	Outer lip of iliac crest and linea alba	Tenses abdominal wall and compresses abdominal contents	Intercostal nerves 7–12
Internal oblique	Crest of ilium and inguinal ligament	Cartilages of lower ribs, linea alba, and crest of pubis	Tenses abdominal wall and compresses abdominal contents	Intercostal nerves 7–12
Transversus abdominis	Costal cartilages of lower ribs, processes of lumbar vertebrae, lip of iliac crest, and inguinal ligament	Linea alba and crest of pubis	Tenses abdominal wall and compresses abdominal contents	Intercostal nerves 7–12
Rectus abdominis	Crest of pubis and pubic symphysis	Xiphoid process of sternum and costal cartilages	Same as above; also flexes vertebral column	Intercostal nerves 7–12

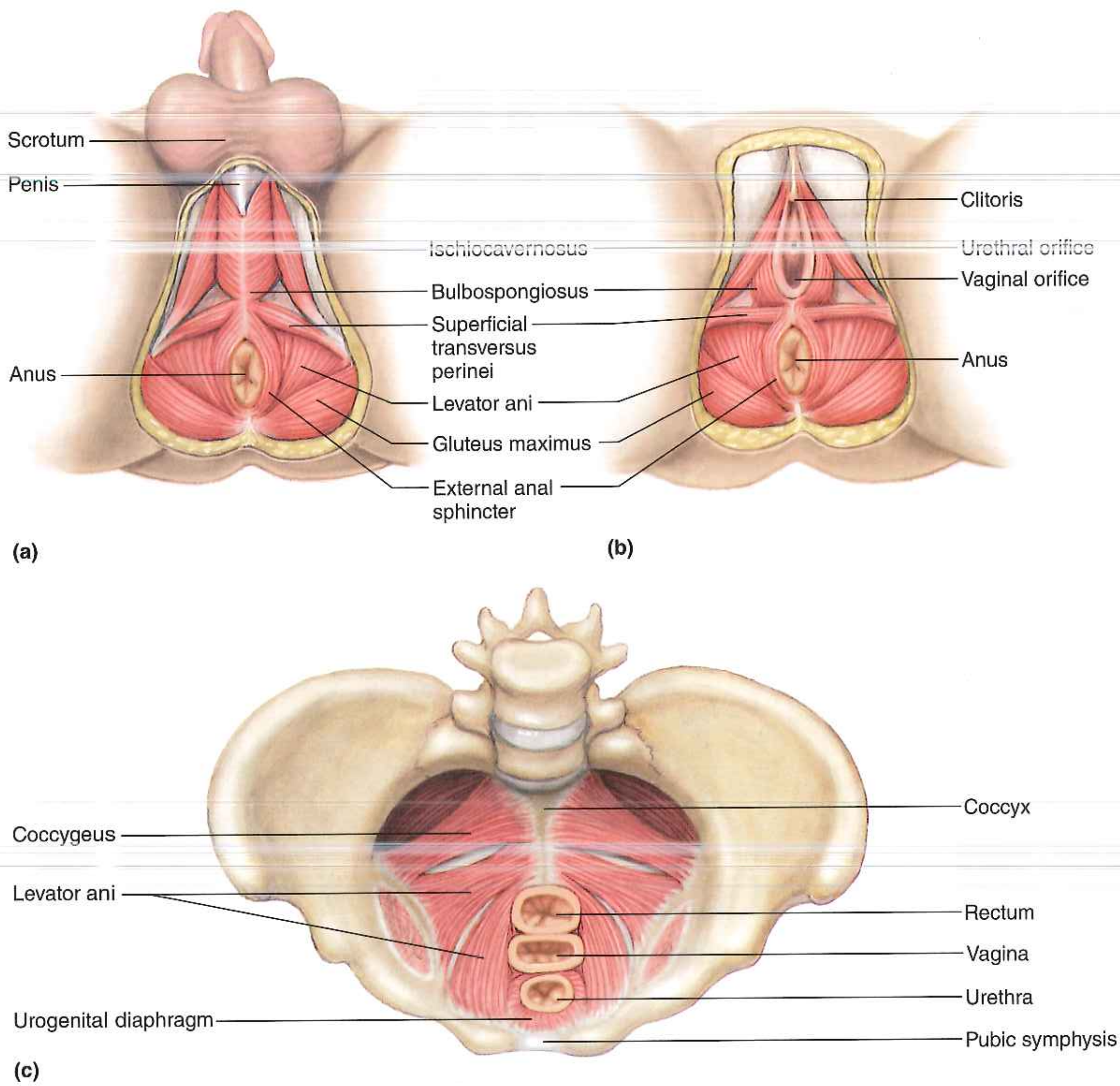


FIGURE 9.36 APR External view of muscles of (*a*) the male pelvic outlet and (*b*) the female pelvic outlet. (*c*) Internal view of female pelvic and urogenital diaphragms.

blood in veins, which helps maintain an erection of the penis in the male and of the clitoris in the female.

The **ischiocavernosus** (is″ke-o-kav″er-no′sus) muscle is a tendinous structure that extends from the ischial tuberosity to the margin of the pubic arch. It assists erection of the penis in males and the clitoris in females.

The **sphincter urethrae** (sfingk′ter u-re′thrē) are muscles that arise from the margins of the pubic and ischial bones. Each arches around the urethra and unites with the one on the other side. Together they act as a sphincter that closes the urethra by compression and opens it by relaxation, helping control the flow of urine.

TABLE 9.11 | Muscles of the Pelvic Outlet

Muscle	Origin	Insertion	Action	Nerve Supply
Levator ani	Pubic bone and ischial spine	Coccyx	Supports pelvic viscera and provides sphincterlike action in anal canal and vagina	Pudendal nerve
Coccygeus	Ischial spine	Sacrum and coccyx	Supports pelvic viscera and provides sphincterlike action in anal canal and vagina	S4 and S5 nerves
Superficial transversus perinei	Ischial tuberosity	Central tendon	Supports pelvic viscera	Pudendal nerve
Bulbospongiosus	Central tendon	Males: Urogenital diaphragm and fascia of penis Females: Pubic arch and root of clitoris	Males: Assists emptying of urethra and assists in erection of penis Females: Constricts vagina and assists in erection of clitoris	Pudendal nerve
Ischiocavernosus	Ischial tuberosity	Pubic arch	Males: Contributes to erection of the penis Females: Contributes to erection of the clitoris	Pudendal nerve
Sphincter urethrae	Margins of pubis and ischium	Fibers of each unite with those from other side	Closes urethra	Pudendal nerve

Muscles That Move the Thigh

The muscles that move the thigh are attached to the femur and to part of the pelvic girdle. (Important exceptions are the sartorius and rectus femoris, described later.) The muscles can be separated into an anterior group that primarily flexes the thigh and a posterior group that extends, abducts, or rotates the thigh. Figures 9.37, 9.38, 9.39, 9.40 and reference plates 71 and 72 (pp. 357–358) show the muscles in these groups, and table 9.12 lists them. Muscles that move the thigh include the following:

Anterior Group	Posterior Group
Psoas major	Gluteus maximus
Iliacus	Gluteus medius
	Gluteus minimus
	Piriformis
	Tensor fasciae latae

Another group of muscles, attached to the femur and pelvic girdle, adducts the thigh. This group includes the following:

Pectineus	Adductor magnus
Adductor brevis	Gracilis
Adductor longus	

Anterior Group

The **psoas** (so'as) **major** is a long, thick muscle that connects the lumbar vertebrae to the femur. It flexes the thigh (see fig. 9.37).

The **iliacus** (il'e-ak-us), a large, fan-shaped muscle, lies along the lateral side of the psoas major. The iliacus and the psoas major are the primary flexors of the thigh, and they advance the lower limb in walking movements (see fig. 9.37).

Posterior Group

The **gluteus maximus** (gloo'te-us mak'si-mus) is the largest muscle in the body and covers a large part of each buttock. It connects the ilium, sacrum, and coccyx to the femur by fascia of the thigh and extends the thigh. The gluteus maximus helps to straighten the lower limb at the hip when a person walks, runs, or climbs. It is also used to raise the body from a sitting position (see fig. 9.38).

The **gluteus medius** (gloo'te-us me'de-us) is partly covered by the gluteus maximus. Its fibers extend from the ilium to the femur, and they abduct the thigh and rotate it medially (see fig. 9.38).

The **gluteus minimus** (gloo'te-us min'ĭ-mus) lies beneath the gluteus medius and is its companion in attachments and functions (see fig. 9.38).

The **piriformis** (pir-ĭ-for'mis) is shaped like a pyramid and located inferior to the gluteus minimus. It abducts and laterally rotates the thigh and is part of the posterior group of muscles that stabilizes the hip.

The **tensor fasciae latae** (ten'sor fash'e-e lah-tē) connects the ilium to the iliotibial tract (fascia of the thigh), which continues downward to the tibia. This muscle abducts and flexes the thigh and rotates it medially (see fig. 9.38).

> The gluteus medius and gluteus minimus help support and maintain the normal position of the pelvis. If these muscles are paralyzed on one side as a result of injury or disease, the pelvis tends to drop on the contralateral side when that foot is raised. Consequently, the person walks with a waddling movement called the *gluteal gait*.

Thigh Adductors

The **pectineus** (pek-tin'e-us) muscle runs from the spine of the pubis to the femur. It flexes and adducts the thigh (see fig. 9.37).

The **adductor brevis** (ah-duk'tor brev'ĭs) is a short, triangular muscle that runs from the pubic bone to the femur. It adducts and assists in flexing the thigh (see fig. 9.37).

The **adductor longus** (ah-duk'tor long'gus) is a long, triangular muscle that runs from the pubic bone to the femur. It adducts the thigh and assists in flexing and rotating it laterally (see fig. 9.37).

The **adductor magnus** (ah-duk'tor mag'nus) is the largest adductor of the thigh. It is a triangular muscle that connects

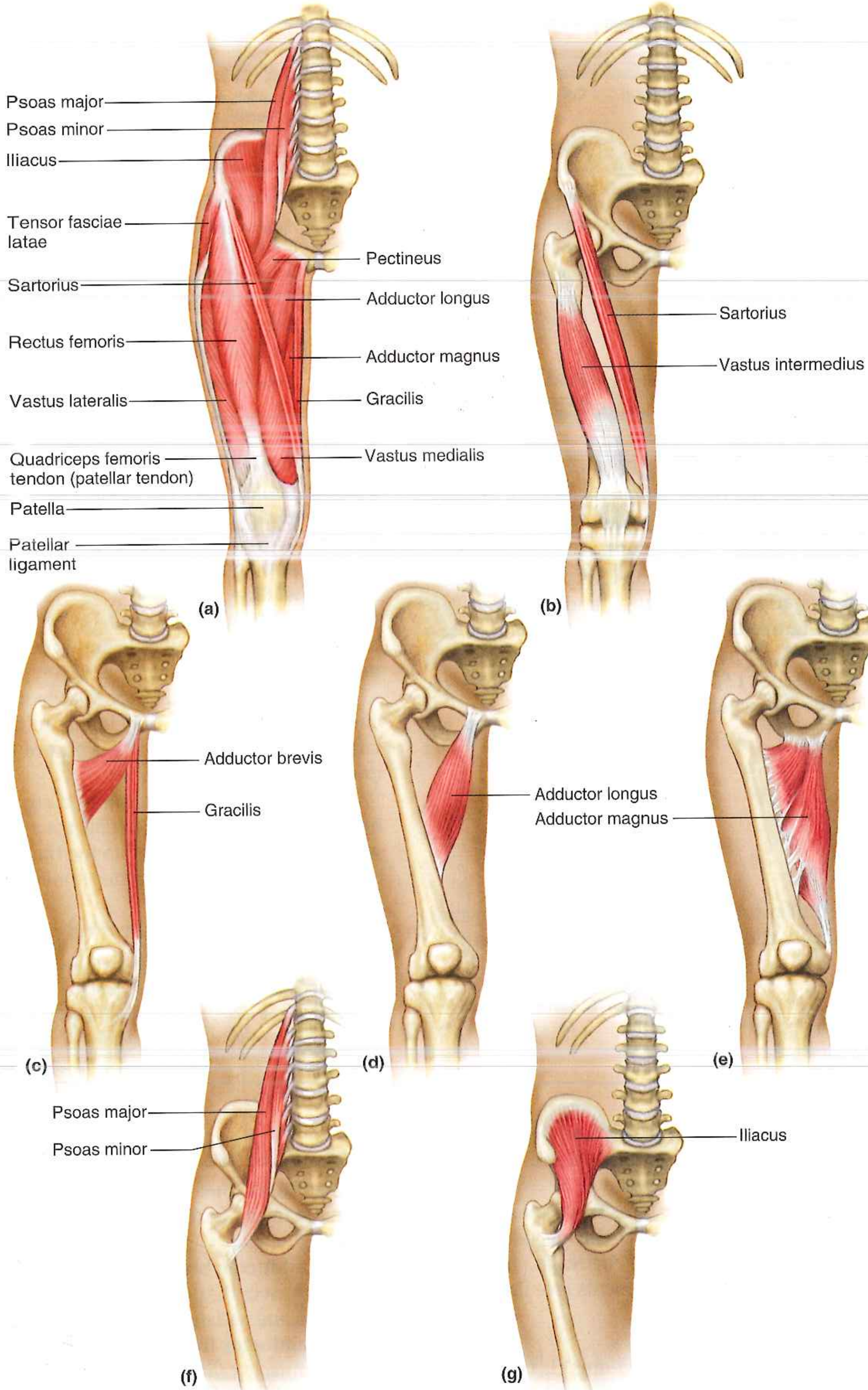


FIGURE 9.37 AP|R Muscles of the thigh and leg. (*a*) Muscles of the anterior right thigh. Isolated views of (*b*) the vastus intermedius, (*c–e*) adductors of the thigh, (*f–g*) flexors of the thigh.

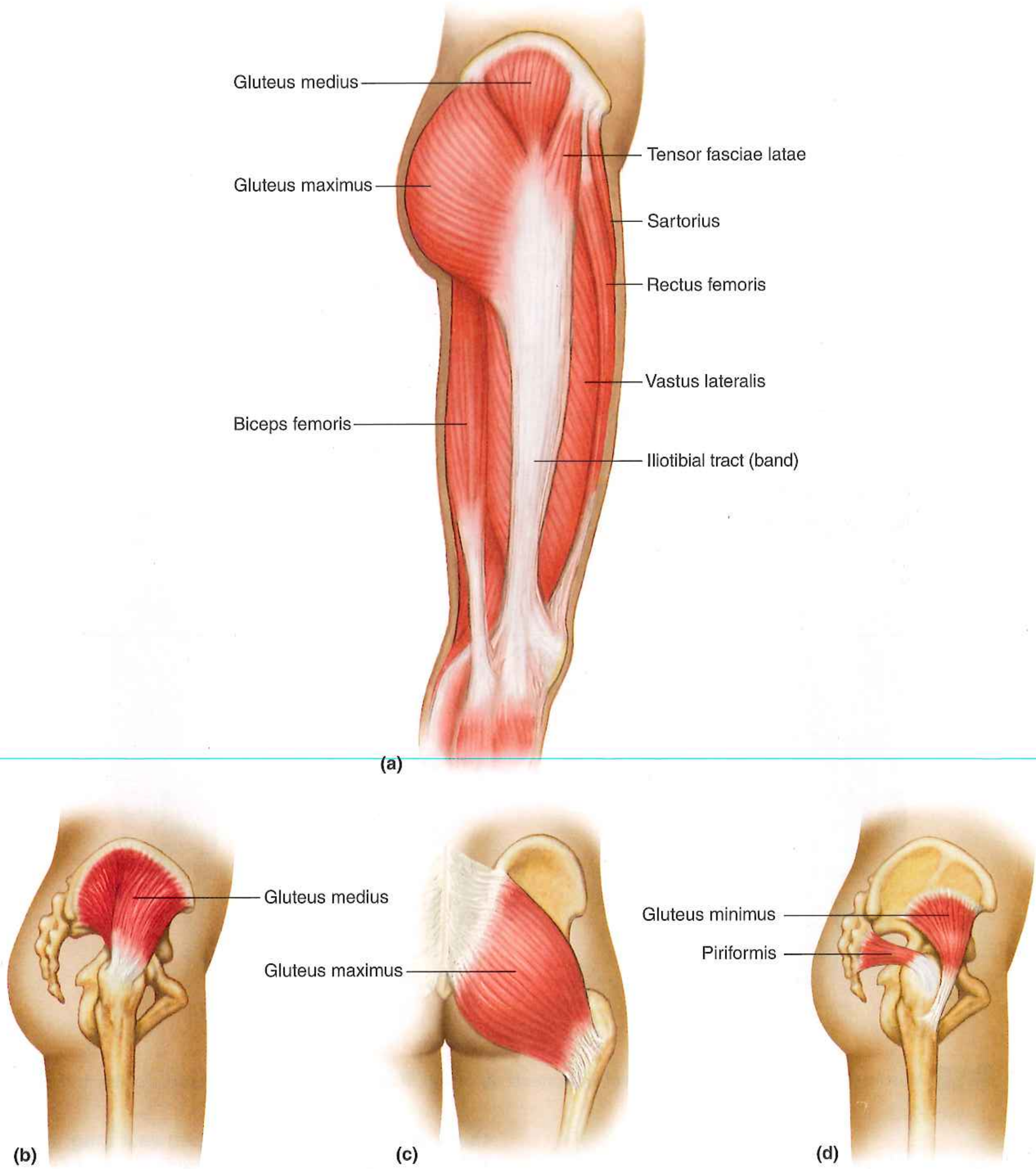


FIGURE 9.38 Muscles of the thigh and leg. (*a*) Muscles of the lateral right thigh. (*b–d*) Isolated views of the gluteal muscles.

the ischium to the femur. It adducts the thigh and portions assist in flexing and extending the thigh (see fig. 9.37).

The **gracilis** (gras'il-is) is a long, straplike muscle that passes from the pubic bone to the tibia. It adducts the thigh and flexes the leg at the knee (see fig. 9.37).

Muscles That Move the Leg

The muscles that move the leg connect the tibia or fibula to the femur or to the pelvic girdle. They fall into two major groups—those that flex the knee and those that extend it. The muscles of these groups are shown in figures 9.37, 9.38, 9.39, 9.40, in reference plates 71 and 72 (pp. 357–358), and are listed in table 9.13. Muscles that move the leg include the following:

Flexors	**Extensor**
Biceps femoris	Quadriceps femoris group
Semitendinosus	
Semimembranosus	
Sartorius	

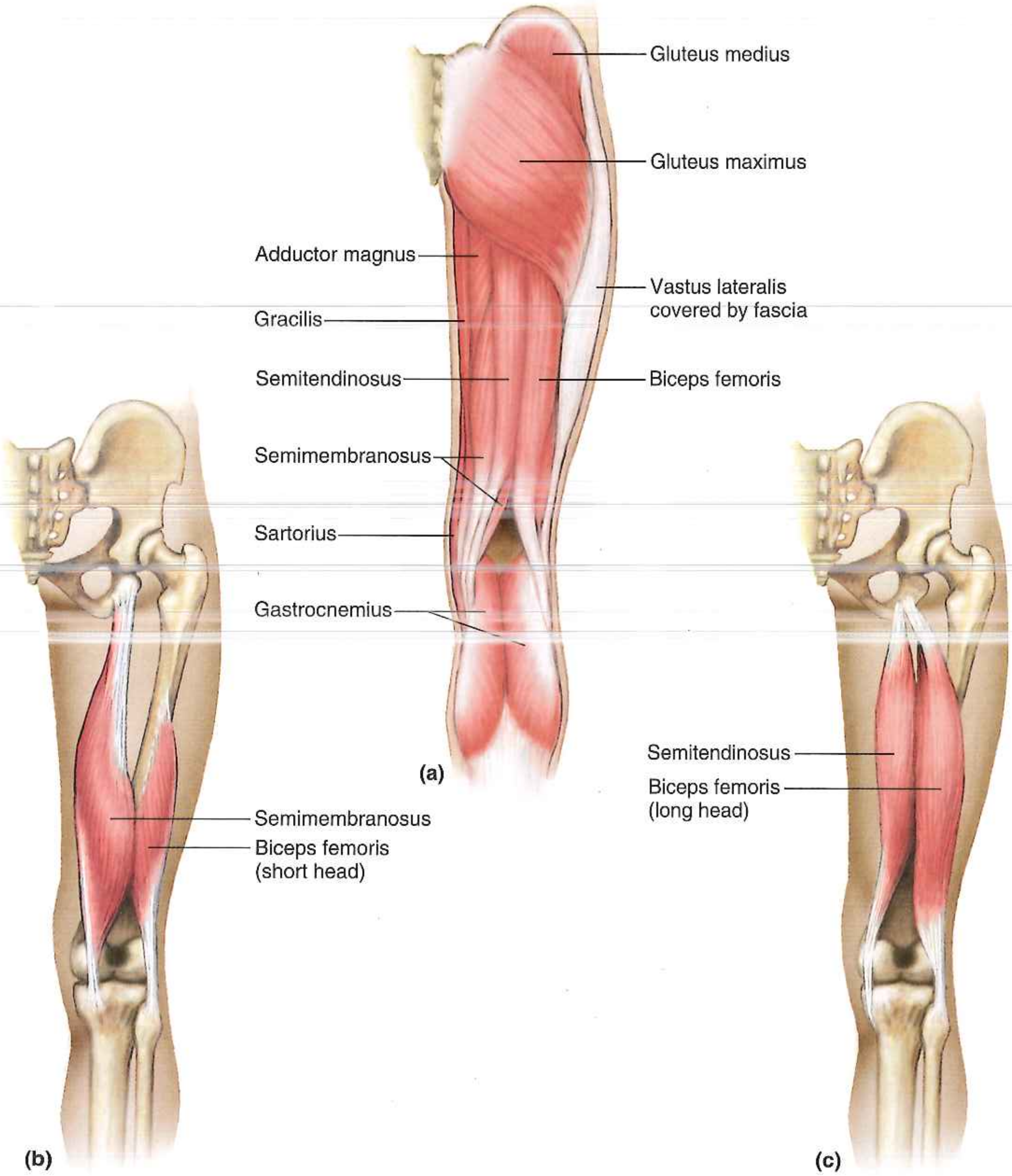


FIGURE 9.39 AP|R Muscles of the thigh and leg. (*a*) Muscles of the posterior right thigh. (*b* and *c*) Isolated views of muscles that flex the leg at the knee.

Flexors

As its name implies, the **biceps femoris** (bi′seps fem′or-is) has two heads, one attached to the ischium and the other attached to the femur. This muscle passes along the back of the thigh on the lateral side and connects to the proximal ends of the fibula and tibia. The biceps femoris is one of the hamstring muscles, and its tendon (hamstring) feels like a lateral ridge behind the knee. This muscle flexes and rotates the leg laterally and extends the thigh (see figs. 9.38 and 9.39).

The **semitendinosus** (sem″e-ten′dĭ-no-sus) is another hamstring muscle. It is a long, bandlike muscle on the back of the thigh toward the medial side, connecting the ischium to the proximal end of the tibia. The semitendinosus is so named because it becomes tendinous in the middle of the thigh, continuing to its insertion as a long, cordlike tendon. It flexes and rotates the leg medially and extends the thigh (see fig. 9.39).

The **semimembranosus** (sem″e-mem′brah-no-sus) is the third hamstring muscle and is the most medially located muscle in the back of the thigh. It connects the ischium to the tibia and flexes and rotates the leg medially and extends the thigh (see fig. 9.39).

Strenuous running or kicking motions can tear the tendinous attachments of the hamstring muscles to the ischial tuberosity. Internal bleeding from damaged blood vessels that supply the muscles usually occurs with this painful injury, commonly called a *pulled hamstring.*

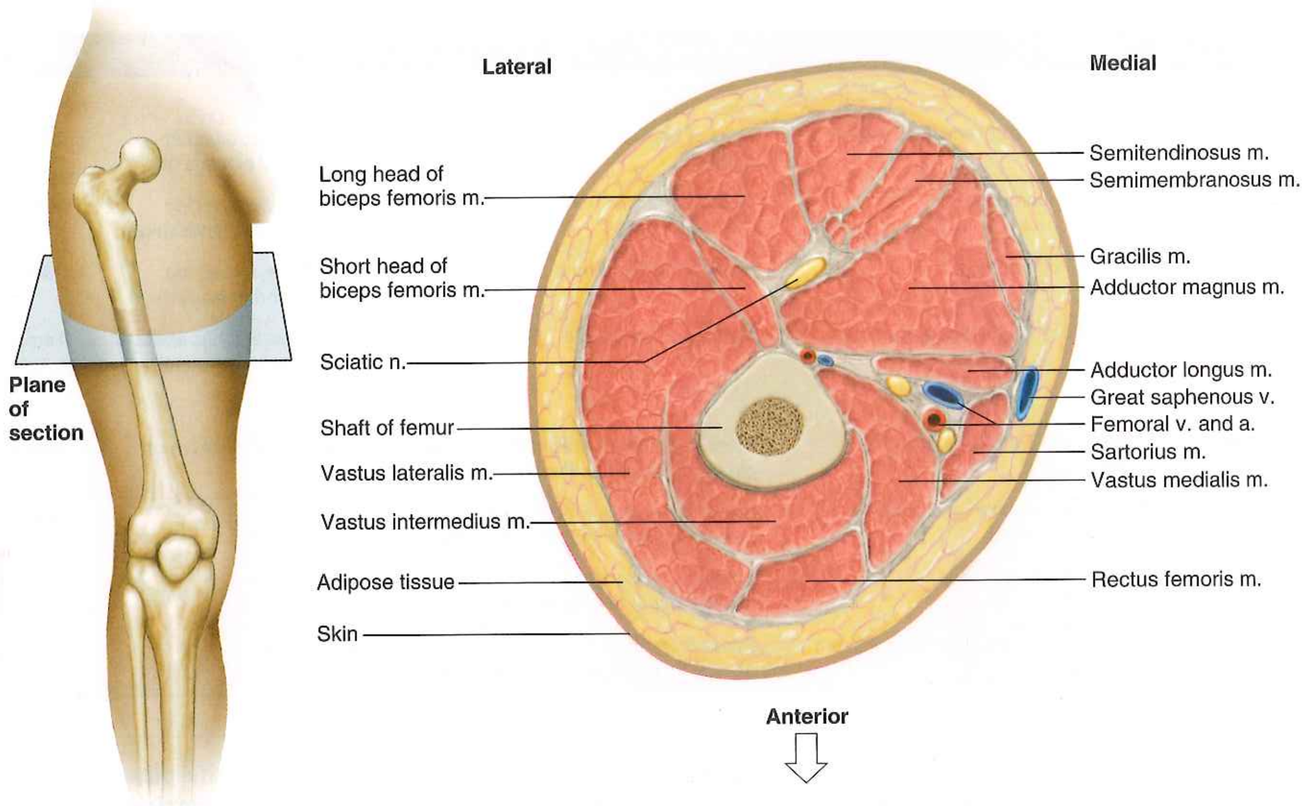


FIGURE 9.40 A cross section of the thigh (superior view). (*a.* stands for artery, *m.* stands for muscle, *n.* stands for nerve, and *v.* stands for vein.)

TABLE 9.12 | Muscles That Move The Thigh APR

Muscle	Origin	Insertion	Action	Nerve Supply
Psoas major	Lumbar intervertebral discs; bodies and transverse processes of lumbar vertebrae	Lesser trochanter of femur	Flexes thigh	Branches of L1–3 nerves
Iliacus	Iliac fossa of ilium	Lesser trochanter of femur	Flexes thigh	Femoral nerve
Gluteus maximus	Sacrum, coccyx, and posterior surface of ilium	Posterior surface of femur and fascia of thigh	Extends hip	Inferior gluteal nerve
Gluteus medius	Lateral surface of ilium	Greater trochanter of femur	Abducts and rotates thigh medially	Superior gluteal nerve
Gluteus minimus	Lateral surface of ilium	Greater trochanter of femur	Abducts and rotates thigh medially	Superior gluteal nerve
Piriformis	Anterior surface of sacrum	Greater trochanter of femur	Abducts and rotates thigh laterally	L5, S1, and S2 nerves
Tensor fasciae latae	Anterior iliac crest	Iliotibial tract (fascia of thigh)	Abducts, flexes, and rotates thigh medially	Superior gluteal nerve
Pectineus	Spine of pubis	Femur distal to lesser trochanter	Flexes and adducts thigh	Obturator and femoral nerves
Adductor brevis	Pubic bone	Posterior surface of femur	Adducts and flexes thigh	Obturator nerve
Adductor longus	Pubic bone near pubic symphysis	Posterior surface of femur	Adducts and flexes thigh	Obturator nerve
Adductor magnus	Ischial tuberosity	Posterior surface of femur	Adducts thigh, posterior portion extends and anterior portion flexes thigh	Obturator and branch of sciatic nerves
Gracilis	Lower edge of pubic symphysis	Medial surface of tibia	Adducts thigh and flexes knee	Obturator nerve

TABLE 9.13 | Muscles That Move the Leg APIR

Muscle	Origin	Insertion	Action	Nerve Supply
Hamstring Group				
Biceps femoris	Ischial tuberosity and linea aspera of femur	Head of fibula and lateral condyle of tibia	Flexes knee, rotates leg laterally and extends thigh	Tibial nerve
Semitendinosus	Ischial tuberosity	Medial surface of tibia	Flexes knee, rotates leg medially and extends thigh	Tibial nerve
Semimembranosus	Ischial tuberosity	Medial condyle of tibia	Flexes knee, rotates leg medially and extends thigh	Tibial neve
Sartorius	Anterior superior iliac spine	Medial surface of tibia	Flexes knee and hip, abducts and rotates thigh laterally	Femoral nerve
Quadriceps Femoris Group				
Rectus femoris	Spine of ilium and margin of acetabulum	Patella by tendon, which continues as patellar ligament to tibial tuberosity	Extends knee, flexes thigh	Femoral nerve
Vastus lateralis	Greater trochanter and posterior surface of femur	Patella by tendon, which continues as patellar ligament to tibial tuberosity	Extends knee	Femoral nerve
Vastus medialis	Medial surface of femur	Patella by tendon, which continues as patellar ligament to tibial tuberosity	Extends knee	Femoral nerve
Vastus intermedius	Anterior and lateral surfaces of femur	Patella by tendon, which continues as patellar ligament to tibial tuberosity	Extends knee	Femoral nerve

The **sartorius** (sar-to're-us) is an elongated, straplike muscle that passes obliquely across the front of the thigh and then descends over the medial side of the knee. It connects the ilium to the tibia and flexes the leg and the thigh. It can also abduct the thigh and rotate it laterally (see figs. 9.37 and 9.38).

Extensor

The large muscle group called the **quadriceps femoris** (kwod'rĭ-seps fem'or-is) occupies the front and sides of the thigh and is the primary extensor of the knee. It is composed of four parts—*rectus femoris, vastus lateralis, vastus medialis,* and *vastus intermedius* (see figs. 9.38 and 9.40). These parts connect the ilium and femur to a common *patellar tendon,* which passes over the front of the knee and attaches to the patella. This tendon then continues as the *patellar ligament* to the tibia. Because the rectus femoris originates on the ilium, it can flex the thigh.

In a traumatic injury that compresses a muscle, such as the quadriceps femoris, against an underlying bone, new bone tissue may begin to develop in the damaged muscle. This condition is called *myositis ossificans.* Surgery can remove the newly formed bone when it matures several months after the injury.

Muscles That Move the Foot

Movements of the foot include movements of the ankle and toes. A number of muscles that move the foot are in the leg. They attach the femur, tibia, and fibula to bones of the foot and move the foot upward (dorsiflexion) or downward (plantar flexion) and turn the foot so the plantar surface faces medially (inversion) or laterally (eversion). These muscles are shown in figures 9.41, 9.42, 9.43, and 9.44, in reference plates 73, 74, 75 (pp. 358–359), and are listed in table 9.14. Muscles that move the foot include the following:

Dorsal Flexors
Tibialis anterior
Fibularis tertius
Extensor digitorum longus
Extensor hallucis longus

Invertor
Tibialis posterior

Plantar Flexors
Gastrocnemius
Soleus
Plantaris
Flexor digitorum longus

Evertor
Fibularis longus

Dorsal Flexors

The **tibialis anterior** (tib"e-a'lis ante're-or) is an elongated, spindle-shaped muscle located on the front of the leg. It arises from the surface of the tibia, passes medially over the distal end of the tibia, and attaches to bones of the foot. Contraction of the tibialis anterior causes dorsiflexion and inversion of the foot (see fig. 9.41).

The **fibularis** (peroneus) **tertius** (fib"u-la'ris ter'shus) is a muscle of variable size that connects the fibula to the lateral side of the foot. It functions in dorsiflexion and eversion of the foot (see fig. 9.41).

The **extensor digitorum longus** (eks-ten'sor dij"ĭ-to'rum long'gus) is situated along the lateral side of the leg just behind the tibialis anterior. It arises from the proximal end of the tibia and the shaft of the fibula. Its tendon divides into

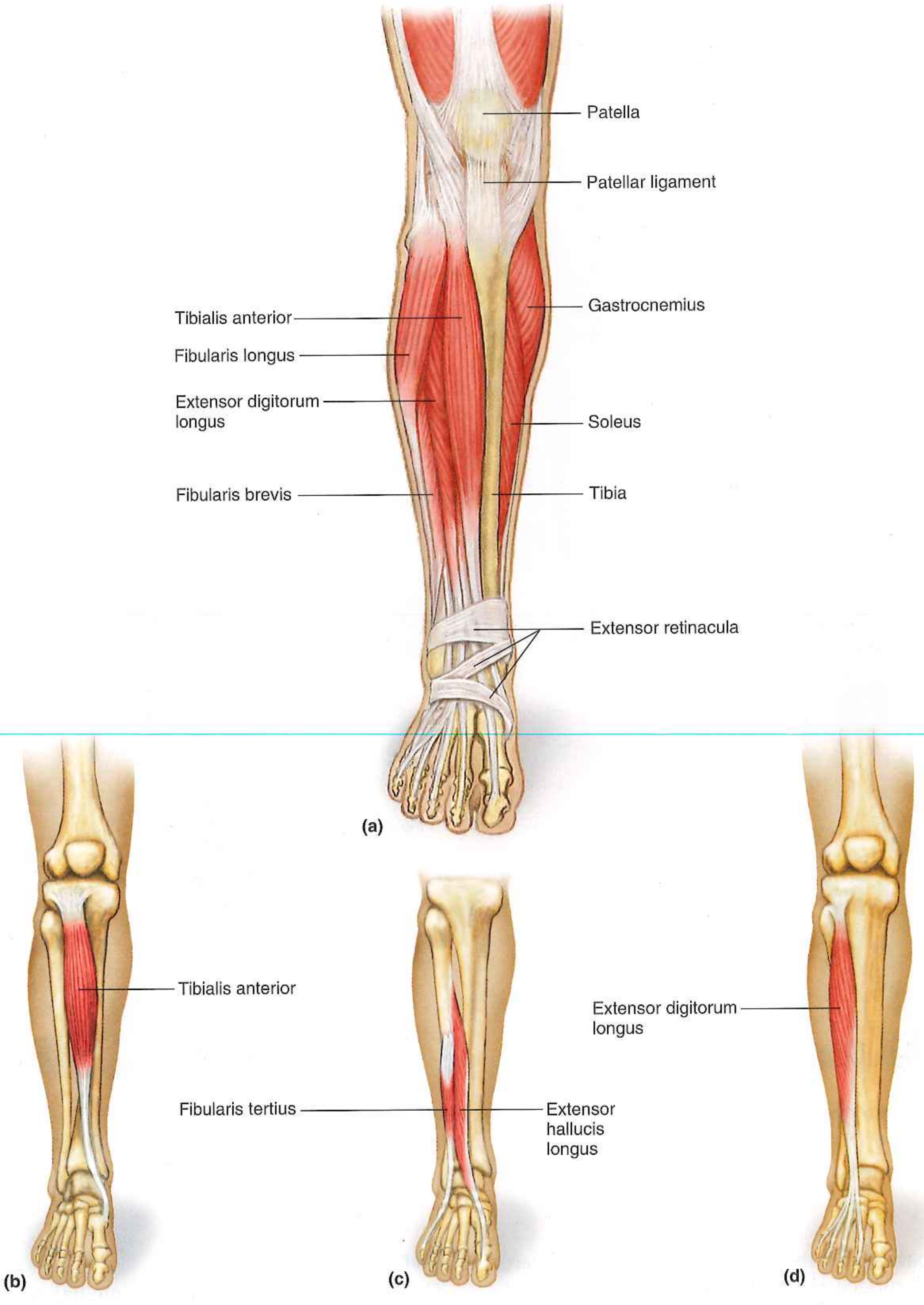


FIGURE 9.41 APR Muscles of the leg. (*a*) Muscles of the anterior right leg. (*b–d*) Isolated views of muscles associated with the anterior right leg.

FIGURE 9.42 Muscles of the leg. (*a*) Muscles of the lateral right leg. Isolated views of (*b*) fibularis longus and (*c*) fibularis brevis.

four parts as it passes over the front of the ankle. These parts continue over the surface of the foot and attach to the four lateral toes. The actions of the extensor digitorum longus include dorsiflexion of the foot, eversion of the foot, and extension of the toes (see figs. 9.41 and 9.42).

The **extensor hallucis longus** (eks-ten′sor hal′lu-sis long′gus) connects the anterior fibula with the great toe. Contraction extends the great toe, dorsiflexes and inverts the foot (see fig. 9.41).

Plantar Flexors

The **gastrocnemius** (gas″trok-ne′me-us) on the back of the leg forms part of the calf. It arises by two heads from the femur. The distal end of this muscle joins the strong *calcaneal tendon* (Achilles tendon), which descends to the heel and attaches to the calcaneus. The gastrocnemius is a powerful plantar flexor of the foot that aids in pushing the body forward when a person walks or runs. It also flexes the leg at the knee (see figs. 9.42 and 9.43).

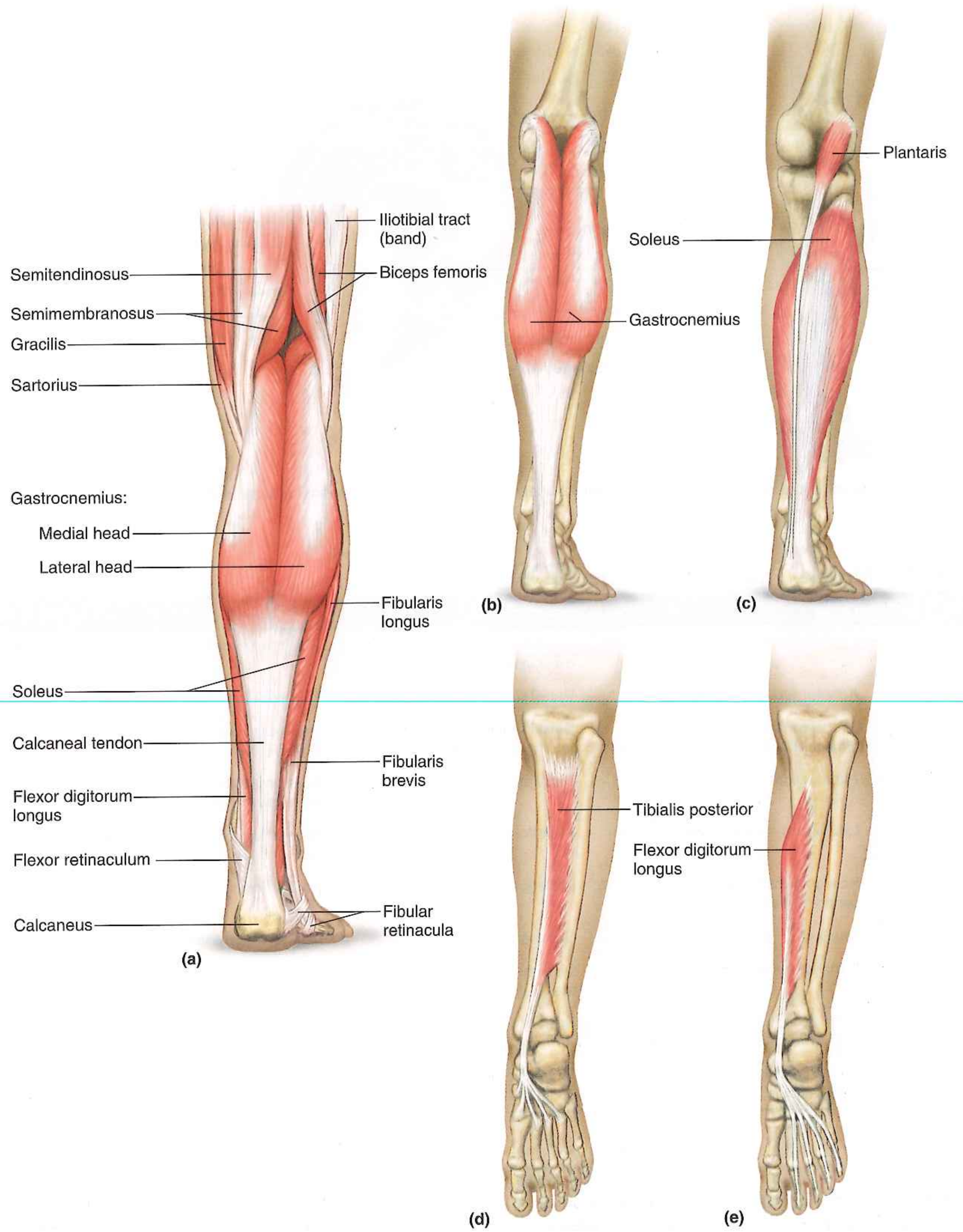


FIGURE 9.43 APR Muscles of the leg. (*a*) Muscles of the posterior right leg. (*b–e*) Isolated views of muscles associated with the posterior right leg.

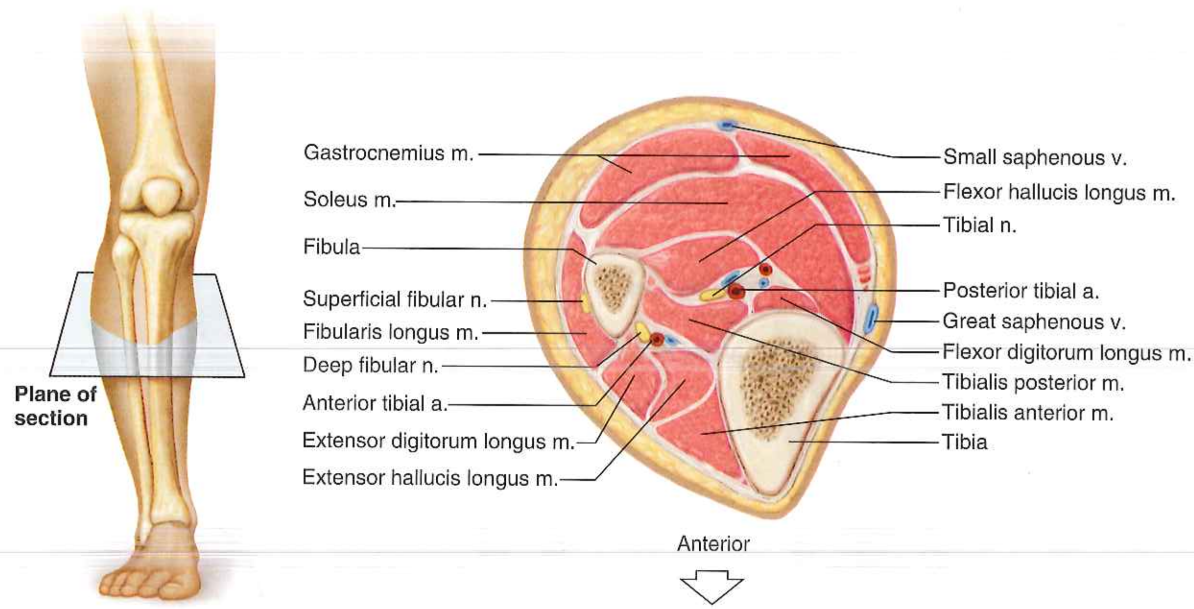


FIGURE 9.44 A cross section of the leg (superior view). (*a.* stands for artery, *m.* stands for muscle, *n.* stands for nerve, and *v.* stands for vein.)

TABLE 9.14 | Muscles That Move the Foot APR

Muscle	Origin	Insertion	Action	Nerve Supply
Tibialis anterior	Lateral condyle and lateral surface of tibia	Tarsal bone (cuneiform) and first metatarsal	Dorsiflexion and inversion of foot	Deep fibular nerve
Fibularis tertius	Anterior surface of fibula	Dorsal surface of fifth metatarsal	Dorsiflexion and eversion of foot	Deep fibular nerve
Extensor digitorum longus	Lateral condyle of tibia and anterior surface of fibula	Dorsal surfaces of second and third phalanges of four lateral toes	Dorsiflexion and eversion of foot, extends toes	Deep fibular nerve
Extensor hallucis longus	Anterior surface of fibula	Distal phalanx of the great toe	Extends great toe, dorsiflexion and inversion of foot	Deep fibular nerve
Gastrocnemius	Lateral and medial condyles of femur	Posterior surface of calcaneus	Plantar flexion of foot, flexes knee	Tibial nerve
Soleus	Head and shaft of fibula and posterior surface of tibia	Posterior surface of calcaneus	Plantar flexion of foot	Tibial nerve
Plantaris	Femur	Calcaneus	Plantar flexion of foot, flexes knee	Tibial nerve
Flexor digitorum longus	Posterior surface of tibia	Distal phalanges of four lateral toes	Plantar flexion and inversion of foot, flexes four lateral toes	Tibial nerve
Tibialis posterior	Lateral condyle and posterior surface of tibia and posterior surface of fibula	Tarsal and metatarsal bones	Plantar flexion and inversion of foot	Tibial nerve
Fibularis longus	Lateral condyle of tibia and head and shaft of fibula	Tarsal and metatarsal bones	Plantar flexion and eversion of foot, also supports arch	Superficial fibular nerve

Strenuous athletic activity may partially or completely tear the calcaneal (Achilles) tendon. This injury occurs most frequently in middle-aged athletes who run or play sports that involve quick movements and directional changes. A torn calcaneal tendon usually requires surgical treatment.

The **soleus** (so′le-us) is a thick, flat muscle located beneath the gastrocnemius, and together these two muscles form the calf of the leg. The soleus arises from the tibia and fibula, and it extends to the heel by way of the calcaneal tendon. It acts with the gastrocnemius to cause plantar flexion of the foot (see figs. 9.42 and 9.43).

The **plantaris** (plan-ta′ris) connects the femur to the heel, where it inserts with the gastrocnemius and soleus via the calcaneal tendon. When the plantaris contracts it flexes the foot, and because it crosses the knee joint, it also flexes the knee.

The **flexor digitorum longus** (flek′sor dij″ĭ-to′rum long′gus) extends from the posterior surface of the tibia to the foot. Its tendon passes along the plantar surface of the foot. There the tendon divides into four parts that attach to the terminal bones of the four lateral toes. This muscle assists in plantar flexion of the foot, flexion of the four lateral toes, and inversion of the foot (see fig. 9.43).

Invertor

The **tibialis posterior** (tib″e-a′lis pos-tēr′e-or) is the deepest of the muscles on the back of the leg. It connects the fibula and tibia to the ankle bones by means of a tendon that curves under the medial malleolus. This muscle assists in inversion and plantar flexion of the foot (see fig. 9.43). The dorsiflexor *extensor hallucis longus*, because it pulls up on the medial portion, also inverts the foot (see fig. 9.41).

Evertor

The **fibularis** (peroneus) **longus** (fib″u-la′ris long′gus) is a long, straplike muscle located on the lateral side of the leg. It connects the tibia and the fibula to the foot by means of a stout tendon that passes behind the lateral malleolus. It everts the foot, assists in plantar flexion, and helps support the arch of the foot (see figs. 9.42 and 9.44).

Fascia in various regions of the ankle thicken to form retinacula, as in the wrist. Anteriorly, for example, *extensor retinacula* connect the tibia and fibula as well as the calcaneus and fascia of the sole. These retinacula form sheaths for tendons crossing the front of the ankle (see figs. 9.41 and 9.42).

Posteriorly, on the inside, a *flexor retinaculum* runs between the medial malleolus and the calcaneus and forms sheaths for tendons passing beneath the foot (see fig. 9.43). *Fibular retinacula* connect the lateral malleolus and the calcaneus, providing sheaths for tendons on the lateral side of the ankle (see fig. 9.42).

PRACTICE

31 Which muscles provide facial expression? ability to chew? head movements?

32 Which muscles move the pectoral girdle? the arm, forearm, and hand?

33 Which muscles move the thigh, legs, and foot?

9.9 LIFE-SPAN CHANGES

Signs of aging in the muscular system begin to appear in one's forties, although a person can still be active. At a microscopic level, supplies of the molecules that enable muscles to function—myoglobin, ATP, and creatine phosphate—decline. The diameters of some muscle fibers may decrease as the muscle layers in the walls of veins thicken, making the vessels more rigid and less elastic. Gradually, the muscles become smaller, drier, and capable of less forceful contraction. Connective tissue and adipose cells begin to replace some muscle tissue. By age eighty, nearly half the muscle mass has atrophied, due to a decline in motor neuron activity. Diminishing muscular strength slows reflexes.

Exercise can help maintain a healthy muscular system throughout life, countering the less effective oxygen delivery that results from the decreased muscle mass that accompanies aging. Exercise can even lead to formation of new muscle by stimulating skeletal muscle cells to release interleukin-6 (IL-6), a type of proinflammatory molecule called a cytokine. The IL-6 stimulates satellite cells, which function as muscle stem cells. They divide and migrate, becoming incorporated into the muscle fiber. Exercise also maintains the flexibility of blood vessels, which helps to keep blood pressure at healthy levels. A physician should be consulted before starting any exercise program.

According to the National Institute on Aging, exercise should include strength training and aerobics. Strength training consists of weight lifting or using a machine that works specific muscles against a resistance, performed so that the same muscle is not exercised on consecutive days. Strength training increases muscle mass, and the resulting stronger muscles can alleviate pressure on the joints, which may lessen arthritis pain. Aerobic exercise improves oxygen use by muscles and increases endurance. A side benefit of regular exercise, especially among older individuals, is fewer bouts of depression.

PRACTICE

34 What changes are associated with an aging muscular system?

35 Describe two types of recommended exercise.

CHAPTER SUMMARY

9.1 INTRODUCTION (PAGE 293)

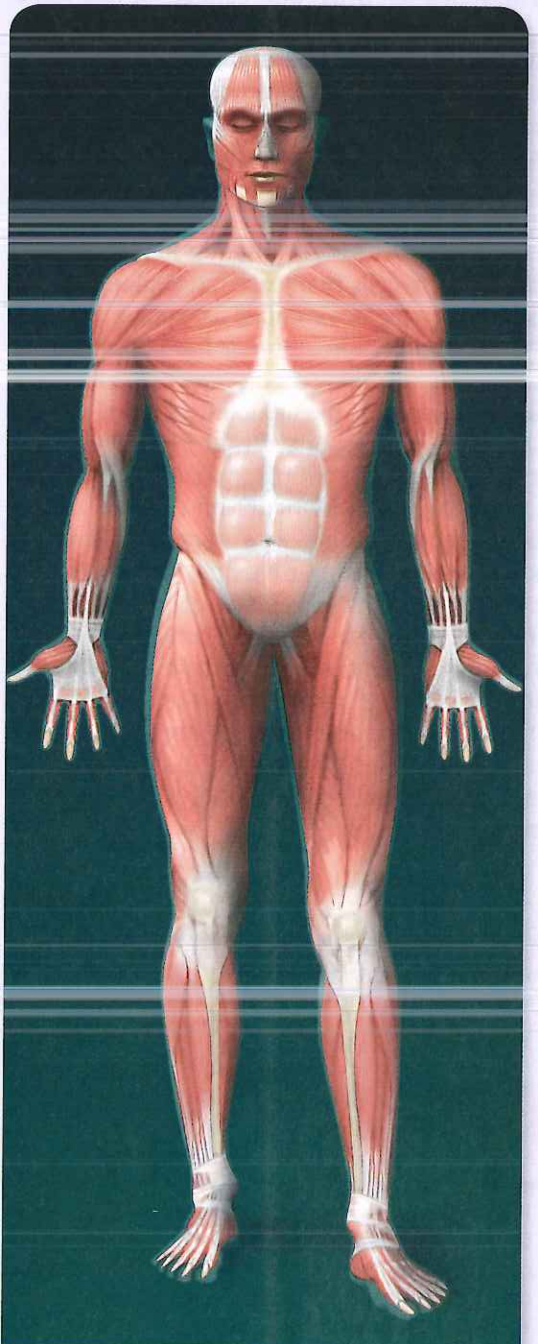
All movements require muscles. The three types of muscle tissue are skeletal, smooth, and cardiac.

9.2 STRUCTURE OF A SKELETAL MUSCLE (PAGE 293)

Skeletal muscles are composed of nervous, vascular and various other connective tissues, as well as skeletal muscle tissue.

1. Connective tissue coverings
   a. Fascia covers each skeletal muscle.
   b. Other connective tissues surround cells and groups of cells within the muscle's structure (epimysium, perimysium, endomysium).
   c. Fascia is part of a complex network of connective tissue that extends throughout the body.
2. Skeletal muscle fibers
   a. Each skeletal muscle fiber is a single muscle cell, the unit of contraction.
   b. Muscle fibers are cylindrical cells with many nuclei.

INNERCONNECTIONS ●●● Muscular System



Muscular System

Muscles provide the force for moving body parts.

Integumentary System

The skin increases heat loss during skeletal muscle activity. Sensory receptors function in the reflex control of skeletal muscles.

Skeletal System

Bones provide attachments that allow skeletal muscles to cause movement.

Nervous System

Neurons control muscle contractions.

Endocrine System

Hormones help increase blood flow to exercising skeletal muscles.

Cardiovascular System

Blood flow delivers oxygen and nutrients and removes wastes. Cardiac muscle pumps blood, smooth muscle in vessel walls enables vasoconstriction, vasodilation.

Lymphatic System

Muscle action pumps lymph through lymphatic vessels.

Digestive System

Skeletal muscles are important in swallowing. Smooth muscle moves food through the digestive tract. The digestive system absorbs needed nutrients.

Respiratory System

Breathing depends on skeletal muscles. The lungs provide oxygen for energy releasing reactions in muscle cells and excrete carbon dioxide waste from those reactions.

Urinary System

Skeletal muscles help control expulsion of urine from the urinary bladder.

Reproductive System

Skeletal muscles are important in sexual activity.

c. The cytoplasm contains mitochondria, sarcoplasmic reticulum, and myofibrils of actin and myosin.
d. The arrangement of the actin and myosin filaments causes striations. (I bands, Z lines, A bands, H zone and M line)
e. Heads of myosin filaments form linkages called cross-bridges with actin filaments. The reaction between actin and myosin filaments provides the basis for contraction.
f. When a fiber is at rest, troponin and tropomyosin molecules interfere with cross-bridge formation. Calcium ions remove the inhibition.
g. Transverse tubules extend from the cell membrane into the cytoplasm and are associated with the cisternae of the sarcoplasmic reticulum.

9.3 SKELETAL MUSCLE CONTRACTION (PAGE 297)

Muscle fiber contraction results from a sliding movement of actin and myosin filaments overlapping that shortens the muscle fiber.

1. Neuromuscular junction
   a. Motor neurons stimulate muscle fibers to contract.
   b. The motor end plate of a muscle fiber lies on one side of a neuromuscular junction.
   c. One motor neuron and the muscle fibers associated with it constitute a motor unit.
   d. In response to an action potential, the end of a motor neuron axon releases a neurotransmitter, which diffuses across the junction and stimulates the muscle fiber.
2. Stimulus for contraction
   a. Acetylcholine released from the end of a motor neuron axon stimulates a muscle fiber.
   b. Acetylcholinesterase decomposes acetylcholine, preventing continuous stimulation.
   c. Stimulation causes a muscle fiber to conduct an impulse that travels over the surface of the sarcolemma and reaches the deep parts of the fiber by means of the transverse tubules.
3. Excitation contraction coupling
   a. A muscle impulse signals the sarcoplasmic reticulum to release calcium ions.
   b. Calcium ions combine with troponin, causing the tropomyosin to shift and expose active sites on the actin for myosin binding.
   c. Cross-bridges form between myosin and actin, and the actin filaments move inward, shortening the sarcomere.
4. The sliding filament model of muscle contraction
   a. The sarcomere, defined by striations, is the functional unit of skeletal muscle.
   b. When the overlapping thick and thin myofilaments slide past one another, the sarcomeres shorten. The muscle contracts.
5. Cross-bridge cycling
   a. A myosin head can attach to an actin binding site to form a cross-bridge which pulls on the actin filament. The myosin head can then release the actin and attach to another active binding site farther down the actin filament and pull again.
   b. The breakdown of ATP releases energy that provides the repetition of the cross-bridge cycle.
6. Relaxation
   a. Acetylcholinesterase rapidly decomposes acetylcholine remaining in the synapse, preventing continuous stimulation of a muscle fiber.
   b. The muscle fiber relaxes when calcium ions are transported back into the sarcoplasmic reticulum.
   c. Cross-bridge linkages break and do not re-form—the muscle fiber relaxes.
7. Energy sources for contraction
   a. ATP supplies the energy for muscle fiber contraction.
   b. Creatine phosphate stores energy that can be used to synthesize ATP as it is decomposed.
   c. Active muscles require cellular respiration for energy.
8. Oxygen supply and cellular respiration
   a. Anaerobic reactions of cellular respiration yield few ATP molecules, whereas aerobic reactions of cellular respiration provide many ATP molecules.
   b. Hemoglobin in red blood cells carries oxygen from the lungs to body cells.
   c. Myoglobin in muscle cells temporarily stores some oxygen.
9. Oxygen debt
   a. During rest or moderate exercise, oxygen is sufficient to support the aerobic reactions of cellular respiration.
   b. During strenuous exercise, oxygen deficiency may develop, and lactic acid may accumulate as a result of the anaerobic reactions of cellular respiration.
   c. The oxygen debt includes the amount of oxygen required to react accumulated lactic acid to form glucose and to restore supplies of ATP and creatine phosphate.
10. Muscle fatigue
    a. A fatigued muscle loses its ability to contract.
    b. Muscle fatigue is due in part to the effects of accumulation of lactic acid.
    c. Athletes usually produce less lactic acid than nonathletes because of their increased ability to supply oxygen and nutrients to muscles.
11. Heat production
    a. Muscular contraction generates body heat.
    b. Most of the energy released by cellular respiration is lost as heat.

9.4 MUSCULAR RESPONSES (PAGE 304)

1. Threshold stimulus is the minimal stimulus needed to elicit a muscular contraction.
2. Recording of a muscle contraction
   a. A twitch is a single, short contraction of a muscle fiber.
   b. A myogram is a recording of the contraction of an electrically stimulated isolated muscle or muscle fiber.
   c. The latent period is the time between stimulus and responding contraction.
   d. During the refractory period immediately following contraction, a muscle fiber cannot respond.
   e. The length to which a muscle is stretched before stimulation affects the force it will develop.
      (1) Normal activities occur at optimal length.
      (2) Too long or too short decreases force.

f. Sustained contractions are more important than twitch contractions in everyday activities.
3. Summation
   a. A rapid series of stimuli may produce summation of twitches and sustained contraction.
   b. At higher frequencies of stimulation, contraction with little time for relaxation is called partial tetany.
   c. Forceful, sustained contraction without any relaxation is a complete (fused) tetanic contraction.
4. Recruitment of motor units
   a. Muscles whose motor units have few muscle fibers produce finer movements.
   b. Motor units respond in an all-or-none manner.
   c. At low intensity of stimulation, relatively few motor units contract.
   d. At increasing intensities of stimulation, other motor units are recruited until the muscle contracts with maximal tension.
5. Sustained contractions
   a. Tetanic contractions are common in everyday activities.
   b. Even when a whole muscle appears at rest, some of its fibers undergo sustained contraction. This is called muscle tone.
6. Types of contractions
   a. One type of isotonic contraction occurs when a muscle contracts and its ends are pulled closer together. Because the muscle shortens, it is called a concentric contraction.
   b. In another type of isotonic contraction, the force a muscle generates is less than that required to move or lift an object. This lengthening contraction is an eccentric contraction.
   c. When a muscle contracts but its attachments do not move, the contraction is isometric.
   d. Most body movements involve both isometric and isotonic contractions.
7. Fast-and-slow twitch muscle fibers
   a. The speed of contraction is related to a muscle's specific function.
   b. Slow-contracting, or red, muscles can generate ATP fast enough to keep up with ATP breakdown and can contract for long periods.
   c. Fast-contracting, or white, muscles have reduced ability to carry on the aerobic reactions of cellular respiration and tend to fatigue rapidly.

9.5 SMOOTH MUSCLES (PAGE 308)

The contractile mechanisms of smooth and cardiac muscles are similar to those of skeletal muscle.

1. Smooth muscle fibers
   a. Smooth muscle cells contain filaments of myosin and actin.
   b. They lack transverse tubules, and the sarcoplasmic reticula are not well developed.
   c. Types include multiunit smooth muscle and visceral smooth muscle.
   d. Visceral smooth muscle displays rhythmicity.
   e. Peristalsis aids movement of material through hollow organs.
2. Smooth muscle contraction
   a. In smooth muscles, calmodulin binds to calcium ions and activates the contraction mechanism.
   b. Both acetylcholine and norepinephrine are neurotransmitters for smooth muscles.
   c. Hormones and stretching affect smooth muscle contractions.
   d. With a given amount of energy, smooth muscle can maintain a contraction longer than skeletal muscle.
   e. Smooth muscles can change length without changing tautness.

9.6 CARDIAC MUSCLE (PAGE 309)

1. Cardiac muscle contracts for a longer time than skeletal muscle because transverse tubules supply extra calcium ions.
2. Intercalated discs connect the ends of adjacent cardiac muscle cells and hold the cells together.
3. A network of fibers contracts as a unit and responds to stimulation in an all-or-none manner.
4. Cardiac muscle is self-exciting, rhythmic, and remains refractory to further stimulation until a contraction is completed.

9.7 SKELETAL MUSCLE ACTIONS (PAGE 310)

1. Body movement
   a. Bones and muscles function together as levers.
   b. A lever consists of a rod, a fulcrum (pivot), a resistance, and a force that supplies energy.
   c. Parts of a first-class lever are arranged resistance–fulcrum–force; of a second-class lever, fulcrum–resistance–force; and of a third-class lever, resistance–force–fulcrum.
2. Origin and insertion
   a. The more movable end of attachment of a skeletal muscle to a bone is its insertion, and the less movable end is its origin.
   b. Some muscles have more than one origin or insertion.
3. Interaction of skeletal muscles
   a. Skeletal muscles function in groups.
   b. A prime mover is a muscle responsible for most of a movement; any muscle that causes a specific movement is an agonist for that movement; synergists work together to perform a specific movement; antagonists can resist a movement.
   c. Smooth movements depend upon antagonists giving way to the actions of agonists.

9.8 MAJOR SKELETAL MUSCLES (PAGE 313)

Muscle names often describe sizes, shapes, locations, actions, number of attachments, or direction of fibers.

1. Muscles of facial expression
   a. These muscles lie beneath the skin of the face and scalp and are used to communicate feelings through facial expression.
   b. They include the epicranius, orbicularis oculi, orbicularis oris, buccinator, zygomaticus major, zygomaticus minor, and platysma.
2. Muscles of mastication
   a. These muscles are attached to the mandible and are used in chewing.
   b. They include the masseter, temporalis, medial pterygoid, and lateral pterygoid.

3. Muscles that move the head and vertebral column
   a. Muscles in the neck and back move the head.
   b. They include the sternocleidomastoid, splenius capitis, semispinalis capitis, quadratus lumborum, and erector spinae.
4. Muscles that move the pectoral girdle
   a. Most of these muscles connect the scapula to nearby bones and are closely associated with muscles that move the arm.
   b. They include the trapezius, rhomboid major, rhomboid minor, levator scapulae, serratus anterior, and pectoralis minor.
5. Muscles that move the arm
   a. These muscles connect the humerus to various regions of the pectoral girdle, ribs, and vertebral column.
   b. They include the coracobrachialis, pectoralis major, teres major, latissimus dorsi, supraspinatus, deltoid, subscapularis, infraspinatus, and teres minor.
6. Muscles that move the forearm
   a. These muscles connect the radius and ulna to the humerus and pectoral girdle.
   b. They include the biceps brachii, brachialis, brachioradialis, triceps brachii, supinator, pronator teres, and pronator quadratus.
7. Muscles that move the hand
   a. These muscles arise from the distal end of the humerus and from the radius and ulna.
   b. They include the flexor carpi radialis, flexor carpi ulnaris, palmaris longus, flexor digitorum profundus, flexor digitorum superficialis, extensor carpi radialis longus, extensor carpi radialis brevis, extensor carpi ulnaris, and extensor digitorum.
   c. An extensor retinaculum forms sheaths for tendons of the extensor muscles.
8. Muscles of the abdominal wall
   a. These muscles connect the rib cage and vertebral column to the pelvic girdle.
   b. They include the external oblique, internal oblique, transversus abdominis, and rectus abdominis.
9. Muscles of the pelvic outlet
   a. These muscles form the floor of the pelvic cavity and fill the space of the pubic arch.
   b. They include the levator ani, coccygeus, superficial transversus perinei, bulbospongiosus, ischiocavernosus, and sphincter urethrae.
10. Muscles that move the thigh
   a. These muscles are attached to the femur and to some part of the pelvic girdle.
   b. They include the psoas major, iliacus, gluteus maximus, gluteus medius, gluteus minimus, piriformis, tensor fasciae latae, pectineus, adductor brevis, adductor longus, adductor magnus, and gracilis.
11. Muscles that move the leg
   a. These muscles connect the tibia or fibula to the femur or pelvic girdle.
   b. They include the biceps femoris, semitendinosus, semimembranosus, sartorius, rectus femoris, vastus lateralis, vastus medialis, and vastus intermedius.
12. Muscles that move the foot
   a. These muscles attach the femur, tibia, and fibula to various bones of the foot.
   b. They include the tibialis anterior, fibularis tertius, extensor digitorum longus, extensor hallucis longus, gastrocnemius, soleus, plantaris, flexor digitorum longus, tibialis posterior, and fibularis longus.
   c. Retinacula form sheaths for tendons passing to the foot.

9.9 LIFE-SPAN CHANGES (PAGE 341)

1. Beginning in one's forties, supplies of ATP, myoglobin, and creatine phosphate begin to decline.
2. By age eighty, muscle mass may be halved. Reflexes slow. Adipose cells and connective tissue replace some muscle tissue.
3. Exercise is beneficial in maintaining muscle function.

CHAPTER ASSESSMENTS

PART A

9.1 Introduction

1 List three outcomes of muscle actions. (p. 293)

9.2 Structure of a Skeletal Muscle

2 Describe the difference between a tendon and an aponeurosis. (p. 293)

3 Describe how connective tissue is part of the structure of a skeletal muscle. (p. 294)

4 Distinguish among deep fascia, subcutaneous fascia, and subserous fascia. (p. 295)

5 Identify the major parts of a skeletal muscle fiber and describe the functions of each. (p. 295)

9.3 Skeletal Muscle Contraction

6 Describe the neuromuscular junction. (p. 298)

7 A neurotransmitter ______________. (p. 297)
   a. binds actin filaments, causing them to slide
   b. diffuses across a synaptic cleft from a neuron to a muscle cell
   c. transports ATP across the synaptic cleft
   d. breaks down acetylcholine at the synapse
   e. is a contractile protein in the muscle fiber

8 Describe the neural control of skeletal muscle contraction. (p. 298)

9 Identify the major events that occur during skeletal muscle fiber contraction. (p. 299)

10 Explain how ATP and creatine phosphate function in skeletal muscle fiber contraction. (p. 302)
11 Describe how oxygen is supplied to skeletal muscle. (p. 302)
12 Describe how oxygen debt may develop. (p. 303)
13 Explain how a muscle may become fatigued, and how a person's physical condition may affect tolerance to fatigue. (p. 304)

9.4 Muscular Responses
14 Define *threshold stimulus.* (p. 304)
15 Distinguish between a twitch and a sustained contraction. (p. 304)
16 Define *motor unit* and explain how the number of fibers in a unit affects muscular contractions. (p. 306)
17 Which of the following describes addition of muscle fibers to take part in a contraction? (p. 306)
a. summation
b. recruitment
c. tetany
d. twitch
e. relaxation
18 Explain how a skeletal muscle can be stimulated to produce a sustained contraction. (p. 306)
19 Distinguish between a complete tetanic contraction and muscle tone. (p. 306)
20 Distinguish between concentric and eccentric contractions, and explain how each is used in body movements. (p. 307)
21 Distinguish between fast- and slow-twitch muscle fibers. (p. 307)

9.5 Smooth Muscle
22 Distinguish between multiunit smooth muscle and visceral smooth muscle. (p. 308)
23 Define *peristalsis* and explain its function. (p. 309)
24 Compare the characteristics of skeletal and smooth muscle fiber contractions. (p. 309)

9.6 Cardiac Muscle
25 Compare the characteristics of skeletal and cardiac muscle fiber contractions. (p. 309)

9.7 Skeletal Muscle Actions
26 Describe a lever, and explain how its parts may be arranged to form first-class, second-class, and third-class levers. (p. 310)
27 Explain how limb movements function as levers. (p. 311)
28 Distinguish between a muscle's origin and its insertion. (p. 312)
29 Define *prime mover, agonist, synergist,* and *antagonist.* (p. 312)

PART B

9.8 Major Skeletal Muscles
30 Match the muscle with its description or action. (pp. 314–341)

(1) buccinator
(2) epicranius
(3) lateral pterygoid
(4) platysma
(5) rhomboid major
(6) splenius capitis
(7) temporalis
(8) zygomaticus major
(9) biceps brachii
(10) brachialis
(11) deltoid
(12) latissimus dorsi
(13) pectoralis major
(14) pronator teres
(15) teres minor
(16) triceps brachii
(17) biceps femoris
(18) external oblique
(19) gastrocnemius
(20) gluteus maximus
(21) gluteus medius
(22) gracilis
(23) rectus femoris
(24) tibialis anterior

A. inserted on the coronoid process of the mandible
B. draws the corner of the mouth upward
C. can raise and adduct the scapula
D. can pull the head into an upright position
E. consists of two parts—the frontalis and the occipitalis
F. compresses the cheeks
G. extends over the neck from the chest to the face
H. pulls the jaw from side to side
I. primary extensor of the elbow
J. pulls the shoulder back and downward
K. abducts the arm
L. rotates the arm laterally
M. pulls the arm forward and across the chest
N. rotates the arm medially
O. strongest flexor of the elbow
P. strongest supinator of the forearm
Q. inverts the foot
R. a member of the quadriceps femoris group
S. a plantar flexor of the foot
T. compresses the contents of the abdominal cavity
U. largest muscle in the body
V. a hamstring muscle
W. adducts the thigh
X. abducts the thigh

PART C

31 Label as many muscles as you can identify in these photos of a model whose muscles are enlarged by exercise. Describe the action of each muscle identified. (pp. 314–341)

9.9 Life-Span Changes

32 Describe three aging-related changes in the muscular system. (p. 341)

33 Explain the benefits of exercise for maintaining muscular health while aging. (p. 341)

INTEGRATIVE ASSESSMENTS / CRITICAL THINKING

OUTCOMES 7.11, 9.8

1. Several important nerves and blood vessels course through the muscles of the gluteal region. To avoid the possibility of damaging such parts, intramuscular injections are usually made into the lateral, superior portion of the gluteus medius. What landmarks would help you locate this muscle in a patient?

OUTCOMES 9.2, 9.3

2. Millions of people take drugs called statins to lower serum cholesterol levels. In a small percentage of people taking these drugs, muscle pain, termed myopathy, is an adverse effect. In a small percentage of these individuals, the condition progresses to rhabdomyolysis, in which the sarcolemma breaks down.
   a. Describe the structure and state the function of the sarcolemma.
   b. Physicians can measure a patient's levels of creatine phosphokinase to track the safety of using a statin. Enzyme levels that exceed 10 times normal indicate possible rhabdomyolysis. Explain what this elevated enzyme level indicates about the physiology of the muscle cell.
   c. Explain why a dusky, dark color in the urine, resulting from the presence of myoglobin, also indicates muscle breakdown.

OUTCOMES 9.2, 9.3, 9.4

3. What steps might be taken to minimize atrophy of skeletal muscles in patients confined to bed for prolonged times?

OUTCOME 9.3

4. As lactic acid and other substances accumulate in an active muscle, they stimulate pain receptors, and the muscle may feel sore. How might the application of heat or substances that dilate blood vessels help relieve such soreness?

OUTCOMES 9.3, 9.4, 9.6

5. Why do you think athletes generally perform better if they warm up by exercising lightly before a competitive event?

OUTCOMES 9.3, 9.4, 9.7

6. Following an injury to a nerve, the muscles it supplies with motor nerve fibers may become paralyzed. How would you explain to a patient the importance of moving the disabled muscles passively or contracting them with electrical stimulation?

OUTCOMES 9.4, 9.8

7. Following childbirth, a woman may lose urinary control (incontinence) when sneezing or coughing. Which muscles of the pelvic floor should be strengthened by exercise to help control this problem?