3.4 Skeletal Muscle Mechanics

Learning Objectives

- Contrast skeletal, cardiac, and smooth muscles
- Describe an isometric contraction
- Describe a muscle twitch
- Distinguish between slow-twitch and fast-twitch muscle fibers on the basis of their contractile behavior
- Define the motor unit
- Describe how recruitment increases muscle force
- Describe how a muscle responds to increased frequency of stimulation
- Define tetany
- Describe the size principle of motor unit recruitment
- Describe the relative importance of frequency coding versus population coding for grading muscle force
- Define the innervation ratio and explain how the size principle creates proportional control of muscle force
- Define passive and active tension and show how they vary with muscle length
- Define afterload
- Describe an isotonic contraction
- Draw the force—velocity curve for fast-twitch and slow-twitch muscles
- Show how power varies with velocity of contraction
- Distinguish among concentric, isometric, and eccentric contractions
- Describe muscle pinnation and how this contributes to muscle function
- Define muscle fatigue
- Describe Burke's system of muscle classification based on contractile properties

MUSCLES EITHER SHORTEN OR PRODUCE FORCE

The primary action of a muscle is **to contract**. Usually this word means to shorten, but physiologists often use it in a broader sense, meaning **to activate** the muscle. Activation of the muscles can produce force without actually shortening, as you might do when holding something really heavy. As we shall see later, there is a trade-off between shortening and producing force, and both originate from the same mechanism. In everyday motion, some muscle contractions occur while the mus-cle actually lengthens. These are called **eccentric** contractions.

MUSCLES PERFORM DIVERSE FUNCTIONS

Muscles that are connected to the skeleton are called **skeletal muscles**. Because they are connected to the bones via their tendons, these muscles transfer force to the skeleton and move one bone relative to another. Coordinated activation of muscles allows for the various movements of the joints (flexion and extension; abduction and adduction; protraction and retraction; elevation and depression; pronation and supination; medial rotation and lateral rotation; and circumduction). Skeletal muscles allow us to lift weights and to move ourselves from place to place. These muscles also include the tongue, the muscles that move the eyeballs, and the upper third of the esophagus. A secondary function of these skeletal muscles is the production of body heat. During vigorous exercise, the heat produced by the skeletal muscles raises body temperature and the excess heat must be removed from the body.

Other muscles surround hollow organs. These include the heart, urinary bladder, gallbladder, and uterus. Contraction of the muscles in the walls of these organs develops a tension in the walls and so develops pressure within the organ. Still other muscles are present in the long hollow tubes of the body. Contraction of the muscles in these tubes sets the diameter of a tube and thereby controls flow through it. Examples include the muscular sphincters of the gastrointestinal tract, the arterioles, the ureters, and the airways of the lungs. Contraction of the muscular layers of the intestine also propels material through the intestine.

MUSCLES ARE CLASSIFIED ACCORDING TO FINE STRUCTURE, NEURAL CONTROL, AND ANATOMICAL ARRANGEMENT

STRIATED MUSCLES HAVE STRIPES

Under the microscope, some muscles appear to have stripes running across them. These are said to be **striated** (from the Latin meaning channel or furrow). All of the skeletal muscle and cardiac muscle are striated.

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Muscles lacking stripes are called **smooth** muscles (Figure 3.4.1).

SKELETAL MUSCLES ARE USUALLY ACTIVATED VOLUNTARILY

Most skeletal muscles are normally activated by a motor neuron that resides in the anterior or ventral horn of the spinal cord. Commands for the activation of the motor neuron can come from sensory input, as in the spinal reflexes, or from the motor cortex in the cerebrum. These muscles are organized as **motor units**, with nerve fibers providing the signal for activation. In contrast, cardiac and visceral smooth muscles are intrinsically active and do not require neural initiation of activation. However, these muscles are innervated and their activity is modulated by nerves and sometimes by humoral factors. These different types of control are broadly classed as **voluntary** and **involuntary**. Breathing and blinking the eyelids are largely automatic events that occur involuntarily, but we can consciously suppress these activities for some time and we must be able to control breathing voluntarily in order to speak, sing, or swim. This chapter is devoted to voluntary skeletal muscles.
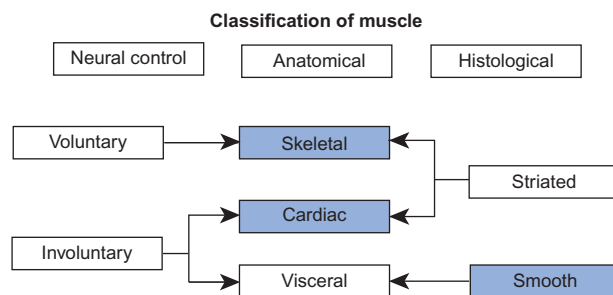

FIGURE 3.4.1 Classification of muscles can be based on control properties, anatomical properties, or the fine structure observed histologically. The preferred classification is that highlighted in the figure, which is a mixture of several classification schemes.

ISOMETRIC FORCE IS MEASURED WHILE KEEPING MUSCLE LENGTH CONSTANT

A muscle can be dissected free from its **origin** and **insertion** (the places where the tendons attach to the bones) and connected to a device to measure the force developed upon activation, as shown in Figure 3.4.2. Here the experimental setup measures force at a nearly constant length, and so these are called **isometric contractions** (from "iso," meaning "the same," and "metric" meaning "distance"). When a stimulus is turned on very briefly (3 ms), a single muscle contraction, called the **muscle twitch**, is recorded. Force rises and falls without muscle shortening. It takes some time for force to rise and generally a longer time for it to fall back to resting levels. When a **gastrocnemius** muscle of a rat is used, the twitch time is about 70 ms. When the **soleus** is used, the twitch time is over 150 ms. Muscles can be distinguished on the basis of their contractile properties, including their twitch times. The gastrocnemius is an example of a fast-twitch muscle; the soleus is a slow-twitch muscle.

The recording in Figure 3.4.2 also shows that the action potential on the muscle lasts only a few ms, whereas the twitch lasts much longer. The action potential is a **trigger** for the muscle contraction.

MUSCLE FORCE DEPENDS ON THE NUMBER OF *MOTOR UNITS* THAT ARE ACTIVATED

The stimulus applied to the nerve can be varied by increasing its voltage or changing its duration, delay, or frequency. When the voltage strength of the stimulus is gradually increased, the force of the twitch also increases until the force reaches a plateau, as shown in Figure 3.4.3. Why should muscle force depend on the voltage of the stimulus?
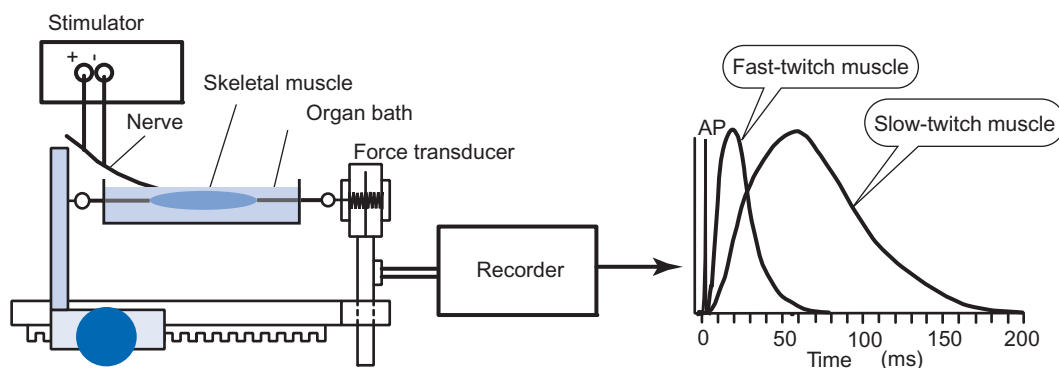

FIGURE 3.4.2 Experimental setup for measuring isometric tension in an isolated muscle. In this preparation, the nerve that usually activates the muscle is severed and action potentials on the motor nerve axon must be initiated by an external stimulator. The muscle is tied at one end to a rigid support and at the other end to a force transducer. When the muscle contracts, it pulls against a stiff spring located in the transducer. The transducer turns its slight movement into an electrical signal that can be recorded. Because the actual shortening of the spring, and its attached muscle, is extremely small, this contraction is called an isometric contraction. A single stimulation results in an action potential in the nerve and subsequently in the muscle that activates the muscle to produce a single contraction called a twitch. Different muscles differ markedly in the time course of force development and relaxation.
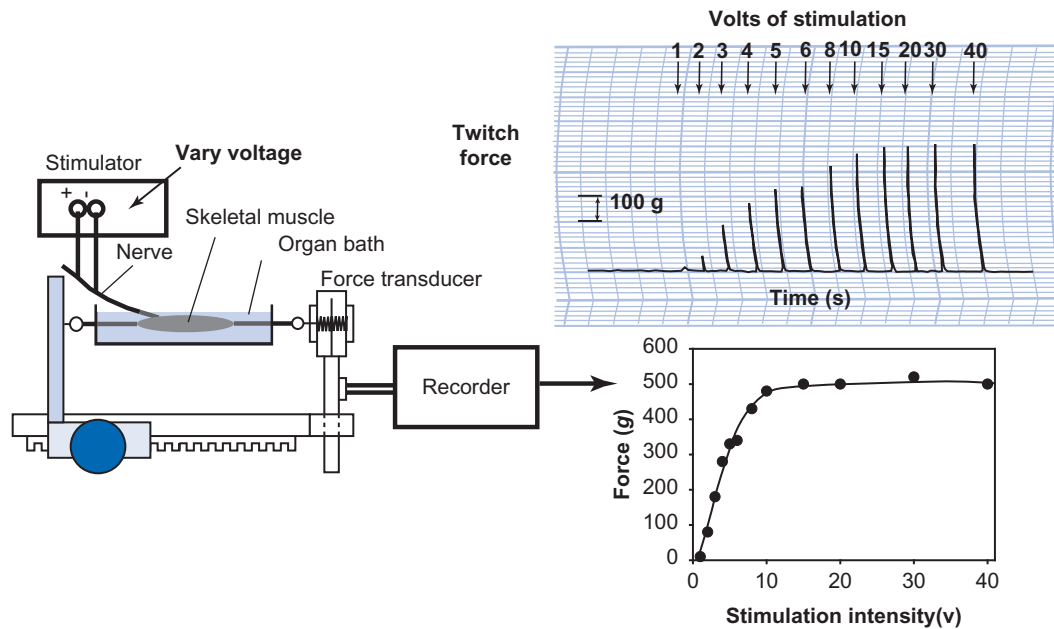
FIGURE 3.4.3 Increase in the muscle twitch with increased recruitment of motor fibers by increasing the strength of the external stimulus. Data obtained from electrical stimulation of the sciatic nerve serving the gastrocnemius muscle of the rat.
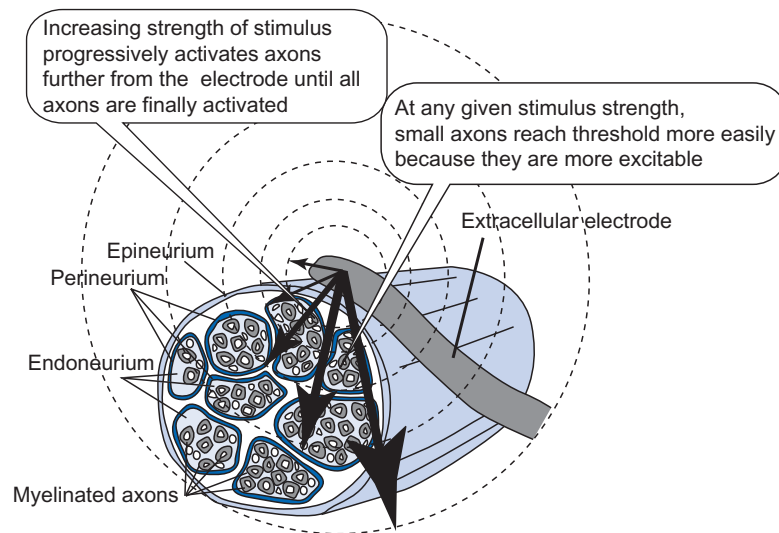

FIGURE 3.4.4 Intact nerve and the extracellular electrode that stimulates it. The whole nerve is a bundle of axons originating in either sensory or motor neurons. As the strength of stimulus increases, more axons are activated until, eventually, all axons in the nerve fire action potentials. Since each axon innervates a set of muscle fibers, called its motor unit, progressive activation of axons causes progressive increases in the number of activated muscle fibers, and progressive increases in the total force produced by the muscle. The smaller axons are more excitable, and they are activated first.

The motor nerve supplying the muscle is actually a bundle of axons from motor neurons carrying excitation to the muscle and sensory nerve fibers that return information to the central nervous system about the state of the muscle. The proportion of motor nerve axons within the bundle varies from 40% to 70% in different muscles, with the remaining being axons carrying sensory information. The motor axons come in two general types: small and large diameter axons (see Figure 3.4.4). The stimulus that we apply is an extracellular stimulus that depolarizes the axons by passing an inward current across their membranes. But the current from the extracellular electrode has many places to go, and most of the current does not go across the axon membrane. Thus higher voltages are necessary to depolarize all of the axons in the bundle. This is why volts are necessary for the external stimulus, when only a few millivolts of membrane depolarization are sufficient to initiate an action potential. Further, the different sized motor neuron axons differ in their rheobase—the amount of current for an infinite time that will bring the axons to threshold (see Figure 3.2.8). Increasing the stimulus
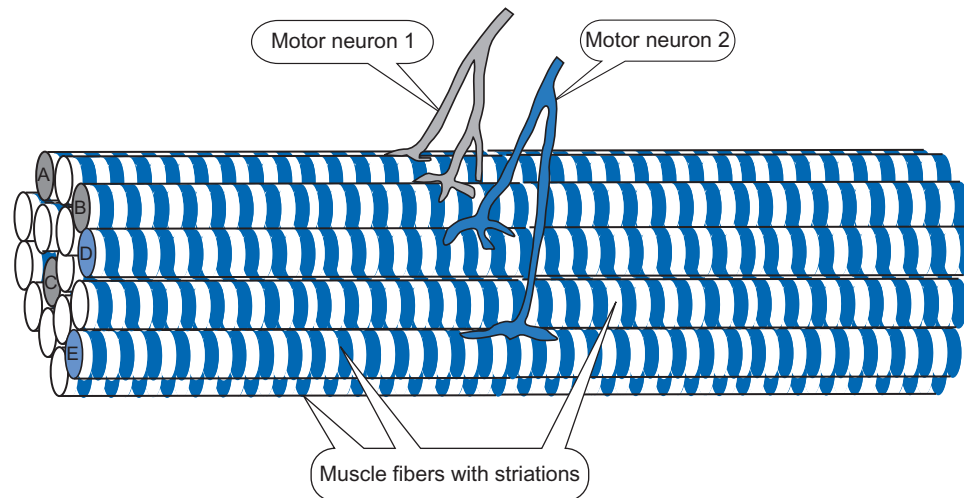
FIGURE 3.4.5 The motor unit consists of the motor neuron and all of the muscle fibers innervated by it. Here motor neuron 1 innervates fibers A, B, and C; motor neuron 2 innervates fibers D and E. When only motor neuron 1 fires an action potential, only fibers A, B, and C contribute to the force. When only motor neuron 2 fires an action potential, only fibers D and E contribute to the force developed by the muscle. When both motor neurons fire an action potential, all of the muscle fibers contribute to the force. Thus the force is greater when more motor units are recruited.

strength (voltage) increases the number of motor neurons that are activated, which increases the number of muscle fibers that are activated, which increases force. Each motor nerve branches and connects to a set of muscle fibers, making a neuromuscular junction with each of them. **The motor neuron and the set of muscle fibers it innervates make up a motor unit**. The entire muscle consists of a large number of muscle fibers that are each typically innervated by a single motor neuron making a junction in the middle of the muscle fiber. Motor neurons typically innervate more than one muscle fiber, but each muscle fiber is innervated by only one motor neuron. The motor unit is designed for 100% fidelity: each time the motor neuron is activated, all of its muscle fibers are subsequently activated. Thus motor units are indivisible quantal elements in all movements (see Figures 3.4.4 and 3.4.5).

The increase in force by activating increasing number of motor units is called **recruitment**. The nearly continuous variation in force from small to large forces means that this force is not all or none; it is **graded**. Although the gradation is fine, it is not really continuous because muscle fibers are activated in a discrete (as opposed to continuous) way. Because there are so many muscle fibers, the force appears to vary nearly continuously. It is important to note that the method of recruitment here, increasing the voltage of stimulation of the nerve, is *not physiological*. Ordinarily motor units are recruited through neuronal connections to the motor neurons, particularly by the activation of command signals originating from the primary motor cortex in the brain, located in the precentral gyrus (see Chapter 4.5). This area of the brain contains "upper" motor neurons that provided excitation to the "lower" motor neurons that are located in the ventral horn of the spinal cord and directly activate muscle fibers. The motor unit specifically refers to a lower motor neuron and the set of muscle fibers that it innervates. Which lower motor neurons

that are activated depends on the output of the primary motor cortex, along with modulating influences from other brain areas and from sensory information. The neural control of movement is discussed in Chapter 4.5.

THE *SIZE PRINCIPLE* STATES THAT MOTOR UNITS ARE RECRUITED IN THE ORDER OF THEIR SIZE

Large motor units are innervated by large motor neurons, and smaller motor units are innervated by smaller motor neurons. The small motor neurons are more excitable, so these are recruited first. This corresponds to our everyday experience. When trying to perform delicate movements that require dexterity but little force, control of muscle force must be fine. This is accomplished by recruiting small numbers of muscle fibers. When performing gross motor movements involving a lot of force, the increments of force are large and we recruit successively larger motor units. The recruitment of motor units in order of their sizes is accomplished through other nerves that make connections to the lower motor neurons.

MUSCLE FORCE CAN BE GRADED BY THE FREQUENCY OF MOTOR NEURON FIRING

The action potential on the motor neuron is very short, between 1 and 3 ms. The action potential on the muscle cell membrane is also short, on the order of 3−5 ms. The muscle twitches are long by comparison, some 30−300 ms. This means that it is possible to stimulate the muscle with another action potential before the muscle has relaxed. Indeed, we can stimulate a muscle again before it reaches its peak tension. When a muscle is stimulated before it has completely relaxed,
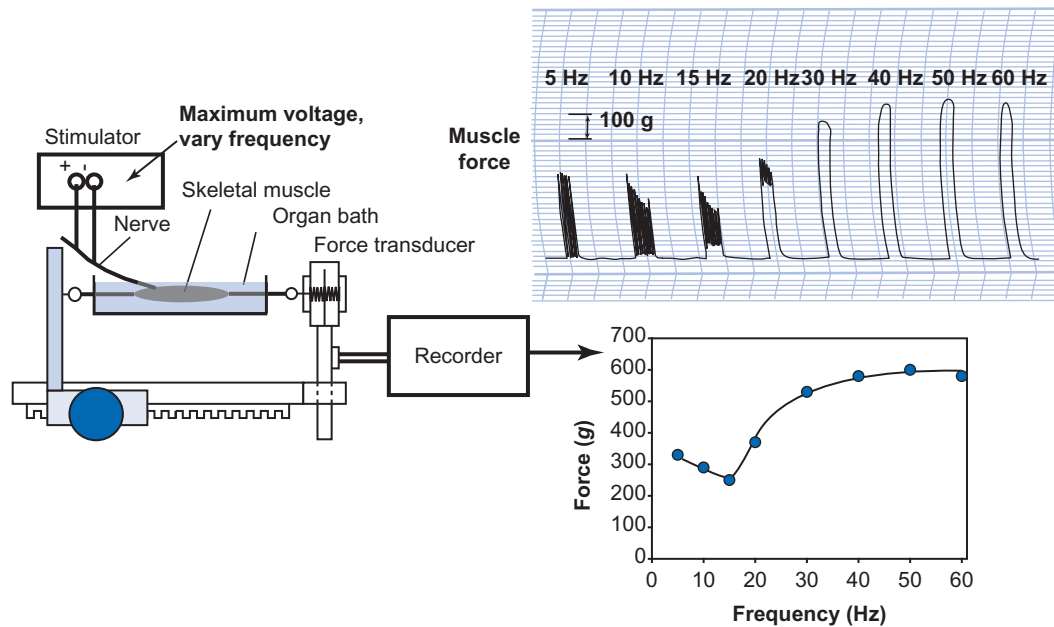
FIGURE 3.4.6 Gradation of muscle force by the frequency of stimulation. Increasing the frequency of stimulation at low frequencies does not increase the force; it merely increases the frequency of the same twitch wave form. When the period of the stimulation frequency is shorter than the period of the twitch, however, force begins to summate. With continued increases in frequency, there is added force until tetany is reached. Data obtained from electrical stimulation of the sciatic nerve serving intact gastrocnemius muscle of the rat.

a new twitch begins force where the first twitch left off (see Figure 3.4.6). The resulting force is greater than with a single twitch. Thus muscle force **summates** with repetitive stimulation. When the frequency of stimulation is great enough, the muscle produces a single forceful contraction with no waviness in the force. This condition is called **tetany**.

The frequency required to reach tetany depends on how fast the muscle contracts and relaxes. If the muscle twitch is 100 ms long, then summation will just begin when the next stimulation arrives at the end of relaxation. Since there are 10 100 ms-intervals in a second, summation for such a fiber should begin at a stimulation frequency of about 10 Hz. (1 Hz is hertz, meaning a cycle per second; 10 Hz is therefore 10 cycles or events per second.) Typically most muscles in the human tetanize between 20 and 100 Hz. **Summation begins when stimulation frequency just exceeds the inverse of the twitch time.**

Although the results shown in Figure 3.4.6 are a laboratory observation involving an isolated nerve and its muscle, the same phenomenon also occurs in living, breathing people. We can grade the force of a muscular contraction, or vary force more or less continuously, by altering the frequency of motor neuron firing. This is one of the principal ways of physiological control of muscle force. Since action potentials are an all-or-none phenomenon, information can be coded only through the frequency of action potentials (frequency code) and in the population of neurons carrying it (population code—this is the same as recruitment). In the case of muscle, high-frequency neuronal activity is converted to high intensity of muscle force.

As you can see from Figure 3.4.6, the tetanic force is much greater than the twitch force. In general, **tetanic force is about five times the twitch force**, but the twitch ratio varies from 2 to 10 in different muscle types.

MUSCLE FORCE DEPENDS ON THE LENGTH OF THE MUSCLE

The device shown in Figures 3.4.2, 3.4.3, and 3.4.6 can be adjusted to vary the length of the muscle. When muscles are relaxed, they exert no force. When the relaxed muscles are stretched passively, without activation by a nerve stimulus, they produce a **passive force**. This is due to elastic properties of the muscle material itself. This passive force increases steeply and nonlinearly with increases in length (see Figure 3.4.7).

When a stretched muscle is stimulated tetanically, it produces a force in addition to the passive force. This increment in force is called the **active tension** because it depends on activation of the muscle by the tetanic stimulation. The additional active force produced by stimulation depends on the length of the muscle. The active force increases to a maximum and then declines with further increases in muscle length. The relationship between active force and muscle length is the **length–tension curve**, originally determined in isolated muscle fibers by Robert Ramsey and Sybil Street. This data became an important observation for explaining the mechanism by which muscles produce force.

The resting length of a muscle is usually designated as L_0. Because muscles are attached to the skeleton, their
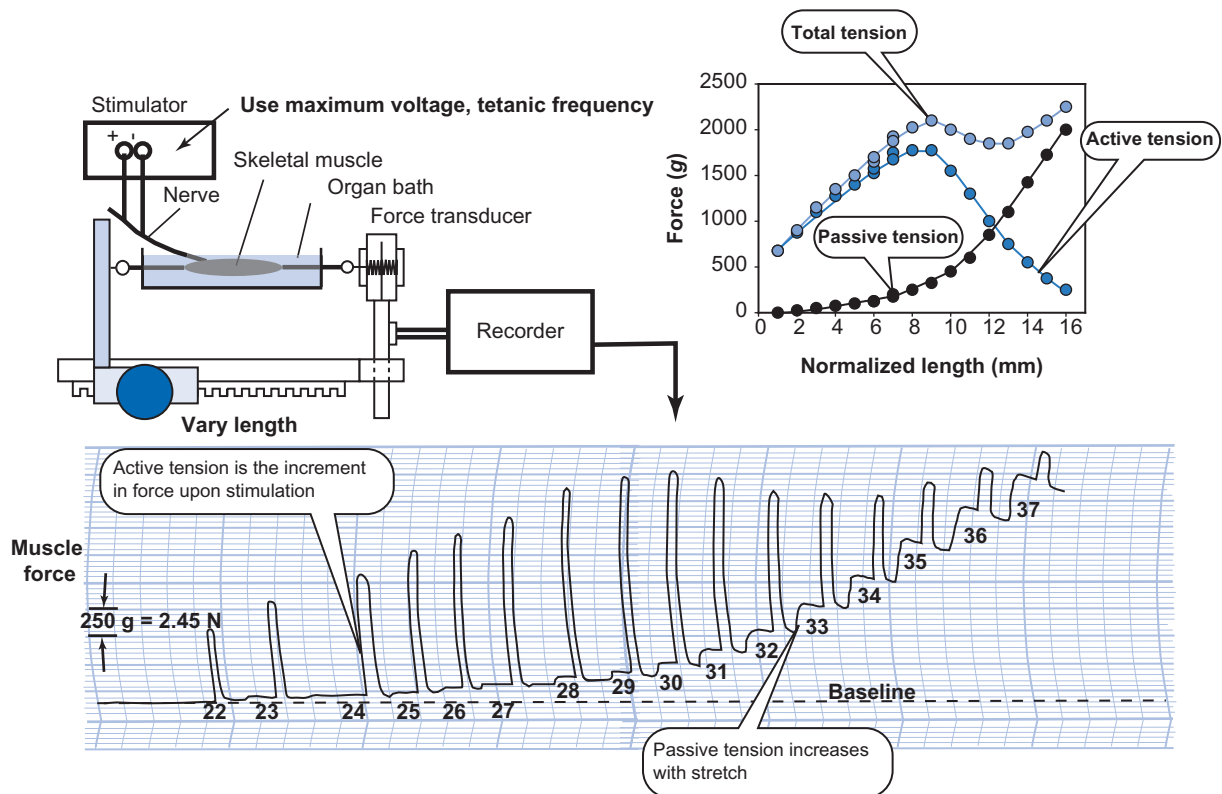
FIGURE 3.4.7 The length−tension relationship in muscle. Increasing muscle length from slack length to relatively long lengths causes a passive force or tension that does not require activation of the muscle. Activation of the muscle at maximum recruitment and tetanic frequency (so that recruitment or frequency response does not confound the results) causes an increment in the force called the active force or tension. Muscle length was increased in increments of 1 mm as indicated by the Vernier scale readings under each tetanic stimulation. Active tension increases biphasically with muscle length. Passive tension increases progressively with muscle length—muscles do not obey Hooke's law, in which force is proportional to length. The total tension is the sum of the passive and active forces. Data obtained by electrical stimulation of the sciatic nerve innervating the gastrocnemius muscle of the rat.

degree of shortening is defined by the movement of the bones and the attachment points of the muscles. Most muscles do not shorten or lengthen by more than about 25% of their rest length. Thus although muscle length can determine muscle force, typically the muscle is physiologically arranged near the top of the length−tension curve, and muscle length changes are relatively unimportant compared to recruitment and frequency of stimulation.

RECRUITMENT PROVIDES THE GREATEST GRADATION OF MUSCLE FORCE

We have described three distinct ways to vary muscle force: (1) recruit muscle fibers by activating larger numbers of motor units, (2) vary the frequency of activation of the activated motor units, and (3) vary the length. As mentioned above, muscle length typically does not vary significantly, and the resting length of muscles is situated at the top of the active length−tension curve, so that varying muscle length is not an important way of varying muscle force in the whole person. Most activation of muscle is not by a single action potential to produce a twitch, but by a train of impulses (see

Chapter 3.7) interrupted by rest periods. These series of activations increase force by wave summation. Although this is important, it provides a range of forces that scale according to the tetanus−twitch ratio, which varies from about 2−10, depending on the muscle. Therefore, the frequency of activation provides at most about a 10-fold range of variation in muscle force. Skeletal muscles often have a range of forces that varies 20,000 fold, from the weakest contraction to the most forceful. Thus rate coding or frequency coding provides an important part of muscle force gradation, but population coding (recruitment) provides the greater part of muscle force gradation.

MUSCLE FIBERS DIFFER IN CONTRACTILE, METABOLIC AND PROTEOMIC CHARACTERISTICS

As shown in Figure 3.4.2, muscles differ in their contractile properties. This mechanical difference derives from differences in their constituent motor units. Each motor neuron innervates a number of muscle fibers. The muscle fibers themselves are heterogeneous, and several classification schemes have been devised to describe them. Based on contractile behavior, muscle

fibers can be broadly classified as being S, FR, FI and FF: these mean S = slow; FR = fast, fatigue resistant; FI = fast, intermediate in fatigability; FF = fast, fatigable. The differences in the muscle fibers come from their expression of different protein isoforms or from differing quantities of the same proteins or from differing quantities and composition of subcellular organelles. The muscle fibers differ in metabolic ability that shows up in their gross appearance: red muscle contains a lot of myoglobin, a protein that binds oxygen within the cytoplasm of the muscle fiber and aids in oxygen delivery to mitochondria, which are also rich in red muscles. White muscle fibers rely less on oxidative metabolism and use anaerobic pathways more. So muscles can be classified according to their metabolic properties as being SO = slow, oxidative; FOG = fast, oxidative and glycolytic; and FG = fast, glycolytic. Muscles are also differentiated on the basis of myosin isoform expression as type I (equivalent to SO), type IIa (equivalent to FOG), and type IIb (FG). We will return to these different muscle fiber types in Chapters 3.5 and 3.7.

MOTOR UNITS CONTAIN A SINGLE TYPE OF MUSCLE FIBER

Muscle fibers are heterogeneous, differing in contractile and metabolic properties, but all of those muscle fibers that are innervated by a single motor neuron are of a single type. This fact suggests that there is some kind of communication that passes between the motor neuron and the muscle fibers that directs their expression of protein isoforms. In short, the motor neuron establishes the kind of muscle fibers it innervates and maintains them in that form.

THE INNERVATION RATIO OF MOTOR UNITS PRODUCES A PROPORTIONAL CONTROL OF MUSCLE FORCE

The tetanic force produced by a single motor unit is given as

[3.4.1] $$F_{MU} = NF_{MF} = NAF_S$$

where F_{MU} is the force of the motor unit, N is the number of muscle fibers that the motor neuron innervates, A is the area per muscle fiber, and F_S is the specific force or the force per unit area of muscle fiber. **N is the innervation ratio.** Although some reports suggest that there might be differences in the specific force for different muscle fiber types, the effect is not large. Typically the force per unit area for a muscle fiber is about 20 N cm^{-2}. The total force developed by a muscle is given as

[3.4.2] $$F = \sum_{i=1}^{i=j} N_i A_i F_S$$

indicating that the forces of the motor units from unit 1 to j sum linearly, and that the innervation ratio and area of the muscle fibers vary with motor unit. Typically the small motor units have low innervation ratios and
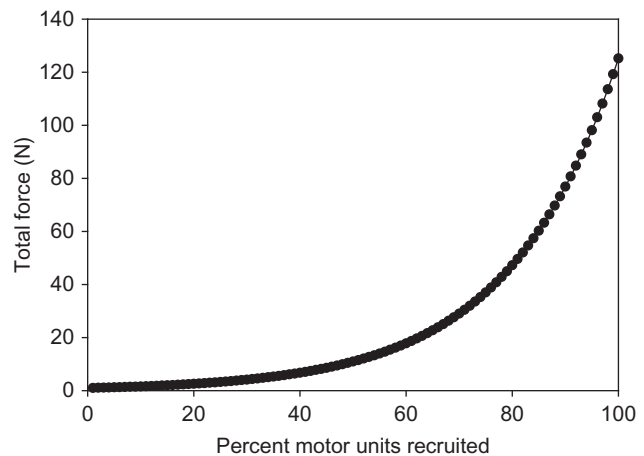

FIGURE 3.4.8 Simulated active force of a muscle as a fraction of motor units that are activated. The muscle was simulated as a population of 100 motor units whose aggregate muscle fiber area was given as $A_{i+1} = 1.05\ A_i$, with a constant specific force of 20 N cm^{-2}.

their muscle fibers have a smaller cross-sectional area. The first recruited motor units typically have Type I muscle fibers (slow twitch, oxidative metabolism) and the last recruited motor units innervate large muscle fibers of Type IIB (fast, glycolytic metabolism). Innervation ratios vary with the type of muscle from about 5 in the lateral rectus muscle that moves the eyeball to over 2000 muscle fibers for a single motor unit in the medial gastrocnemius in the calf. According to the size principle, the small motor units are recruited first, and progressively larger motor units are recruited until all motor units are recruited in maximal voluntary contractions. The theoretical consequence of the dispersion of motor unit innervation ratios and the orderly recruitment of motor units is shown in Figure 3.4.8. The total active force produced by the muscle increases progressively with the recruitment of the motor units in a process referred to as proportional control. In this process, force is added in steps that are proportional to the amount of force already present. During weak contractions, force is adjusted by changing it slightly (e.g., in steps of 5%) whereas strong contractions are adjusted by making large incremental changes that remain 5% of the force already present. The proportional control is accomplished by recruiting motor units in order of increasing strength.

MUSCLE FORCE VARIES INVERSELY WITH MUSCLE VELOCITY

The experimental setups illustrated in Figures 3.4.2, 3.4.3, 3.4.6, and 3.4.7 were all performed using isometric contractions in which muscle length did not change. We now change this situation and hook up one end of the muscle to a pulley system connected to an **afterload** (see Figure 3.4.9). An afterloaded muscle cannot shorten until it produces a force equal to the afterload. When stimulated, the muscle contracts isometrically during the time it takes to develop force equal to the
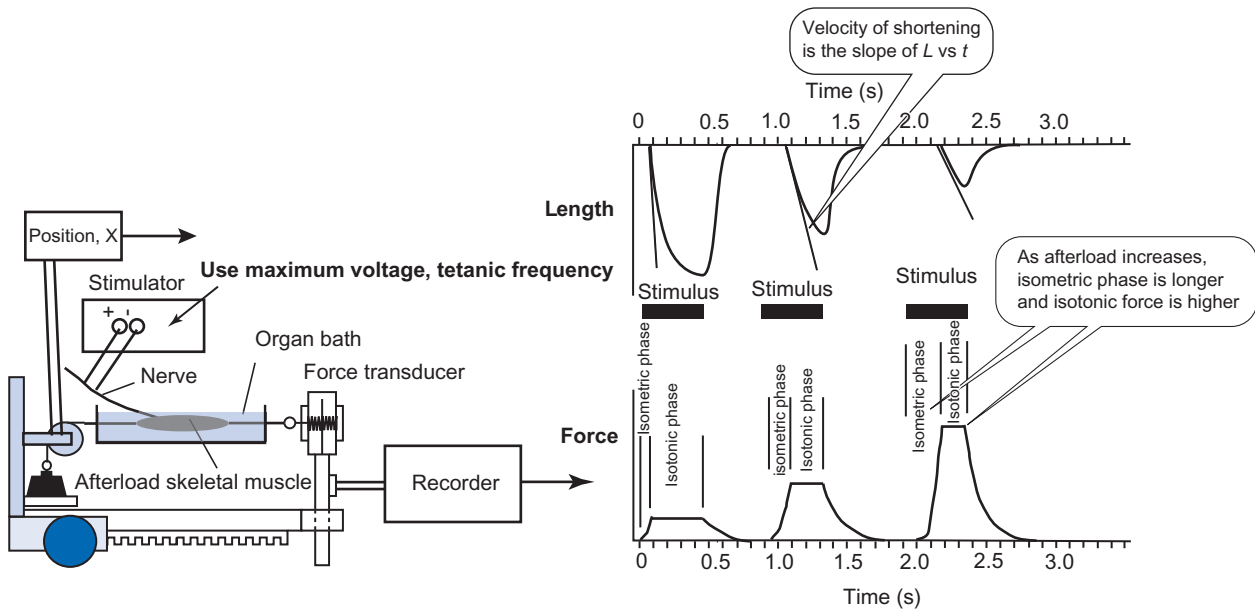
FIGURE 3.4.9 Experimental setup for measuring the force and velocity of isotonic contractions. The afterload is supported by a shelf prior to the activation of the muscle and thus it is not felt by the muscle until all slack in the line are taken up by muscle shortening. When the size of the afterload is increased, the muscle takes longer to develop sufficient force to lift the load, and the velocity of shortening is less. The initial velocity of shortening is inversely related to the afterload or the force developed by the muscle.

afterload. After the muscle develops a force equal to the afterload, it lifts the afterload and continues to shorten. For some part of this contraction, the velocity of shortening is approximately constant. Such a contraction is called an **isotonic contraction**. Thus each contraction consists of an isometric part and an isotonic part, as shown in Figure 3.4.9.

Everyday experience shows that the speed of muscle contraction depends on the load that must be moved. We know that we can move a light load quickly, whereas we move a heavy load slowly. The force–velocity curve is produced by measuring the initial velocity and plotting it against the afterload. The initial velocity can be measured using a device such as that shown in Figure 3.4.9, where the afterload is varied. The initial velocity is used because after the muscle shortens it cannot produce as much force, because it moves off the optimum of the length–tension curve. The force–velocity curve is shown in Figure 3.4.10.

MUSCLE POWER VARIES WITH THE LOAD AND MUSCLE TYPE

Power is *defined* as the rate of energy production or consumption and it has the units of energy per unit time. In mechanical terms, energy is work. Work is defined in mechanics as force × distance. Thus we have the following:

[3.4.3A]   Power = Energy/time

[3.4.3B]   Energy = work
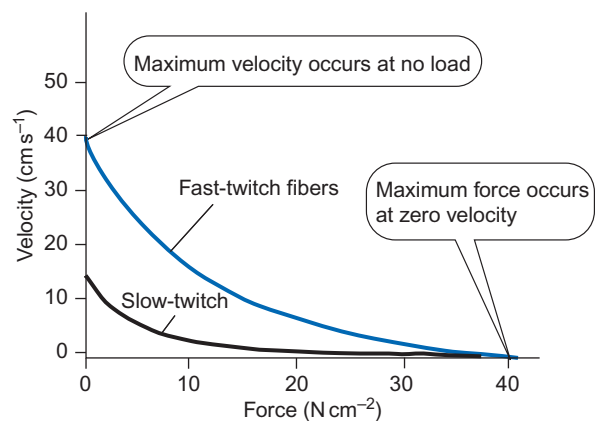
[3.4.3C]   Work = force × distance

FIGURE 3.4.10 The force–velocity curve for an intact fast-twitch or slow-twitch muscle. Fast contractions can occur only with low loads. Higher loads mean slower velocity of muscle contraction, but more force. Thus there is an inverse relationship between force and velocity.

Inserting Eqn [3.4.3C] into Eqn [3.4.3B] and then into Eqn [3.4.3A], we get

[3.4.4]   Power = force × distance/time

From the definition of velocity as distance/time, we get

[3.4.5]   Power = force × velocity

The force–velocity curve obtained experimentally is displayed in Figure 3.4.10. We can obtain the power–force curve by multiplying force and velocity at every point on this curve. This power is the instantaneous power produced during the initial shortening of the muscle. Power is expressed in units of watts or $N \, m \, s^{-1}$, per unit weight of muscle. The power as a function of muscle force is shown in Figure 3.4.11. This shows
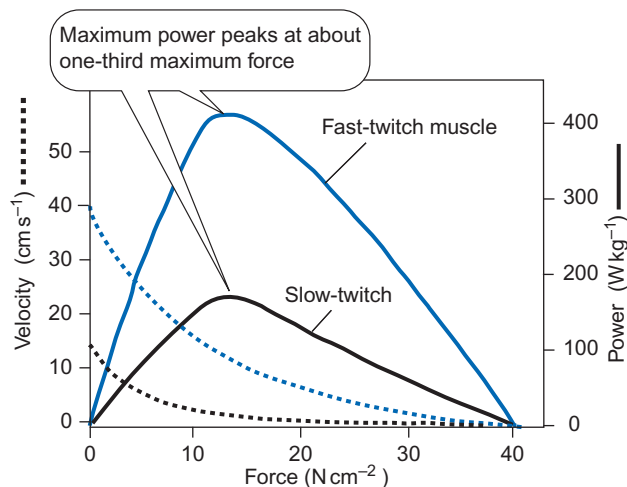
FIGURE 3.4.11 Power as a function of force for slow-twitch and fast-twitch muscles. Velocity is shown as dashes, power as solid lines. Power peaks at about one-third maximum force for both fast-twitch and slow-twitch muscles, but fast-twitch muscles deliver more power due to their faster contractions. These curves are part of the reasons for gears on bicycles, so that a constant power can be delivered to the wheels by keeping the velocity of the muscles and forces near the peak power output when translational velocity of the bike changes going up or down hill.
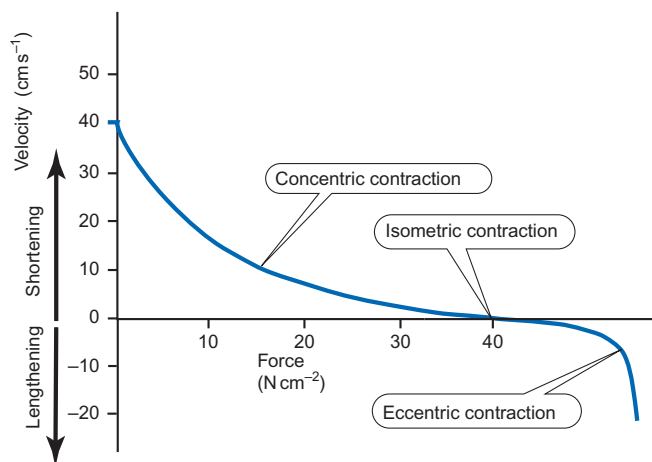

FIGURE 3.4.12 Concentric, isometric, and eccentric contractions. Concentric contractions involve a shortening of the muscle. Eccentric contractions involve a lengthening of the muscle. Isometric contractions occur when the muscle length does not change and occurs at zero velocity. Developed force is greatest for eccentric contractions, next highest for isometric contractions and lowest for concentric contractions.

that the power is about two to three times greater in fast-twitch fibers because of their greater speed of contraction.

ECCENTRIC CONTRACTIONS LENGTHEN THE MUSCLE AND PRODUCE MORE FORCE

According to the way in which we measured velocity, a positive velocity corresponded to a shortening of the muscle. If the support for a *very large* afterload in Figure 3.4.9 is removed, the afterload will cause the muscle to lengthen during contraction. This lengthening is a negative velocity. Contraction of the muscle during a lengthening is called an **eccentric contraction**. Contraction of a muscle that causes a shortening is called a **concentric contraction**. The extension of the force−velocity curve to negative velocities (see Figure 3.4.12) shows that muscles can exert about 40% more force in an eccentric contraction compared to the maximal isometric force measured at zero velocity.

CONCENTRIC, ISOMETRIC, AND ECCENTRIC CONTRACTIONS SERVE DIFFERENT FUNCTIONS

Because concentric contractions shorten, they are useful for the acceleration of one body part relative to another, including parts that are loaded with external objects. Isometric contractions are used to fix joints, usually to produce a platform on which other actions can be made. For example, delicate work by the fingers requires immobilization of the arm and shoulder to hold the hand still while the fingers do the work. Such immobilization is accomplished by simultaneously activating **antagonistic muscles**—those that move joints in opposite directions. Eccentric contractions are used to decelerate body parts, as in activation of the quadriceps muscles in the leg while going downstairs.

Table 3.4.1 shows the three types of contractions, their functions for movement, and the work performed.

MUSCLE ARCHITECTURE INFLUENCES FORCE AND VELOCITY OF THE WHOLE MUSCLE

The force that a muscle develops depends on its size: larger muscles produce greater force. Because muscles

TABLE 3.4.1 Types of Contractions and Their Uses

Types of Contractions	Distance Change	Function	Work
Concentric	Shortening ($+D$)	Acceleration	Positive $W = F \times (+D)$
Isometric	No change ($0\,D$)	Fixation	Zero
Eccentric	Lengthening ($-D$)	Deceleration	Negative $W = F \times (-D)$

are not right cylinders but take on complicated shapes, determinants of the size present something of a problem. The usual estimate of size is the muscle's cross-sectional area at the belly, or widest part, of the muscle. The maximum force expressed per unit area is typically from 15 to 40 N cm^{-2}. This is enough to lift about 1.5−4 kg cm^{-2}. The variation in this force per unit area derives from the orientation of the muscle fibers within the muscle.

There are three major orientations of the muscle fibers within muscles: **parallel fibers**, **fusiform**, and **pinnate**. The parallel arrangement is present in muscles shaped like a strap or in parts of flat-shaped muscles. In fusiform muscles, the fibers are generally parallel to the longitudinal axis of the muscle, but their number varies with distance from the belly of the muscle. In pinnate muscles, the fibers are oriented at an angle to the tendon or aponeurosis. Because they resemble a feather, these muscles are called pinnate or pennate (see Figure 3.4.13).

The consequence of orienting the muscle fibers at an angle with respect to the tendon is to increase the effective cross-sectional area of the muscle while reducing the distance the muscle can contract along the lines of the tendons. To see this, we consider two muscles, a strap muscle with parallel fibers having a volume of 300 cm^3 and a resting length of 36.8 cm and a second muscle with pinnate architecture with fibers 12 cm long and overall length of 36.8 cm. The pinnate muscle fibers are oriented 15° to the line of action. The geometry of these is shown in Figures 3.4.14 and 3.4.15. The fibers in the strap muscle do not span the distance from tendon to tendon. Instead, long strap muscles are divided into compartments by fibrous bands called **inscriptions**. The sartorius muscle (originating on the lateral hip, wrapping around to the inner thigh, and inserting on the medial tibia) has three inscriptions, giving four compartments; the semitendinosus (part of the hamstring muscles, originating on the medial tuberosity of the ischium and inserting its long tendon on the medial tibia) has three compartments and the biceps femoris (in the back of the thigh, originating in two places and inserting on the lateral side of the head of the fibula) and gracilis (most superficial muscle on the inner thigh, originating on the symphysis pubis and inserting on the medial tibia) have two compartments each.

The conclusion from the calculations in Examples 3.4.1 and 3.4.2 is that the pinnate arrangement of the muscle fibers allows many more muscle fibers to attach to the aponeurosis. The consequence is that the muscle can develop more force, but it does so by reducing its velocity.
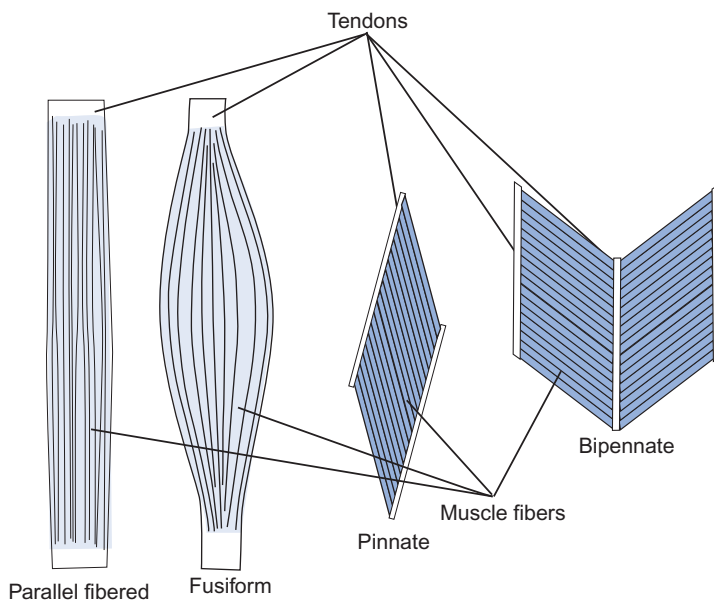

FIGURE 3.4.13 Different arrangement of muscle fibers. Parallel fibers are oriented longitudinally in the direction of the muscle. Fusiform muscles are tapered. Pinnate fibers are parallel but oriented at an angle to the action of the muscle.
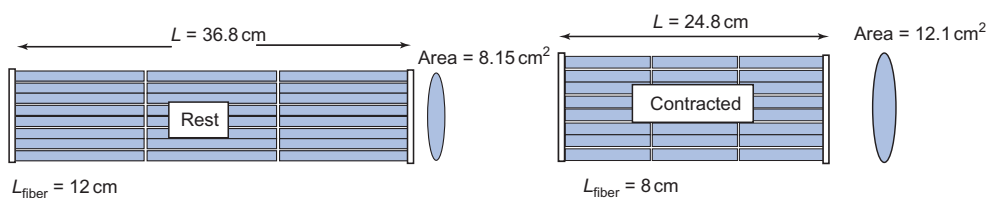

FIGURE 3.4.14 Geometry of a strap muscle with two inscriptions, fiber length = 12 cm and volume = 300 cm^2.
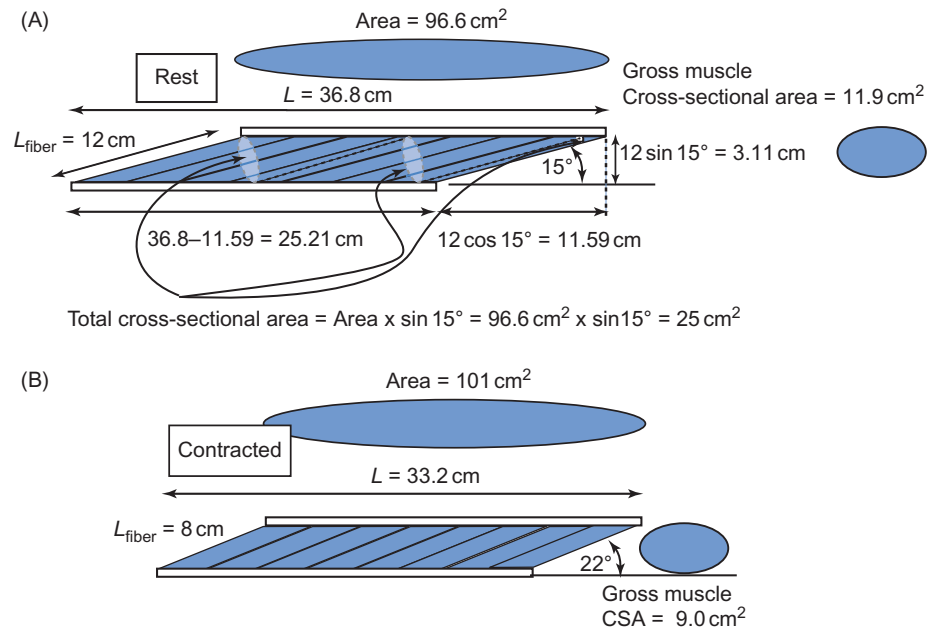
FIGURE 3.4.15 Geometry of a pinnate muscle fiber at rest (A) and contracted (B).

EXAMPLE 3.4.1 Calculate the Isometric Force and Maximal Velocity of a Parallel Muscle

We use the strap muscle shown in Figure 3.4.14 as an example. Its maximal force is its cross-sectional area times the force developed per unit cross-sectional area. Since its volume is 300 cm^3 and its length is 36.8 cm, its cross-sectional area is 300 cm^3/36.8 cm = 8.15 cm^2.

The typical isometric force per unit area is 20 N cm^{-2}. The isometric force of this muscle would be

$$F = 8.15 \text{ cm}^2 \times 20 \text{ Ncm}^{-2} = \textbf{163 N}$$

Taking the unloaded contraction time as 0.033 s for the muscle fibers to contract from 12 to 8 cm, we get an unloaded velocity = (36.8 cm − 24.8 cm)/0.033 s = **364 cm s^{-1}**.

EXAMPLE 3.4.2 Calculate the Isometric Force and Maximal Velocity of a Unipinnate Muscle

An unipinnate muscle with the same volume and rest length as the strap muscle has fibers oriented at 15° to the direction of force. The fiber rest length is 12 cm; thus the aggregate cross-sectional area of the fibers is 300 cm^3/12 cm = 25 cm^2, which can also be obtained from the area of the aponeurosis × sin 15°. This is not the gross cross-sectional area of the muscle. The gross cross-sectional area can be estimated from the volume and length of the muscle. From the geometry in Figure 3.4.15, the overall length of the muscle is 36.8 cm, but each aponeurosis is 25.21 cm long; the thickness of the muscle is 3.11 cm. From these numbers, the area of the aponeuroses is 96.6 cm^2 and the gross cross-sectional area of the muscle is 11.9 cm^2. Total force generated by the fibers

is the cross-sectional area of the fibers × the force per unit area = 25 cm^2 × 20 N cm^{-2} = 500 N. This force is not directed along the lines of the aponeurosis; the force transmitted to the tendons will be 500 N × cos 15° = **483 N**.

The apparent isometric force of the muscle, using its gross cross-sectional area, is 483 N/11.9 cm^2 = 40.6 N cm^{-2}.

When the fibers shorten from 12 to 8 cm, the pinnation angle changes. The overall length of the muscle changes from 36.8 to 33.2 cm, or by 3.6 cm, in 0.033 s, giving an unloaded velocity of 3.6 cm/0.033 s = **109 cm s^{-1}**.

MUSCLES DECREASE FORCE UPON REPEATED STIMULATION; THIS IS *FATIGUE*

Everyday experience shows us that maximal effort can be sustained only briefly. The more intense the effort, the faster one fatigues. Intense efforts rely predominantly on fast-twitch fibers. These are generally larger than the slow-twitch fibers and belong to larger motor units, so that these are recruited last. This makes subjective sense, because these large muscle fibers in large motor units increase force in the greatest increments when they are recruited. These fast-twitch fibers are also more easily fatigued than the slow-twitch fibers. Fatigue of slow-twitch muscles takes longer to produce. Therefore, it makes sense that these slow-twitch fibers, which are smaller and belong to smaller motor units, are recruited early on and so are active almost every time the muscle is activated, even for tasks requiring little force. The differences in fatiguability of different muscles led Burke to propose a system of classification of muscles based on four types:

1. S = slow-twitch fibers
2. FR = fast, fatigue resistant
3. FI = fast, intermediate fatigue resistant
4. FF = fast, fatiguable.

Most muscles consist of thousands of muscle fibers. Most muscles contain all of the different fiber types, but they differ in their relative number. The soleus muscle in the human consists predominantly of slow-twitch muscle fibers, whereas the gastrocnemius consists mainly of fast-twitch fibers. However, there is considerable individual variation in the fiber types that are present in individual muscles. Transformation of muscle types appears to be limited and obeys a strict progression. Increased use of a muscle invariably tends to convert muscle fibers into more fatigue-resistant fibers, but conversion of fast fatigable fibers all the way to slow-twitch fibers does not occur.

SUMMARY

Skeletal muscles consist of thousands of muscle fibers which are large multinucleated cells. Each muscle fiber is controlled by a single motor neuron that forms a neuromuscular junction approximately in the middle of the fiber. Motor neurons branch and form junctions with one-to-many muscle fibers. All of the muscle fibers innervated by a single motor neuron constitute the motor unit. Large motor units typically have large motor neurons in the spinal cord, and small motor units have small motor neurons. The small motor neurons are more excitable and are recruited first.

A single action potential on a motor neuron produces a twitch. Brief twitches characterize fast-twitch muscles: they develop force rapidly and relax rapidly. Slow-twitch fibers develop force more slowly and relax more slowly. Muscle force can be graded three ways: (1) by recruiting more motor units; (2) by increasing the frequency of stimulation; and (3) by changing the length of the muscle. Changing the length of the muscle is not so important because muscles are restrained by the position of their origins and insertions on the skeleton. Recruitment follows the size principle: small motor units are recruited first. Increasing frequency of neuronal action potentials excites the muscle again before it has time to relax because the twitch is usually much longer than the action potential. Thus muscle force can summate when excitation frequency exceeds $1/t$, where t is the period of the twitch. The tetanic frequency is the frequency at which all waviness disappears from the force record. Typically tetanic force is about five times the twitch force. Recruitment is usually the most important way of grading muscle force and can be responsible for a 100-fold or greater range of muscle force.

Stretching a muscle produces a passive force that increases nonlinearly with stretch. The active force, the increment of force caused by excitation, changes biphasically with muscle length. It increases with increasing muscle length when the muscle is short, reaches a maximum, and then decreases with further stretch of the muscle.

The velocity of muscle shortening depends on the load. Maximal velocity occurs at zero load, and maximum force develops at zero velocity. The power output of muscle varies biphasically with muscle force, being maximal at about $1/3 F_{max}$. Both fast- and slow-twitch muscles show this behavior. Power output also varies with velocity, being maximal at about $1/3 V_{max}$. During rapid movements, almost all power derive from fast-twitch muscle.

Muscle activation can produce force while the muscle shortens, and this is called a concentric contraction. Isometric contractions refer to the activation of muscle under conditions in which it does not change length. In some cases, muscle activation develops a force while the muscle lengthens. This is an eccentric contraction. Concentric contractions are used to accelerate objects or body parts. Isometric contractions are used to fix joints in some configuration, whereas eccentric contractions are used to decelerate objects or body parts.

Muscle fibers often are oriented at an angle with respect to the direction of muscle action. This is called the pinnation angle. This allows more muscle fibers to fit into the volume occupied by the muscle and increases force but decreases muscle velocity.

Fatigue is the loss of muscle force due to prolonged use. There are two types of fatigue: rapid onset of fatigue brought about by continuous maximal stimulation and slower onset of fatigue brought about by repetitive but submaximal activation of the muscles.

Muscles can be classified on the basis of their contractile activities. Thus there are slow-twitch fibers, fast and fatigue-resistant fibers, fast intermediate (with respect to fatigue) fibers, and fast fatiguable fibers.

REVIEW QUESTIONS

1. What is a muscle twitch? What is tetany?
2. Name three ways that the body varies muscle force. Are all equally important physiologically?
3. What is a motor unit? What is recruitment? How is recruitment usually affected? How much stimulation can be achieved through recruitment?
4. What is tetany? What is the most rapid train of twitches possible without increasing force? By how much can force be increased by increasing the frequency of stimulation?
5. What is active tension? What is passive tension? How do they vary with muscle length? Is this an important way of varying muscle strength?
6. What is the relationship between force and velocity? Is a negative velocity of muscle contraction possible? If so, what do you call such a contraction?
7. What do we mean by "fast-twitch" and "slow-twitch" fibers? Why is muscle power higher in fast-twitch than in slow-twitch fibers?
8. What are concentric, isometric, and eccentric contractions? What are these used for?
9. What advantage does fiber pinnation afford? What is its disadvantage?