The Sarcomere

The sarcomere is the functional unit of the contractile system in muscle, and the events that take place in one sarcomere are duplicated in the others. Various sarcomeres build a myofibril, myofibrils build the muscle fiber, and muscle fibers build a muscle. The sarcomere is composed of thin filaments composed of two proteins, actin and myosin. Six other proteins have been identified that have a structural or physiologic purpose. The contractile unit of the entire myofibril is known as the sarcomere.

Gross Structure of Skeletal Muscle

Each of more than 430 voluntary muscles in the body consists of various layers of connective tissue. Figure 5-1 illustrates a cross section of a muscle consisting of thousands of muscle cells called muscle fibers (Fig. 5-1A and B). These multinucleated muscle fibers lie parallel to one another and are separated by the innermost layer of connective tissue, called the endomysium. As many as 150 fibers are arranged into bundles called fasciculi. Fasciculi are surrounded by perimysium, the next layer of connective tissue. The entire muscle is encased by the outermost layer of connective tissue, the epimysium. This connective tissue sheath tapers at the ends as it blends into and joins the intramuscular tissue sheaths forming the tendons. The tendons connect to the outermost covering of the bone, the periosteum. The force of muscle contraction is transmitted directly from the muscle's connective tissue to the point of attachment on the bone. Beneath the endomysium and surrounding each muscle fiber is a thin, elastic membrane, called the sarcolemma, enclosing the fiber's cellular contents. The aqueous protoplasm or sarcoplasm contains the contractile proteins, enzymes, fat and glycogen particles, the nuclei, and various specialized cellular organelles. Embedded in the sarcoplasm is an extensive network of interconnecting tubular channels known as the sarcoplasmic reticulum. This highly specialized system provides the cell with structural integrity and also serves important functions in muscular contractions.

Ultrastructure of Skeletal Muscle

The ultrastructure of skeletal muscle consists of different levels of subcellular organization (see Fig. 5-1). Each muscle fiber consists of small fibers called myofibrils (see Fig. 5-1C). Myofibrils are composed of even smaller threads called myofilaments (see Fig. 5-1D–F). The myofilaments are composed primarily of two proteins, actin and myosin. Six other proteins have been identified that have a structural or physiologic purpose. The contractile unit of the entire myofibril is known as the sarcomere.

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Therapeutic Exercise: Moving Toward Function

(approximately 5 nm in diameter) formulated from the protein actin and the thick filaments (approximately 15 nm in diameter) formulated from the protein myosin.

Figure 5-1C illustrates the structural pattern of myofila-
ments within a sarcomere. The lighter area is referred to as the I band and contains the portion of the thin filaments that do not overlap with the thick filaments. The darker zone is known as the A band and is the region where actin and myo-
sin overlap. The Z line bisects the I band and adheres to the sarcolemma to give the entire structure stability. The repeating unit between two Z lines represents the sarcomere. The actin and myosin filaments within the sarcomere are primarily involved in the mechanical process of muscular contraction and therefore in force development. Each myosin cross-
bridge is an independent force generator.

Actin-Myosin Orientation
Figure 5-2 illustrates the actin-myosin orientation within a sarcomere at resting and contracted lengths. Actin, the chief component of the thin filament, has the shape of a double helix and appears as two strands of beads spiraling around each other. Two additional proteins, troponin and tropomyosin, are important constituents of the actin helix because they appear to regulate the making and breaking of contacts between the actin and myosin filaments during contraction. Tropomyosin is a long polypeptide chain that lies in the grooves between the helices of actin. Troponin is a globular molecule attached at regular intervals to the tropomyosin (Fig. 5-3).

Intracellular Tubule System
The sarcoplasmic reticulum and transverse tubule (T-tubule) system within the muscle fiber can be seen in Fig. 5-4. The sarcoplasmic reticulum lies parallel to the myofibrils, whereas the T-tubule system runs perpendicular to the myofibril. The lateral end of the sarcoplasmic reticulum terminates in a saclike vesicle that stores calcium. The T-tubule system appears to function as a microtransportation network for spreading the action potential (i.e., wave of depolarization) from the fiber’s outer membrane inward to the deep regions of the cell.

Chemical and Mechanical Events During Contraction and Relaxation
The most widely held theory of muscle contraction is the sliding filament theory. According to this theory, active shortening of the sarcomere, and hence of muscle, results from the relative movement of the actin and myosin filaments past one another while retaining its original length.

Excitation-contraction is the physiologic mechanism whereby an electric discharge at the muscle initiates the chemical events that lead to contraction. When a muscle fiber is stimulated to contract, there is an immediate increase in the intracellular calcium concentration. Arrival of the action potential at the T-tubules causes calcium to be released from the lateral sacs of the sarcoplasmic reticulum. The inhibitory action of troponin (i.e., preventing actin-myosin interaction) ceases when calcium ions bind rapidly with troponin in the actin filaments. The globular head of the myosin cross-bridge provides the mechanical means for the actin and myosin filaments to slide past each other. During contraction, each cross-bridge undergoes many repeated but independent cycles of movement. Thus at any given moment only approximately half of the cross-bridges actively generate force and displacement, and when these detach, others take up the task so that shortening is maintained. Display 5-1 summarizes the events during excitation, contraction, and relaxation of the muscle.

Muscle Fiber Type
Skeletal muscle is not a simple homogenous group of fibers with similar metabolic and functional properties. Distinct fiber types have been identified and classified by their
**DISPLAY 5-1**  
Sequence of Events in Muscular Contraction

The following is a list of the main events in muscular contraction and relaxation. The sequence begins with the initiation of an action potential by the motor nerve. This impulse is propagated over the entire surface of the muscle fiber as the cell membrane becomes depolarized.

1. Depolarization of the T-tubules causes release of calcium from the lateral sacs of the sarcoplasmic reticulum.  
2. Calcium binds to the troponin-tropomyosin complex in the actin filaments, releasing the inhibition that prevented actin from combining with myosin.  
3. Actin combines with myosin-activated myosin ATPase, which splits ATP. The energy that is created produces movement of the cross-bridge, and tension is created.  
4. ATP binds to the myosin cross-bridge, breaking the actin-myosin bond and allowing the cross-bridge to dissociate from actin.  
5. Cross-bridge activation continues as long as the concentration of calcium remains high enough to inhibit the action of the troponin-tropomyosin system.  
6. When stimulation ceases, calcium moves back into the lateral sacs of the sarcoplasmic reticulum.  
7. Removal of calcium restores the inhibitory action of troponin-tropomyosin. In the presence of ATP, actin and myosin remain in the dissociated, relaxed state.

contractile and metabolic characteristics. Slow-twitch fibers, or type I fibers, are characterized by slow speed of contraction, low activity of myosin ATPase, and glycolytic capacity that is less well developed than that of their fast-twitch counterparts. Slow-twitch fibers are well suited for prolonged aerobic exercise.

Fast-twitch fibers are divided into fast oxidative-glycolytic, or type II A, and fast-glycolytic, or type IIB, fibers. Generally, fast-twitch fibers have a high activity level of myosin ATPase associated with their ability to generate energy rapidly for quick, forceful contractions. Fast oxidative-glycolytic fibers are a hybrid between slow-twitch and fast-glycolytic fibers. These fibers combine the ability to produce quick, forceful contractions and sustain them for longer than fast-glycolytic fibers (though not as long as slow-twitch fibers). Compared with fast oxidative-glycolytic fibers, the fast-glycolytic fibers possess a greater anaerobic potential. A third fast-twitch fiber, type IIC, has been identified. The type IIC fiber is normally a rare and undifferentiated fiber that may be involved in reinnervation or motor unit transformation.  

**Motor Unit**

The motor unit consists of the motor neuron, its axon, and the muscle fibers supplied by the motor neuron. The number of muscle fibers belonging to a single motor unit can vary from 5 to 10 to more than 100. As a general rule, small muscles responsible for precision tasks (e.g., intrinsic hand muscles) are composed of motor units supplying few muscle fibers, whereas trunk and proximal limb muscles contain motor units supplying a large number of muscle fibers.

Human motor units with the following characteristics tend to be classified as tonic motor units: long contraction times, low twitch tension, high resistance to fatigue, small-amplitude action potentials, and slow conduction velocities. Conversely, phasic motor units tend to be recruited at high levels of voluntary contraction, display short contraction times and high-twitch tensions, are not fatigue-resistant, and show large-amplitude action potentials and fast conduction velocities.

**Force Gradation**

Motor units are activated to increase force production or deactivated to decrease force production. Force gradation can be likened to a rheostat, through which more motor units are brought on line as the need for force increases or taken off line as the need for force decreases. Force increases can occur by increasing the rate of discharge (i.e., rate coding) or by graded recruitment of higher threshold motor units (i.e., size principle). Rate coding implies high-frequency discharge when high forces are needed, and low-frequency pulses are delivered when low forces are necessary.U The size principle states that, during activation of motor neurons, those with the smallest axons have the lowest thresholds and are recruited first, followed by larger cells with higher thresholds.

In most voluntary everyday contractions, slow (type I) motor units are the first to be recruited. With increasing power output, more fast (type II) units are activated. Trained persons can activate all the motor units in a large limb muscle during a static, maximal, voluntary contraction, whereas this is not possible for untrained persons. The fastest (type IIB) motor units are preferentially activated in fast corrective movements and reflexes. Explosive maximal contractions are thought to activate fast and slow motor units simultaneously.

Violations of the size principle do occur. Two departures occur through neural adaptations related to the specificity of velocity and movement pattern in strength training. High-threshold, fast-twitch motor units are preferentially activated during brief, rapid concentric actions in which the intent is to relax quickly. It has also been demonstrated that fast-twitch motor units are preferentially recruited in eccentric actions performed at moderate to high velocities.

**REFERENCES**