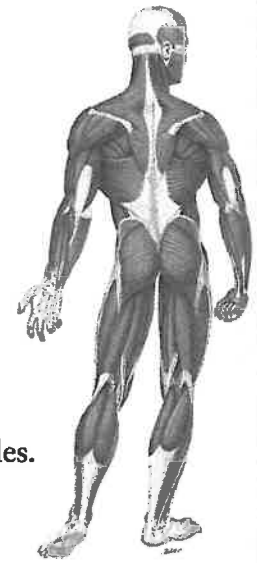
chapter 8

THE MUSCULAR SYSTEM



did you know? ***Strength training exercise results not only in stronger muscles, but in many other health benefits as well. Strength training helps to increase bone strength, increasing the deposition of bone minerals in young adults and helping to prevent, or at least slow, their loss in later life. By increasing muscle mass, strength training raises resting metabolic rate, the amount of energy expended at rest, so you can eat more food without gaining weight. Strength training helps to prevent back injury and injury from participation in sports and other physical activities. Psychological benefits include reductions in feelings of stress and fatigue.***

Focus on Wellness, page 190

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Movements such as throwing a ball, biking, and walking require an interaction between bones and muscles. To understand how muscles produce different movements, you will learn where the muscles attach on individual bones and the types of joints acted on by the contracting muscles. The bones, muscles, and joints together form an integrated system called the ***musculoskeletal system***. The scientific study of muscles is known as ***myology*** (mī-OL-ō-jē; *my-* = muscle; *-logy* = study of). The branch of medical science concerned with the prevention or correction of disorders of the musculoskeletal system is called ***orthopedics*** (or′-thō-PĒ-diks; *ortho-* = correct; *pedi* = child).

looking back to move ahead . . .

- **Muscular Tissue (page 90)**
- **Adenosine Triphosphate (page 38)**
- **Divisions of the Skeletal System (page 124)**
- **Joints (page 157)**
- **Types of Movements at Synovial Joints (page 160)**

OVERVIEW OF MUSCULAR TISSUE

OBJECTIVE • Describe the types and functions of muscular tissue.

Types of Muscular Tissue

Muscular tissue constitutes about 40% to 50% of the total body weight and is composed of highly specialized cells. Recall from Chapter 4 that the three types of muscular tissue are skeletal, cardiac, and smooth. As its name suggests, most ***skeletal muscle tissue*** is attached to bones and moves parts of the skeleton. It is ***striated***; that is, *striations*, or alternating light and dark bands, are visible under a microscope. Because skeletal muscle can be made to contract and relax by conscious control, it is ***voluntary***. Due to the presence of a small number of cells that can undergo cell division, skeletal muscle has a limited capacity for regeneration.

Cardiac muscle tissue, found only in the heart, forms the bulk of the heart wall. The heart pumps blood through blood vessels to all parts of the body. Like skeletal muscle tissue, cardiac muscle tissue is ***striated***. However, unlike skeletal muscle tissue, it is ***involuntary***: Its contractions are not under conscious control. Cardiac muscle can regenerate under certain conditions. This will be explained in Chapter 15.

Smooth muscle tissue is located in the walls of hollow internal structures, such as blood vessels, airways, the stomach, and the intestines. It participates in internal processes such as digestion and the regulation of blood pressure. Smooth muscle is ***nonstriated*** (lacks striations) and ***involuntary*** (not under conscious control). Although smooth muscle tissue has considerable capacity to regenerate when compared with other muscle tissues, this capacity is limited when compared to other types of tissues, for example, epithelium.

Functions of Muscular Tissue

Through sustained contraction or alternating contraction and relaxation, muscular tissue has five key functions: producing body movements, stabilizing body positions, regulating organ volume, moving substances within the body, and generating heat.

1. **Producing body movements.** Body movements such as walking, running, writing, or nodding the head rely on the integrated functioning of skeletal muscles, bones, and joints.
2. **Stabilizing body positions.** Skeletal muscle contractions stabilize joints and help maintain body positions, such as standing or sitting. Postural muscles contract continuously when a person is awake; for example, sustained contractions of your neck muscles hold your head upright.
3. **Regulating organ volume.** Sustained contractions of ringlike bands of smooth muscles called *sphincters* prevent outflow of the contents of a hollow organ. Temporary storage of food in the stomach or urine in the urinary bladder is possible because smooth muscle sphincters close off the outlets of these organs.
4. **Moving substances within the body.** Cardiac muscle contractions pump blood through the body's blood vessels. Contraction and relaxation of smooth muscle in the walls of blood vessels helps adjust their diameter and thus regulate blood flow. Smooth muscle contractions also move food and other substances through the gastrointestinal tract, push gametes (sperm and oocytes) through the reproductive system, and propel urine through the urinary system. Skeletal muscle contractions aid the return of blood to the heart.
5. **Producing heat.** As muscular tissue contracts, it produces heat. Much of the heat released by muscles is used to maintain normal body temperature. Involuntary contractions of skeletal muscle, known as shivering, can help warm the body by greatly increasing the rate of heat production.

■ CHECKPOINT

1. What features distinguish the three types of muscular tissue?
2. What are the general functions of muscular tissue?

SKELETAL MUSCLE TISSUE

OBJECTIVES • Explain the relation of connective tissue components, blood vessels, and nerves to skeletal muscles.

• Describe the histology of a skeletal muscle fiber.

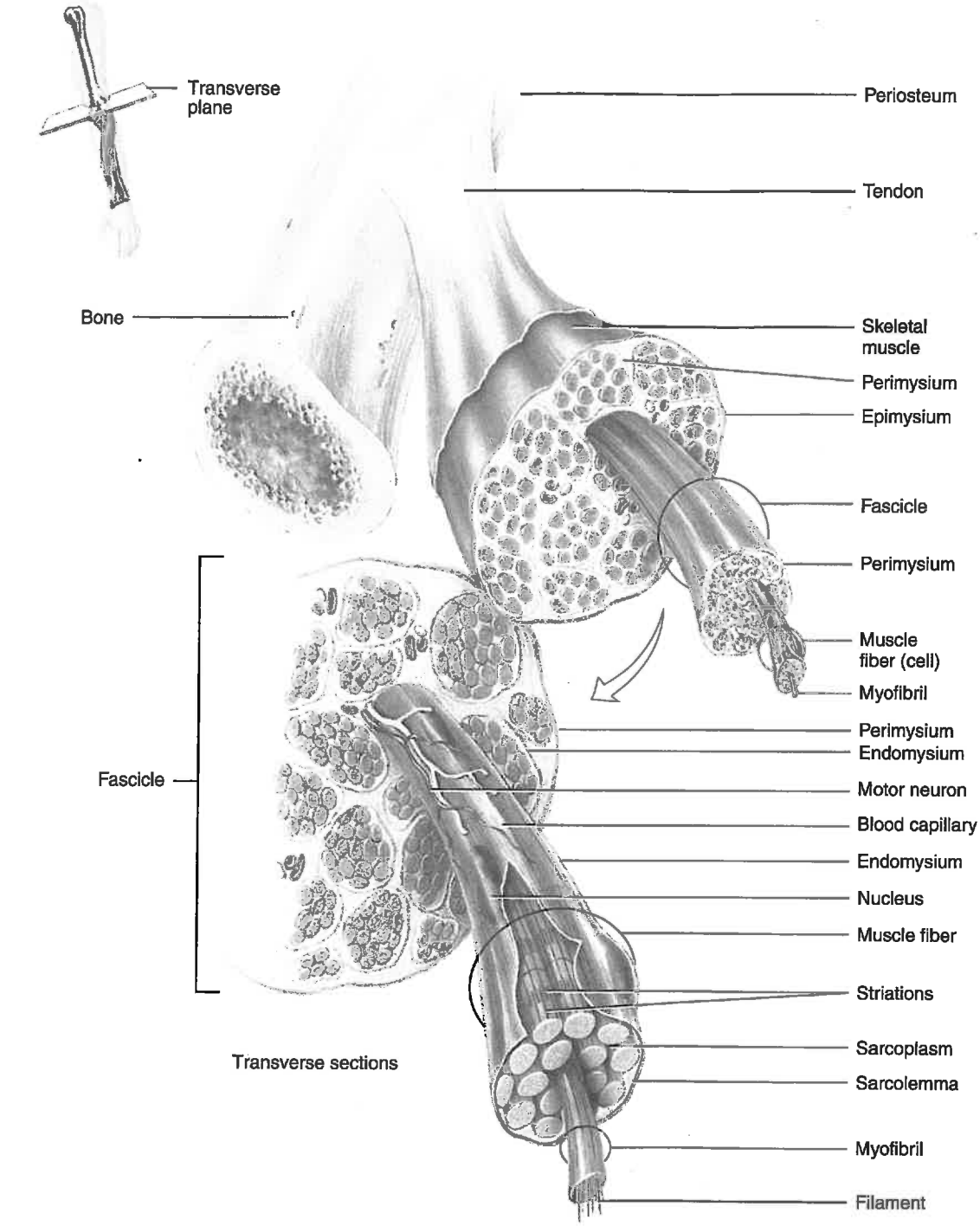
Each skeletal muscle is a separate organ composed of hundreds to thousands of cells, which are called ***muscle fibers*** because of their elongated shapes. Connective tissues surround muscle fibers and whole muscles, and blood vessels and nerves penetrate muscles.

Connective Tissue Components

Several connective tissue coverings are associated with skeletal muscle (Figure 8.1). The entire muscle is wrapped in ***epimysium*** (ep′-i-MĪZ-ē-um; *epi-* = upon). ***Perimysium*** (per′-i-MĪZ-ē-um; *peri-* = around) surrounds bundles of 10 to 100 or more muscle fibers called ***fascicles*** (FAS-i-kuls = little bundle). Finally, ***endomysium*** (en′-dō-MĪZ-ē-um; *endo-* = within) wraps each individual muscle fiber. Epimysium, perimysium, and endomysium extend beyond the muscle as a ***tendon***—a cord of dense regular connective tissue composed of parallel bundles of collagen fibers. Its

Figure 8.1 Organization of skeletal muscle and its connective tissue coverings.

A skeletal muscle consists of individual muscle fibers (cells) bundled into fascicles and surrounded by three connective tissue layers.



Functions of Muscles

1. Produces body motions.
2. Stabilizes body positions.
3. Regulates organ volume.
4. Moves substances within the body.
5. Produces heat.

Starting with the connective tissue that surrounds an individual muscle fiber (cell) and working toward the outside, list the connective tissue layers in order.

function is to attach a muscle to a bone. An example is the calcaneal (Achilles) tendon of the gastrocnemius muscle (see Figure 8.24a).

Nerve and Blood Supply

Skeletal muscles are well supplied with nerves and blood vessels (Figure 8.1), both of which are directly related to contraction, the chief characteristic of muscle. Muscle contraction also requires a good deal of ATP and therefore large amounts of nutrients and oxygen for ATP synthesis. Moreover, the waste products of these ATP-producing reactions must be eliminated. Thus, prolonged muscle action depends on a rich blood supply to deliver nutrients and oxygen and to remove wastes.

Generally, an artery and one or two veins accompany each nerve that penetrates a skeletal muscle. Within the endomysium, microscopic blood vessels called capillaries are distributed so that each muscle fiber is in close contact with one or more capillaries. Each skeletal muscle fiber also makes contact with the terminal portion of a neuron.

Histology

Microscopic examination of a skeletal muscle reveals that it consists of thousands of elongated, cylindrical cells called ***muscle fibers*** arranged parallel to one another (Figure 8.2a). Each muscle fiber is covered by a plasma membrane called the ***sarcolemma*** (*sarco-* = flesh; *-lemma* = sheath). ***Transverse tubules (T tubules)*** tunnel in from the surface toward the center of each muscle fiber. Multiple nuclei lie at the periphery of the fiber, next to the sarcolemma. The muscle fiber's cytoplasm, called ***sarcoplasm***, contains many mitochondria that produce large amounts of ATP during muscle contraction. Extending throughout the sarcoplasm is ***sarcoplasmic reticulum*** (sar′-kō-PLAZ-mik re-TIK-ū-lum), a network of fluid-filled membrane-enclosed tubules (similar to smooth endoplasmic reticulum) that stores calcium ions required for muscle contraction. Also in the sarcoplasm are numerous molecules of ***myoglobin*** (mī′-ō-GLŌ-bin), a reddish pigment similar to hemoglobin in blood. In addition to the characteristic color it lends to skeletal muscle, myoglobin stores oxygen until it is needed by mitochondria to generate ATP.

Extending along the entire length of the muscle fiber are cylindrical structures called ***myofibrils***. Each myofibril, in turn, consists of two types of protein filaments called ***thin filaments*** and ***thick filaments*** (Figure 8.2b), which do not extend the entire length of a muscle fiber. Filaments overlap in specific patterns and form compartments called ***sarcomeres*** (*-meres* = parts), the basic functional units of striated muscle fibers (Figure 8.2b, c). Sarcomeres are separated from one another by zig-zagging zones of dense protein material called ***Z discs***. Within each sarcomere a darker area, called the ***A band***, extends the entire length of the thick filaments. At the center of each A band is a narrow ***H zone***, which contains only the thick filaments. At both ends of the A band, thick and thin filaments overlap. A lighter-colored area to either side of the A band, called the ***I band***, contains the rest of the thin filaments but no thick filaments. Each I band extends into two sarcomeres, divided in half by a Z disc (see Figure 8.4a). The alternating darker A bands and lighter I bands give the muscle fiber its striated appearance.

Thick filaments are composed of the protein ***myosin***, which is shaped like two golf clubs twisted together (Figure 8.3a on page 177). The *myosin tails* (golf club handles) are arranged parallel to each other, forming the shaft of the thick filament. The heads of the golf clubs project outward from the surface of the shaft. These projecting heads are referred to as *myosin heads*.

Thin filaments are anchored to the Z discs. Their main component is the protein ***actin***. Individual actin molecules join to form an actin filament that is twisted into a helix (Figure 8.3b). Each actin molecule contains *a myosin-binding site*, where a myosin head can attach. The thin filaments contain two other proteins, ***tropomyosin*** and ***troponin***. In a relaxed muscle, myosin is blocked from binding to actin because strands of tropomyosin cover the *myosin-binding sites* on actin. The tropomyosin strands, in turn, are held in place by troponin molecules.

Muscular atrophy (A-trō-fē; *a-* = without, *-trophy* = nourishment) is a wasting away of muscles. Individual muscle fibers decrease in size because of progressive loss of myofibrils. The atrophy that occurs if muscles are not used is termed *disuse atrophy*. Bedridden individuals and people with casts experience disuse atrophy because the number of nerve impulses to inactive muscle is greatly reduced. If the nerve supply to a muscle is disrupted or cut, the muscle undergoes *denervation atrophy*. In about 6 months to 2 years, the muscle will be one-quarter of its original size, and the muscle fibers will be replaced by fibrous connective tissue. The transition to connective tissue, when complete, cannot be reversed.

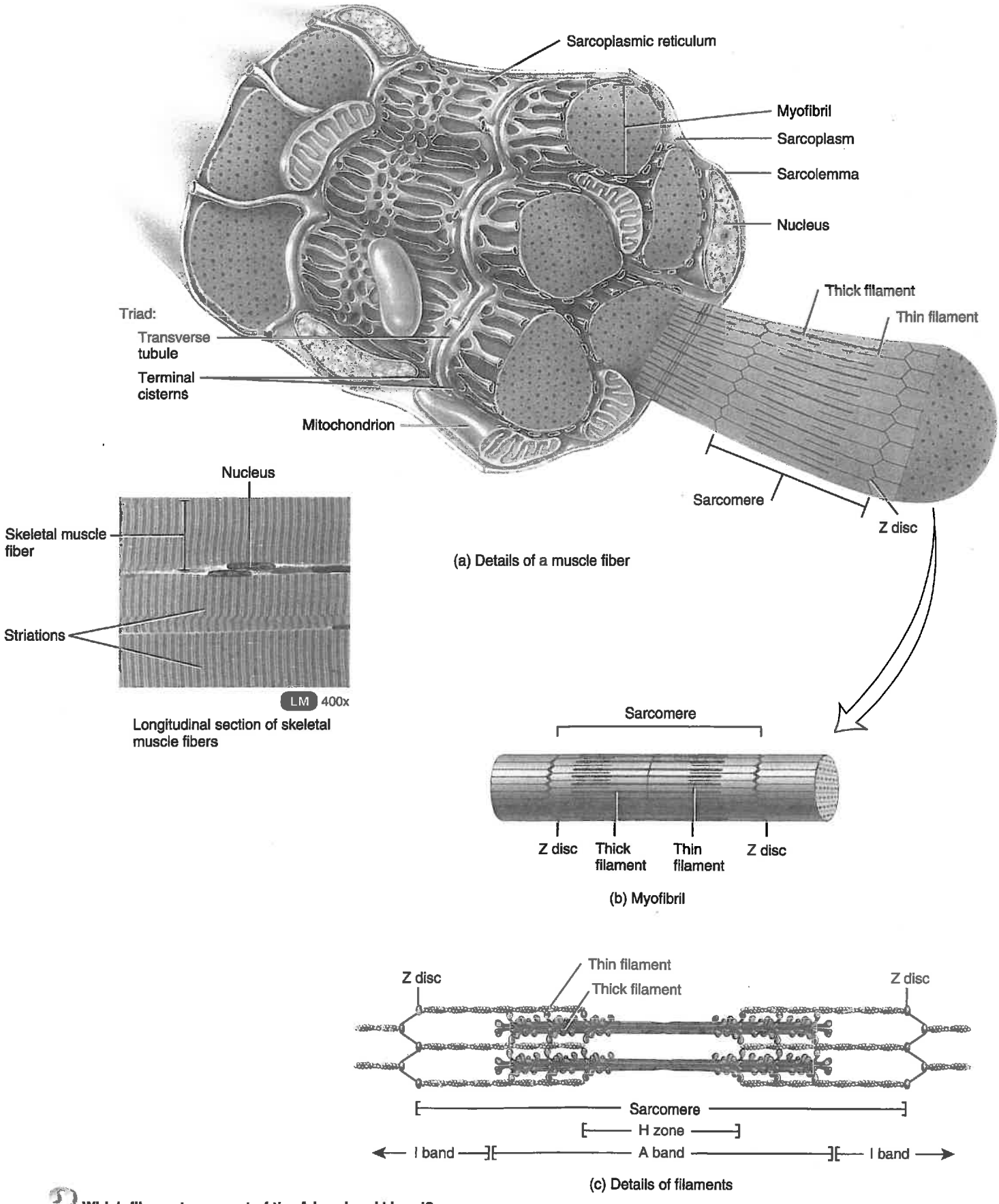
Muscular hypertrophy (hī-PER-trō-fē; *hyper-* = above or excessive) is an increase in muscle fiber diameter owing to the production of more myofibrils, mitochondria, sarcoplasmic reticulum, etc. It results from very forceful, repetitive muscular activity, such as strength training. Because hypertrophied muscles contain more myofibrils, they are capable of contractions that are more forceful.

CHECKPOINT

3. What type of connective tissue coverings are associat with skeletal muscle?
4. Why is a rich blood supply important for mus contraction?
5. What is a sarcomere? What does a sarcomere contain?

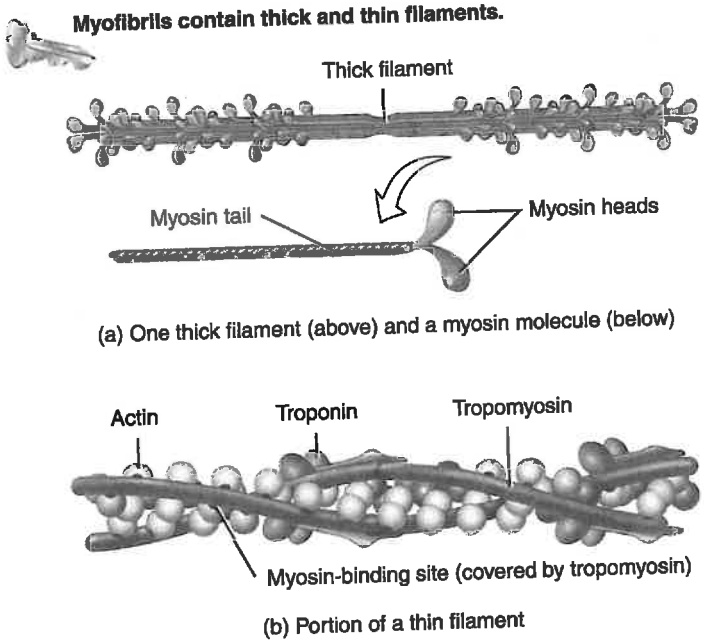
Figure 8.2 Organization of skeletal muscle from gross to molecular levels.

The structural organization of a skeletal muscle from macroscopic to microscopic is as follows: skeletal muscle, fascicle (bundle of muscle fibers), muscle fiber, myofibril, and thin and thick filaments.



Which filaments are part of the A band and I band?

Figure 8.3 Detailed structure of filaments. (a) About 300 myosin molecules compose a thick filament. The myosin tails all point toward the center of the sarcomere. (b) Thin filaments contain actin, troponin, and tropomyosin.



What proteins are present in the A band and in the I band?

CONTRACTION AND RELAXATION OF SKELETAL MUSCLE

OBJECTIVE • Explain how skeletal muscle fibers contract and relax.

Sliding-Filament Mechanism

During muscle contraction, myosin heads of the thick filaments pull on the thin filaments, causing the thin filaments to slide toward the center of a sarcomere (Figure 8.4a, b). As the thin filaments slide, the I bands and H zones become narrower (Figure 8.4b) and eventually disappear altogether when the muscle is maximally contracted (Figure 8.4c).

The thin filaments slide past the thick filaments because the myosin heads move like the oars of a boat, pulling on the actin molecules of the thin filaments. Although the sarcomere shortens because of the increased overlap of thin and thick filaments, the lengths of the thin and thick filaments do not change. The sliding of filaments and shortening of sarcomeres in turn cause the shortening of the muscle fibers. This process, the ***sliding-filament mechanism*** of muscle contraction, occurs only when the level of calcium ions (Ca^{2+}) is high enough and ATP is available, for reasons you will see shortly.

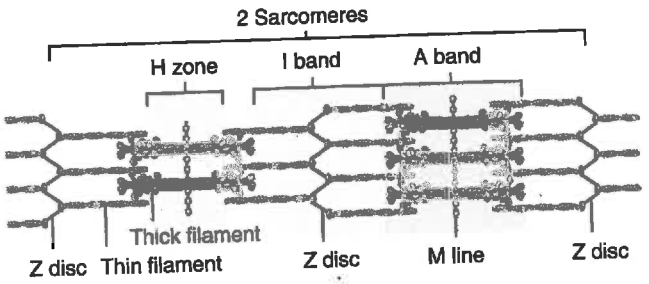
Neuromuscular Junction

Before a skeletal muscle fiber can contract, it must be stimulated by an electrical signal called a ***muscle action potential*** delivered by its neuron called a ***motor neuron***. A single motor neuron along with all the muscle fibers it stimulates is called a ***motor unit***. Stimulation of one motor neuron causes all the muscle fibers in that motor unit to contract at the same time. Muscles that control small, precise movements, such as the muscles that move the eyes, have 10 to 20 muscle fibers per motor unit. Muscles of the body that are responsible for large, powerful movements, such as the biceps brachii in the arm and gastrocnemius in the leg, have as many as 2000 to 3000 muscle fibers in some motor units.

As the *axon* (long process) of a motor neuron enters a skeletal muscle, it divides into branches called *axon terminals* that approach—but do not touch—the sarcolemma of a muscle fiber (Figure 8.5a, b). The ends of the axon terminals

Figure 8.4 Sliding-filament mechanism of muscle contraction.

During muscle contraction, thin filaments move inward toward the H zone.



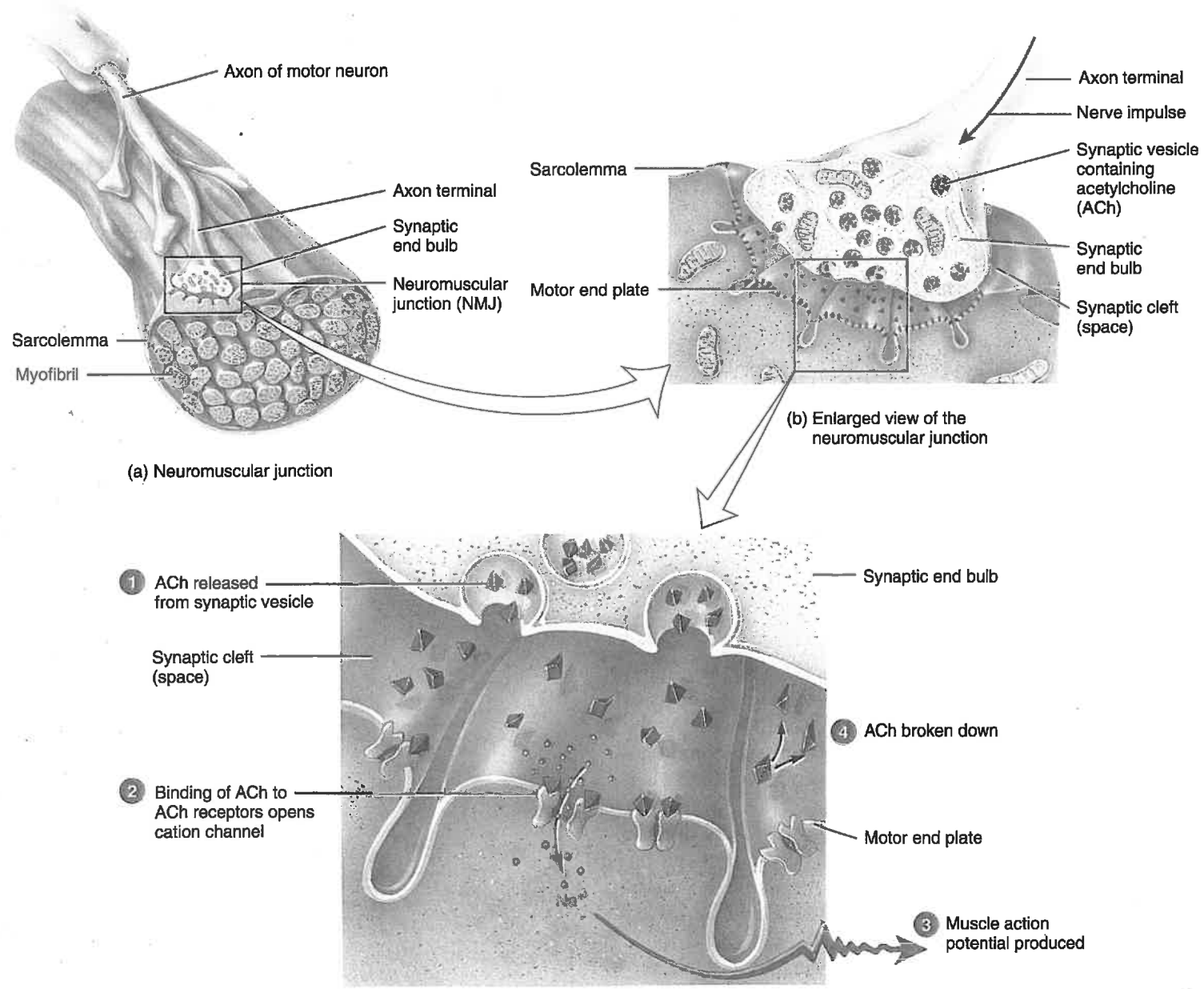
What happens to the I bands as muscle contracts? Do the lengths of the thick and thin filaments change during contracti

enlarge into swellings known as *synaptic end bulbs*, which contain *synaptic vesicles* filled with a chemical *neurotransmitter*. The region of the sarcolemma near the axon terminal is called the ***motor end plate***. The space between the axon terminal and sarcolemma is the ***synaptic cleft***. The synapse formed between the axon terminals of a motor neuron and the motor end plate of a muscle fiber is known as the ***neuromuscular junction (NMJ)***. At the NMJ, a motor neuron excites a skeletal muscle fiber in the following way (Figure 8.5c):

1. **Release of acetylcholine.** Arrival of the nerve impulse at the synaptic end bulbs triggers release of the neurotransmitter ***acetylcholine (ACh)*** (as′-e-til-KŌ-lēn). ACh then diffuses across the synaptic cleft between the motor neuron and the motor end plate.
2. **Activation of ACh receptors.** Binding of ACh to its receptor in the motor end plate opens ion channels that allow small cations, especially sodium ions (Na^+), to flow across the membrane.

Figure 8.5 Neuromuscular junction.

A neuromuscular junction includes the axon terminal of a motor neuron plus the motor end plate of a muscle fiber.



What is the motor end plate?

3. **Generation of muscle action potential.** The inflow of Na^+ (down its concentration gradient) generates a muscle action potential. The muscle action potential then travels along the sarcolemma and through the T tubules. Each nerve impulse normally elicits one muscle action potential. If another nerve impulse releases more acetylcholine, then steps 2 and 3 repeat. See chapter 9 for the details of nerve impulse generation.

4. **Breakdown of ACh.** The effect of ACh lasts only briefly because the neurotransmitter is rapidly broken down in the synaptic cleft by an enzyme called ***acetylcholinesterase (AChE)*** (as′-e-til-kō′-lin-ES-ter-ās).

Functioning of the NMJ can be altered by several toxins and drugs. Botulinum toxin, produced by the bacterium *Clostridium botulinum*, blocks release of ACh. As a result, muscle contraction does not occur. The bacteria proliferate in improperly canned foods, and their toxin is one of the most lethal chemicals known. A tiny amount can cause death by paralyzing the diaphragm, the main muscle that powers breathing. Yet, it is also the first bacterial toxin to be used as a medicine (Botox®). Injections of Botox into the affected muscles can help patients who have strabismus (crossed eyes) or blepharospasm (uncontrollable blinking). It is also used as a cosmetic treatment to relax muscles that cause facial wrinkles and to alleviate chronic back pain due to muscle spasms in the lumbar region.

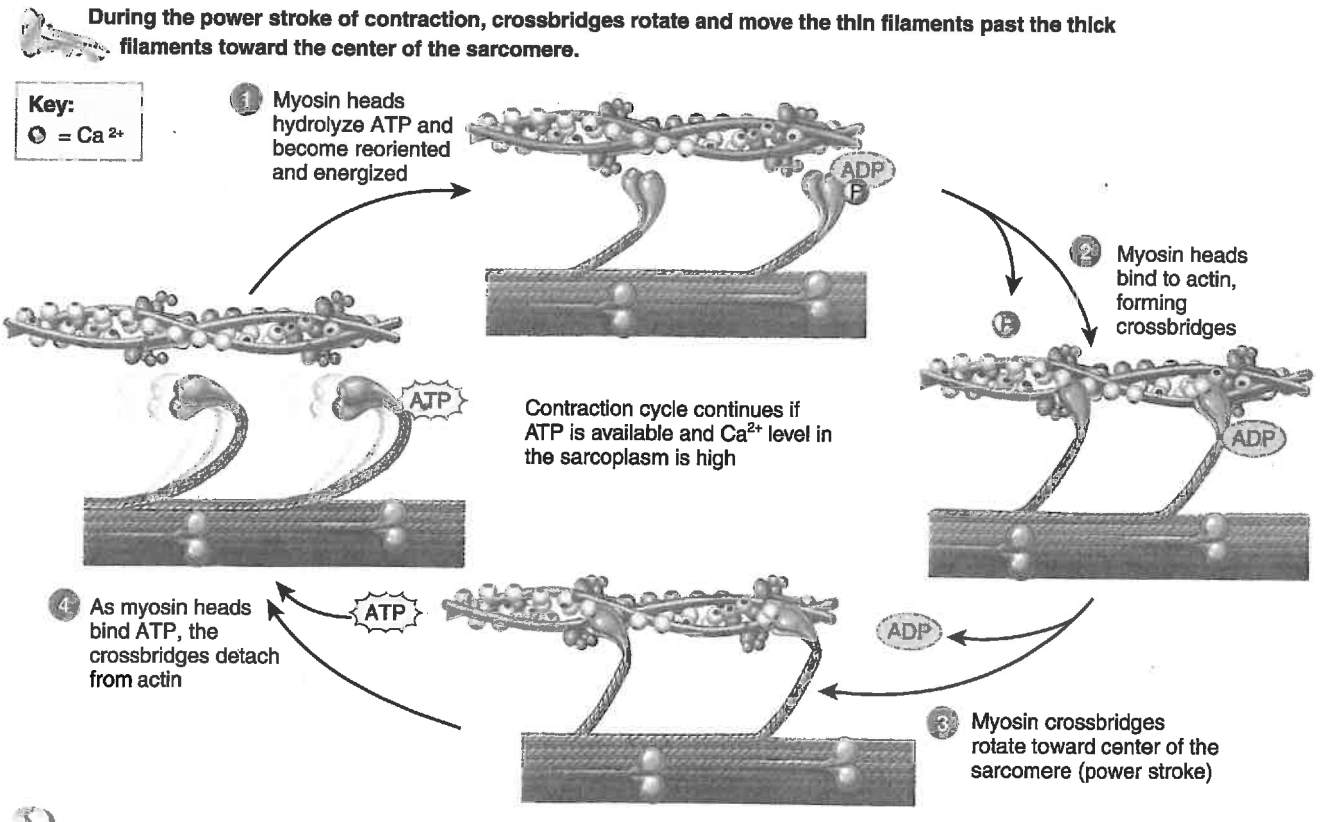
Physiology of Contraction

Both Ca^{2+} and energy, in the form of ATP, are needed for muscle contraction. When a muscle fiber is relaxed (not contracting), there is a low concentration of Ca^{2+} in the sarcoplasm because the membrane of the sarcoplasmic reticulum contains Ca^{2+} active transport pumps that continually transport Ca^{2+} from the sarcoplasm into the sarcoplasmic reticulum (see Figure 8.7 7). However, when a muscle action potential travels along the sarcolemma and into the transverse tubule system, Ca^{2+} release channels open (see Figure 8.7 4), allowing Ca^{2+} to escape into the sarcoplasm. The Ca^{2+} binds to troponin molecules in the thin filaments, causing the troponin to change shape. This change in shape releases the troponin–tropomyosin complex from the myosin-binding sites on actin (see Figure 8.7 5).

Once the myosin-binding sites are uncovered, the ***contraction cycle***—the repeating sequence of events that causes the filaments to slide—begins, as shown in Figure 8.6:

1. **Splitting ATP.** The myosin heads contain ATPase, an enzyme that splits ATP into ADP (adenosine diphos-

Figure 8.6 The contraction cycle. Sarcomeres shorten through repeated cycles in which the myosin heads (crossbridges) attach to actin, rotate, and detach.



What causes crossbridges to detach from actin?

phate) and P (a phosphate group). This splitting reaction transfers energy to the myosin head, although ADP and P remain attached to it.

2. **Forming crossbridges.** The energized myosin heads attach to the myosin-binding sites on actin, and release the phosphate groups. When myosin heads attach to actin during contraction, they are referred to as ***crossbridges***.
3. **Power stroke.** After the crossbridges form, the ***power stroke*** occurs. During the power stroke, the crossbridge rotates or swivels and releases the ADP. The force produced as hundreds of crossbridges swivel slides the thin filament past the thick filament toward the center of the sarcomere.
4. **Binding ATP and detaching.** At the end of the power stroke, the crossbridges remain firmly attached to actin. When they bind another molecule of ATP, the myosin heads detach from actin.

As the myosin ATPase again splits ATP, the myosin head is reoriented and energized, ready to combine with another myosin-binding site farther along the thin filament. The contraction cycle repeats as long as ATP and Ca^{2+} are available in the sarcoplasm. At any one instant, some of the myosin heads are attached to actin, forming crossbridges and generating force, and other myosin heads are detached from actin and getting ready to bind again. During a maximal contraction, the sarcomere can shorten by as much as half its resting length.

After a person dies, Ca^{2+} begins to leak out of the sarcoplasmic reticulum and binds to troponin, causing the thin filaments to slide. ATP production has ceased, however, so the crossbridges cannot detach from actin. The resulting stiffness of the muscles is termed **rigor mortis**, rigidity of death. It begins 3–4 hours after death, lasts about 24 hours, and then disappears as enzymes from lysozymes digest crossbridges.

Relaxation

Two changes permit a muscle fiber to relax after it has contracted. First, the neurotransmitter acetylcholine is rapidly broken down by the enzyme acetylcholinesterase (AChE). When nerve action potentials cease, release of ACh stops, and AChE rapidly breaks down the ACh already present in the synaptic cleft. This ends the generation of muscle action potentials, and the Ca^{2+} release channels in the sarcoplasmic reticulum membrane close.

Second, calcium ions are rapidly transported from the sarcoplasm into the sarcoplasmic reticulum. As the level of Ca^{2+} in the sarcoplasm falls, the tropomyosin–troponin complex slides back over the myosin-binding sites on actin. Once the myosin-binding sites are covered, the thin filaments slip back to their relaxed positions. Figure 8.7 summarizes the events of contraction and relaxation in a muscle fiber.

Muscle Tone

Even when a whole muscle is not contracting, a small number of its motor units are involuntarily activated to produce a sustained contraction of their muscle fibers. This process results in ***muscle tone*** (*tonos* = tension). To sustain muscle tone, small groups of motor units are alternately active and inactive in a constantly shifting pattern. Muscle tone keeps skeletal muscles firm, but it does not result in a contraction strong enough to produce movement. For example, the tone of muscles in the back of the neck keeps the head upright and prevents it from slumping forward on the chest. Recall that skeletal muscle contracts only after it is activated by acetylcholine released by nerve impulses in its motor neurons. Hence, muscle tone is established by neurons in the brain and spinal cord that excite the muscle's motor neurons. When the motor neurons serving a skeletal muscle are damaged or cut, the muscle becomes ***flaccid*** (FLAS-id = flabby), a state of limpness in which muscle tone is lost.

■ CHECKPOINT

6. Explain how a skeletal muscle contracts and relaxes.
7. What is the importance of the neuromuscular junction?

METABOLISM OF SKELETAL MUSCLE TISSUE

OBJECTIVES • **Describe the sources of ATP and oxygen for muscle contraction.**

• **Define muscle fatigue and list its possible causes.**

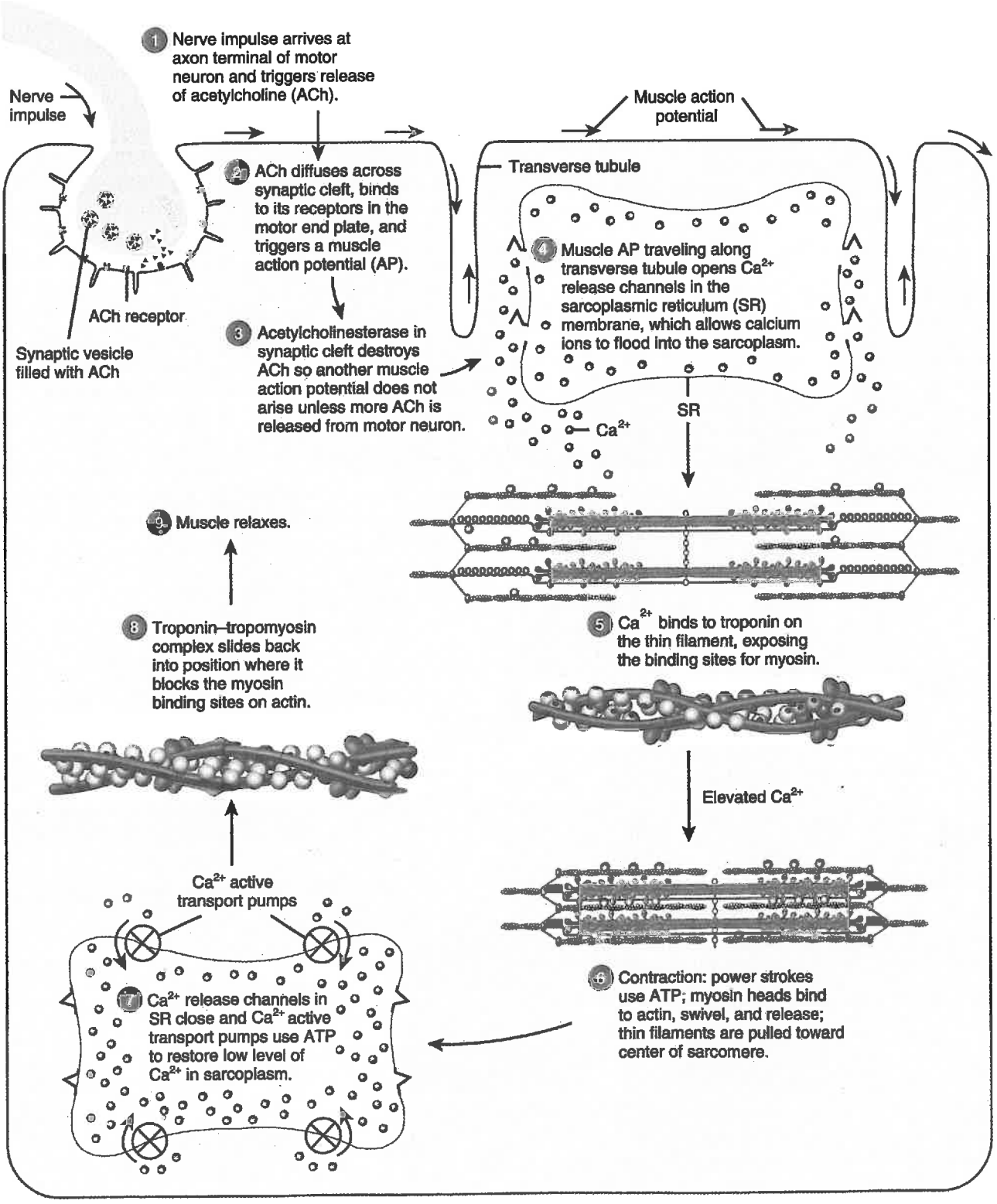
Energy for Contraction

Unlike most cells of the body, skeletal muscle fibers often switch between virtual inactivity, when they are relaxed and using only a modest amount of ATP, and great activity, when they are contracting and using ATP at a rapid pace. However, the ATP present inside muscle fibers is enough to power contraction for only a few seconds. If strenuous exercise is to continue, additional ATP must be synthesized. Muscle fibers have three sources for ATP production: (1) creatine phosphate, (2) anaerobic cellular respiration, and (3) aerobic cellular respiration.

While at rest, muscle fibers produce more ATP than they need. Some of the excess ATP is used to make ***creatine phosphate***, an energy-rich molecule that is unique to muscle

Figure 8.7 Summary of the events of contraction and relaxation in a skeletal muscle fiber.

Acetylcholine released at the neuromuscular junction triggers a muscle action potential, which leads to muscle contraction.



The power stroke occurs during which numbered step in this figure?