Lesson 1 presents little physiology per se, but information that is fundamental to the study of the exercise physiology of skeletal muscle (which comes in the later lessons). Basic terms and concepts are addressed in Lesson 1, as is the essential anatomy of skeletal muscle tissue.

Contents of Lesson 1:

<table>
<thead>
<tr>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Introduction to Unit 3 - Lesson 1</td>
<td>1-2</td>
</tr>
<tr>
<td>Fundamental Concepts</td>
<td>3-15</td>
</tr>
<tr>
<td>Functional Anatomy of Skeletal Muscle Tissue</td>
<td>16-30</td>
</tr>
<tr>
<td>Review of Lesson</td>
<td>31</td>
</tr>
</tbody>
</table>

Outline of Content

I. Fundamental Concepts (Pages 2-16)
   A. Introduction (Page 2)
   B. Muscle as a Tissue and Muscle as an Organ (Pages 3-5)
   C. Muscle Contraction - The Basic Function of Muscle (Pages 6-15)
      1. Definition of contraction
      2. Types of contractions

II. Functional Anatomy of Skeletal Muscle Tissue (Pages 16-32)
- Introduction to Unit 3 - Lesson 1 (cont.)

**Learning Objectives**

After completion of Lesson 1, the student should be able to:

1. Define: primary tissue, striated muscle tissue, skeletal muscle tissue, irritability, conductivity, compliance, stiffness, viscoelasticity, viscosity, elasticity, contractility, muscle contraction, types of muscle contraction (static, dynamic, isometric, concentric, eccentric, isotonic, isokinetic), torque, sliding filament theory of contraction, alpha motor neuron, motor unit.

2. Distinguish between muscle as a primary tissue and muscle as an organ. Give examples of each.

3. Discuss the three major types of skeletal muscle contractions, explaining for each type the relationship between opposing force (torque) and the muscle’s force (torque), and the function of the contraction type. Apply this information to analysis of human movements, such as, moving weights or other objects, walking or running on different grades, and jumping and landing from jumps.

4. Describe and/or draw a diagram to illustrate the basic gross and microscopic anatomy of skeletal muscle. Include the following: endomysium, perimysium, epimysium, tendon, muscle organ, fascicle, fiber, myofibril, myofilament, sarcolemma, sarcoplasmic reticulum, sarcosomes, myoplasm (sarcoplasm), Z-disks, M-line, sarcomere, troponin, tropomyosin, troponin-tropomyosin complex, motor endplate, axon of alpha motor neuron. Define each of these terms.
Fundamental Concepts

Introduction

The work of exercise is done by skeletal muscles. Using the factory analogy I presented in the introduction to the course, skeletal muscles are the machines in the factory. In a manufacturing plant, key machines are the presses that bend and fold metal into desired forms. In a furniture factory, lathes turn pieces of wood into desired shapes and designs. In the exercising body, skeletal muscles turn energy into mechanical forces that bring about desired (hopefully) movements. In this unit we will study how these muscle machines function, that is, the physiology of skeletal muscles.

Muscle as a Tissue and Muscle as an Organ

In the body, atoms make up molecules, molecules make up subcellular structures, subcellular structures make up cells, cells make up tissues, tissues make up organs, organs make up systems, and systems make up the entire organism, the body. There are only four primary tissues in the body. A primary tissue is a group of cells specialized in a common direction and able to perform a common function. Every organ in the body, and therefore ultimately the entire body, is formed from these four primary tissues. Muscle is one of the primary tissues; the others are connective tissue, epithelial tissue, and nervous tissue.

Muscle as a primary tissue refers to the individual muscle cells, which are more commonly referred to as muscle fibers. When we study muscles of the body such as the biceps brachii or the quadriceps femoris muscles, we are studying muscles as organs. The term “organ” is not often applied to muscles, but it is appropriate. Organs are structures that are made up of more than one primary tissue. All four primary tissues contribute to the structure and function of muscles, so whole muscles are organs. In our study of muscle physiology, we will sometimes study individual muscle fibers and sometimes muscle organs.
All muscle tissue shares certain characteristics, but there are also differences among various muscle tissues. The types of muscle tissue are categorized in one of three ways, as noted in the table.

<table>
<thead>
<tr>
<th>Basis of Classification</th>
<th>1. Anatomic Location</th>
<th>2. Microscopic Appearance</th>
<th>3. Nervous Control</th>
</tr>
</thead>
<tbody>
<tr>
<td>Skeletal</td>
<td>Striated</td>
<td>Voluntary</td>
<td></td>
</tr>
<tr>
<td>Visceral</td>
<td>Smooth</td>
<td>Involuntary</td>
<td></td>
</tr>
<tr>
<td>Cardiac</td>
<td></td>
<td>Mixed</td>
<td></td>
</tr>
</tbody>
</table>

In this unit we will study skeletal muscle. As the name indicates, skeletal muscle tissue is part of muscle organs that are attached to bones of the skeleton. Skeletal muscle fibers are striated (as are cardiac muscle fibers); that is, they have striations or stripes when viewed with a microscope. Skeletal muscle fibers are normally under voluntary nervous control. That is, within limits, a person can volitionally determine whether these fibers contract or relax.
Muscle as a Tissue and Muscle as an Organ (cont.)

All muscle tissue has the following characteristics:

- **Irritability** – The ability to respond to a stimulus, especially an electrical stimulus. This is important in the control of muscle activity.

- **Conductivity** – The ability to conduct an electrical impulse. This is essential to translating a nervous stimulus into muscle contraction.

- **Compliance** – The ability to be extended or lengthened. Another term that may be used for this characteristic is stiffness. Normal muscle is very compliant and has low stiffness.

- **Viscoelasticity** – This is really two characteristics that determine how muscle responds to being extended. Viscosity is the resistance of a fluid to flow; muscle is some 70-75% water, so it has certain properties of fluids, including viscosity. Elasticity is the ability to return to original shape (or length) following distortion (or lengthening).

- **Contractility** – The ability to contract, or to actively generate force.

Each of the characteristics listed plays a key role in determining muscle function. We will deal with these characteristics where appropriate in our study of skeletal muscle.

Only one of these characteristics is unique to muscle tissue – contractility. No other tissue can contract. Contraction is the reason muscle tissue exists.
**Muscle Contraction – The Basic Function of Muscle**

Muscle contraction may seem to be a simple term and a simple concept. It is frequently misunderstood, however. Even some exercise physiologists misuse the term at times. In fact, some exercise physiologists are campaigning to replace the term. But the term is fine, IF everyone pays attention to its definition in muscle physiology. In everyday English, “contraction” refers to something getting smaller in length or volume. This IS NOT the definition of contraction in muscle physiology.

- **Muscle contraction** is active development of force by muscle tissue.

It’s that simple. The definition says nothing about change in length or volume of the muscle. “Active” is a key word in the definition. It means that the muscle tissue itself develops the force. No other tissue can do this. Lots of tissues and other materials can passively develop force. An obvious example is a rubber band. It can develop force, but only after some other force has been used to stretch it out. A vaulting pole in track and field is elastic. This elastic force is used to propel the vaulter upwards, hopefully over the bar. But the pole can generate this elastic force only after it has been bent by outside forces. Later in this unit we will study the mechanism by which muscle tissue actively develops force. For now, the important thing is that you understand this definition of muscle contraction.
**Fundamental Concepts (cont.)**

**Muscle Contraction – The Basic Function of Muscle**

There are two general types of muscle contractions: static and dynamic.

Static contractions are commonly referred to as isometric contractions; isometric literally means constant length. Static contractions are contractions during which the muscle does not change in length.

All other contractions are dynamic contractions, which means that the length of the muscle changes during contraction. Sometimes dynamic contractions are called isotonic contractions, but this is a misnomer. “Isotonic” literally means “constant tension.” To truly be an isotonic contraction, the tension or force within the muscle must be constant throughout the entire contraction. Such contractions can occur in experimental situations with isolated muscles, but true constant-tension contractions rarely occur in the intact body.

Dynamic contractions may be of two types, depending on whether the muscle shortens or lengthens during contraction. If the muscle shortens while contracting, the contraction is a concentric contraction. If the muscle lengthens while contracting, the contraction is an eccentric contraction.

It is particularly the eccentric (lengthening) contractions that have prompted some to suggest that the term “contraction” no longer be used. They suggest that a “lengthening contraction” is impossible. But this fails to recognize the definition of “muscle contraction,” which refers simply to active force development and implies nothing at all about changes in muscle length. You will hear and read the term “muscle action” being substituted by some for “muscle contraction.” This is a very poor substitute for a term that does not need replacing.

Once again, muscle contraction simply means the muscle is actively developing force. Whether the muscle’s length stays the same, decreases or increases is entirely determined by the relationship between the force the muscle develops and the force opposing the muscle.
**Muscle Contraction – The Basic Function of Muscle (cont.)**

Let me insert a note here regarding torque. Torque is a rotational force. Since skeletal muscles act on bones and the bones of the skeleton are levers that rotate around joints, the effectiveness of a muscle’s force depends on the torque it generates. This depends on the force developed within the muscle, but it also depends very much on the lever system and how the force is applied to the lever. When analyzing movements of the body and body segments, torque is more important than muscle force per se. For example, if the elbow flexor muscles contract (i.e., actively develop force), whether they shorten, stay the same length, or lengthen is determined by the magnitude of the muscular torques (rather than forces) about the elbow joint compared with the opposing torques (rather than forces), such as provided by a weight held in the hand. For simplicity in this unit, however, I am going to refer to muscle force rather than torque in most cases, including the concept of torque in the term "force," unless otherwise noted.

---

**Fundamental Concepts (cont.)**

**Muscle Contraction – The Basic Function of Muscle (cont.)**

*For practical purposes, there are three types of muscle contractions:* static, concentric and eccentric. Each of these has a unique and important function.

- **Static contractions** are used to fixate a joint or body segment, to prevent movement. Maintaining posture uses static contractions, as does gripping a bat, golf club or racquet, holding the starting position in the blocks before the start of a sprint, and doing a handstand in gymnastics.

- **Concentric contractions cause movement** of a body segment; they impart positive acceleration. Concentric contractions propel the body upward in a vertical jump, accelerate the bat, golf club or racquet in a swing, and propel the body upward and forward in each stride of walking and running.

- **Eccentric contractions resist movement** of a body segment; they decelerate or slow down a body segment. Eccentric contractions resist the force of gravity in landing from a vertical jump, decelerate the bat, golf club or racquet at the end of the swing after contacting the ball, and decelerate the body during “landing” after foot-strike in each stride of walking and running. These contractions are essential for absorbing
Muscle Contraction – The Basic Function of Muscle (cont.)

The types of muscle contractions and their various characteristics are summarized in the table.

<table>
<thead>
<tr>
<th>Type of Contraction</th>
<th>Muscle Force (M.F.) vs. Opposing Force (O.F.)</th>
<th>Change in Muscle Length</th>
<th>Function</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Static (Isometric)</td>
<td>M.F. = O.F.</td>
<td>None</td>
<td>Prevent movement</td>
</tr>
<tr>
<td>2. Dynamic</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>a. Concentric</td>
<td>M.F. &gt; O.F.</td>
<td>Shortening</td>
<td>Cause movement</td>
</tr>
<tr>
<td>b. Eccentric</td>
<td>M.F. &lt; O.F.</td>
<td>Lengthening</td>
<td>Resist movement</td>
</tr>
</tbody>
</table>

Running. These contractions are essential for absorbing the opposing forces, lessening the impact on joints.
Muscle Contraction – The Basic Function of Muscle (cont.)

Let's look at some examples of the different types of muscle contractions.

First, let's consider a person doing arm curls with a 25-pound dumbbell. (Remember that, in reality, torques about the elbow are the important consideration. Whether the weight is lifted, lowered, or held in the same place is determined by the relationship between muscle torque trying to cause elbow flexion and torque due to effect of gravity on the dumbbell and forearm and hand tending to cause elbow extension. For simplicity here, I will refer to the forces as if they were the same as the torques, and I will ignore the weight of the forearm and hand.) If force exerted by the elbow flexor muscles (e.g., biceps brachii muscle) is greater than 25 pounds, the weight is lifted. The muscles shorten in a concentric contraction that causes the weight to move upward. How fast the weight is lifted will depend on how much greater the muscular force is than the weight of the dumbbell. If the muscular force is only slightly more than 25 pounds, the weight will be lifted slowly. If the muscular force is a lot more than 25 pounds, the weight will be lifted rapidly.

After the dumbbell has been lifted, it must be lowered again to complete the repetition and get ready for the next lift. Actually, no muscular force needs to be exerted to do this. If the person simply lets go of the dumbbell, it will fall by itself due to gravity. This would be hard on the floor and perhaps toes, depending on where the dumbbell lands. And it would make doing a set of repetitions more difficult. Plus, it would leave out the important “negative” part of the exercise, the eccentric contractions. So, instead of simply dropping the dumbbell, it is lowered under control, that is, the downward movement is resisted. This is done by reducing the active force of the elbow flexor muscles to less than 25 pounds. Note that these muscles are contracting (developing active force), trying to cause elbow flexion, but now the opposing force of gravity acting on the dumbbell is greater. So elbow extension results, the elbow flexor muscles are forced to lengthen, and the dumbbell is lowered under control. As with the concentric contraction discussed above, the velocity at which the weight is lowered depends on how much less the muscular force is than the weight of the dumbbell.

Finally, imagine that the person stops in the middle of a repetition and holds the dumbbell perfectly still with the angle at the elbow at 90 degrees. This “prevention of movement” is accomplished by static contraction of the elbow flexor muscles – the muscular force exactly equals the opposing force of gravity acting on the dumbbell. The slightest change in muscular force will result in movement at the elbow and a dynamic contraction.
I must say a little more about torque. Anyone who has lifted weights knows that a weight is easier to lift when the joints involved are at certain angles and harder to lift at other angles. The weight of the load being lifted hasn't changed, and usually there has not been an appreciable change in muscular forces during the lift. What has changed is the leverage – leverage of the weight being lifted and of the muscles. Sometimes leverage can be adjusted to make muscular forces more effective. For example, when doing an arm curl, flexing at the wrists moves the weight just a little closer to the elbow joint, reducing its torque and making it easier to lift. This is the same as moving the heavier person closer to the axis of a seesaw, so he/she can be balanced by a lighter person. I do not want to minimize how important leverage is in determining the effectiveness of a force. I simply want to focus on muscle function in this unit and in this course. More detailed treatment of leverage of muscles and opposing forces is usually done in biomechanics courses.

Now let's consider a person running on different grades. Running involves a series of lifting and lowering of the body with each stride cycle. Lifting a weight against gravity requires concentric contractions; lowering a weight, resisting the force of gravity, requires eccentric contractions. Therefore, extensor muscles of the hip, knee and ankle must contract concentrically to accelerate the body upward and forward during the push-off phase of a stride. These same muscles must contract eccentrically to decelerate the body during the landing phase. Just as with the lowering of the dumbbell in the example above, no muscle contractions are needed for the body to fall to the surface with each stride; gravity will do that. But eccentric muscle contractions are essential for controlling this fall, that is, controlling how far the body’s center of mass falls, and dissipating the impact forces over a longer time and over various body structures.

When running on a horizontal surface (i.e., no grade), the body rises and falls the same amount. Therefore, there is the same amount of lifting and lowering, and thus similar components of concentric and eccentric contractions. Of course, during running, some joints are kept motionless, and static contractions do this.
Fundamental Concepts (cont.)

Muscle Contraction – The Basic Function of Muscle (cont.)

What about running uphill or downhill? In general, running uphill biases toward concentric contractions of hip, knee and ankle extensor muscles; that is, there is a relatively greater component of concentric contractions than of eccentric contractions. The reason is that the mass of the body is lifted more than it lowers when running uphill. Therefore, more "concentric force" is needed for this lifting and relatively less "eccentric force" is needed to control lowering of the body. Conversely, in downhill running, in general there is a relatively greater component of eccentric contractions than of concentric contractions by hip, knee and ankle extensor muscles. The reason is that the mass of the body lowers more than it is lifted when running downhill. Therefore, more eccentric force is needed to control lowering of the body and less is needed to lift the body.

It is important to note that I have presented generalizations that apply to the body as a whole when running on grades. With specific muscle groups at certain joints, there can be exceptions to these generalizations. One important exception involves the ankle extensor (plantar flexor) muscles during running on a steep uphill grade. When running up a steep hill, the foot necessarily lands on the ball of the foot, and then the heel tends to fall to the surface (i.e., there is ankle flexion or dorsiflexion). This tendency for dorsiflexion is resisted by eccentric contractions of the plantar flexor muscles. Thus, although overall there is a greater component of concentric contractions by hip, knee and ankle extensor muscles during running up steep hills, there is also a large eccentric component for the ankle extensors. This example points out the importance of analyzing movements carefully, to avoid errors that may result from applying generalizations to specific body segments.
Fundamental Concepts (cont.)

Muscle Contraction – The Basic Function of Muscle (cont.)

You have probably heard references to isokinetic muscle contractions. What are these? And how do they relate to static, concentric and eccentric contractions?

Isokinetic literally means “constant velocity.” Therefore, an isokinetic contraction is a contraction in which the velocity of the contraction stays exactly the same throughout the entire contraction. Technically a static contraction is isokinetic because velocity is constant at zero. But generally, the term "isokinetic" is used to refer to dynamic contractions. So, isokinetic contractions are simply a special type of concentric and eccentric contractions.

In typical movements of the body, muscles rarely contract isokinetically. The use of isokinetic contractions became popular in clinical settings with the advent of isokinetic dynamometers (e.g., Cybex, Kin-Com) some 25 years ago. Dynamometers measure force, and specifically muscle strength. Isokinetic dynamometers keep angular velocity of joint motion constant at selected speeds, no matter how much muscular force or torque is applied. These instruments are useful in orthopedic and sports medicine and physical therapy for evaluating muscular strength over a complete range of joint motion. This in turn is useful in diagnosing injuries, tracking progress of therapeutic interventions, and evaluating success of training programs.

Functional Anatomy of Skeletal Muscle Tissue

In keeping with a course on the physiology of exercise, this unit on skeletal muscle emphasizes function of muscle rather than structure. But, as mentioned in the introduction to the course, one must know a certain amount of anatomy to be able to understand physiology. Therefore, in this section I will present aspects of skeletal muscle structure that are essential to the functioning of muscle during exercise.
Muscle as primary tissue consists of muscle cells or fibers. Skeletal muscle fibers have a cylindrical, thread-like structure that is different from the structure of other muscle fibers. Skeletal muscle fibers are organized into whole muscle organs by a network or “skeleton” of connective tissue that consists primarily of the protein collagen.

Each muscle fiber is surrounded by a sheath of connective tissue called the endomysium (literally, “inside muscle;” this connective tissue is not inside muscle fibers, but it is the innermost connective tissue in a whole muscle).

Bundles or fascicles of fibers are wrapped by a connective tissue sheath known as the perimysium (literally, “around muscle;” not around the entire muscle, but around bundles of fibers).

Finally, all of the fascicles of the entire muscle organ are wrapped by a sheath of connective tissue called the epimysium (literally, “on muscle”).

The endomysium of individual fibers is connected to the surrounding perimysium, which in turn is connected to the surrounding epimysium, which connects to the muscle’s tendons, which connect to bones of the skeleton. This connective tissue structure is perfect for transmitting the force developed by the individual muscle fibers to the bones of the skeleton. This connective tissue is very noncompliant or stiff, which means it resists being stretched. As a result, it faithfully transmits forces, as does a rope in a tug of war, or a tow chain used to pull a car out of a ditch.

So the force developed by a muscle fiber is transmitted to its surrounding endomysium, from the endomysium to the perimysium, from the perimysium to the epimysium, from the epimysium to the tendon, and ultimately from the tendon to the bone.
In addition to the important network of connective tissue that organizes skeletal muscle organs, other components of the muscle organ are located within the network of connective tissue outside the muscle fibers. These include neurons and nerves; blood vessels; and lymph vessels.

Skeletal muscle fibers range from a fraction of an inch to several inches in length, depending on the particular muscle organ the fibers are a part of, and they range from 10 to 100 micrometers (0.01-0.10 mm) in diameter. Thus, the largest fibers are similar to a human hair, just barely visible to the unaided eye. Obviously, then, to look at details of the structure of a muscle fiber requires a microscope.

The components of a skeletal muscle fiber relate to five general functions:

- **Genetics** – Components that are involved in synthesis of proteins and other molecules for the growth of the fiber, repair after injury, and generation of new fibers at certain periods of development of the organism. Nuclei are structures in this category. Skeletal muscle fibers are unique in having many nuclei per fiber. These are normally located on the periphery of the fiber, just beneath the outer cell membrane.

- **Metabolism** – Components involved in energy turnover and especially ATP synthesis. Mitochondria are the primary structures in this category. Muscle mitochondria are also called sarcosomes.

- **Structure** – Components that provide the appropriate structural organization for everything in the fiber, so it can function properly. There are, for example, a number of proteins (e.g., titin, nebulin) that make up the cytoskeleton (“cell skeleton”). Their primary, and perhaps only, function is to organize other components in the proper relationship to each other.

- **Regulation** – Components that are involved in controlling contraction and relaxation of the fiber. The primary subcellular structure in this category is the sarcoplasmic reticulum (SR), which regulates calcium concentration within the cell in response to nervous...
Concentration within the cell in response to nervous stimulation.

- **Contraction** – Components that are directly involved in generating force. Examples include the so-called thick and thin myofilaments, and the proteins myosin and actin.

In the following section, I will deal with basic structures of the muscle fiber that relate primarily to contraction and the regulation of contraction.

**- Functional Anatomy of Skeletal Muscle Tissue (cont.)**

(Ref. Fig. 8.1 & 8.2 in Powers & Howley.)

The textbook has diagrams illustrating the levels of organization of structure of a muscle, from the whole muscle organ down to the muscle fiber and then to subcellular components. You should familiarize yourself with the points illustrated in those diagrams.

I want to emphasize several points. One way to study muscle structure is to start with the largest structure, the whole muscle organ (gross anatomy) and then gradually examine smaller and smaller structures, as though gradually turning up the power of a microscope. By this approach, the order is muscle organ à fascicles à individual fibers à myofibrils à myofilaments à individual molecules of myosin and actin, for example. The opposite approach starts with the smallest substances and structures and proceeds to larger and larger structures. This is more in line with the way muscle is formed during growth and hypertrophy. I will use this latter approach in discussing the structure of a skeletal muscle fiber, starting with molecules and then selected subcellular structures that form the fiber.
The two molecules that directly generate the force in muscle contraction are the proteins myosin and actin, and especially myosin. These are often called contractile proteins or myofibrillar proteins.

Myosin is a long and slender molecule with a tail portion and a head portion. It has a couple of hinge points at which the molecule can bend relatively easily. Myosin has two very important functional characteristics:

(a) On its head is a site that can bind easily with actin under appropriate conditions.

(b) A portion of the myosin head is the enzyme ATPase, the enzyme that hydrolyzes ATP rapidly, making energy available.

Actin exists as spherical globules attached end to end to form a long filament. Actin has two important functional properties that complement myosin’s properties:

(a) Actin has myosin binding sites, that is, locations on the molecule where myosin attaches easily.

(b) Actin stimulates the activity of myosin ATPase.
To make a muscle fiber, very many myosin and actin molecules must be synthesized. Individual amino acids must be attached in just the right sequence to form each molecule. As myosin molecules are formed, the tails of some are attached to a membrane in the fiber known as the M-line. The M-line is also made up of proteins that must be synthesized and attached to each other in a very specific arrangement. Other myosin molecules are attached to the myosins that are attached to the M-line proteins, forming thick filaments that extend away from the M-line on both sides. The main structure of each thick filament is the tail portions of myosin molecules, bundled together like a sheaf of wheat stalks. The head portions of the molecules extend outward from this main structure.

At the same time, actin molecules that are formed are attached to a membrane known as the Z-disk (or Z-line), and thin filaments of actin are formed, extending outward from the Z-disk (on both sides) toward the M-line that is mid-way between one Z-disk and the next. These thin filaments are positioned between the thick filaments. This is by no means random or haphazard. The positions of the thick and thin filaments, as they are formed, are set precisely by structures such as the Z-disks and M-line proteins, as well as the cytoskeletal proteins. As a result, the 3-dimensional structure is very precise: Each thick filament is surrounded by six thin filaments in a perfect hexagon, and each thin filament is surrounded by three thick filaments in a triangle. This arrangement optimizes the positions of myosin-binding sites on actin in relation to the myosin heads that project toward the thin filaments from the thick filaments.

Between the filaments is myoplasm (or sarcoplasm), a fluid consisting mostly of water, but also containing ATP, electrolytes (e.g., calcium), proteins, and other substances.
Functional Anatomy of Skeletal Muscle Tissue (cont.)

(Ref. Fig. 8.1-3, 8.5, & 8.6 in Powers & Howley.)

Many thick and thin myofilaments arranged in parallel with each other are organized into myofibrils (literally, "little fibers"). There are many myofibrils running parallel to each other in each muscle fiber. It is in the "space" between myofibrils that other cell structures are located, especially mitochondria and the SR (sarcoplasmic reticulum). It is critical that these structures be near the contractile proteins, but not where they would interfere with the attachment of myosin heads to actin.

The longitudinal arrangement of thick and thin filaments is precisely controlled too. The distance from one Z-disk to the next Z-disk is called a sarcomere. In each sarcomere, thin filaments extend from the Z-disk at each end towards the middle, but not all the way to the M-line. And thick filaments extend from the M-line in the middle of the sarcomere toward, but not all the way to, the Z-disks. In an entire muscle fiber, many sarcomeres exist in series, like links of a chain. The length of a single sarcomere is about 2 microns (0.002 mm), so you can see that there would have to be many sarcomeres in a fiber. The normal skeletal muscle fiber has a very organized spacing of the elements of each sarcomere and of sarcomeres across fascicles. This is what gives skeletal muscle its striated appearance under the microscope.
To summarize, the essential structures for force development are the thick and thin myofilaments. Thick filaments are essentially strands of myosin molecules, and the filaments project out from M-lines. Thin filaments are primarily actin molecules, and they project out from Z-disks. The very specific arrangement of these structures is also controlled by cytoskeletal proteins. When a muscle fiber is formed or grows, all of these proteins must be synthesized from amino acids and placed in just the right positions. Myofilaments are organized laterally into myofibrils, defined primarily by the surrounding mitochondria and SR. Increasing the cross-sectional diameter of a muscle fiber usually requires adding more myofilaments and myofibrils in parallel with each other. This is like adding strands to a rope to make it thicker and stronger.

Sarcomeres are added end to end as appropriate for the length of the fiber.

(A related side-note: When muscles are fixed in a longer-than-normal position, such as when a limb is in a cast, the muscle will assume a new, longer length by adding sarcomeres on the ends of fibers. Conversely, when a muscle is fixed in a shortened position, the muscle will shorten by eliminating sarcomeres from the ends of fibers. The purpose of this is to keep individual sarcomeres at an optimal or near-optimal length in terms of overlap of thick and thin filaments, and therefore in terms of the relationship between myosin and actin molecules.)

The force that a muscle fiber develops in contraction is the sum of the forces of many myosin molecules attaching to and pulling on actin molecules. In dynamic contractions, the thick and thin filaments slide across each other, the so-called sliding-filament mechanism of contraction.
- Functional Anatomy of Skeletal Muscle Tissue (cont.)

(Ref. Fig. 8.6 in Powers & Howley.)

The thin myofilaments contain two other important proteins, troponin and tropomyosin. As a fiber develops, these proteins must also be synthesized and placed in their proper positions on the thin filaments. These proteins are sometimes referred to as the troponin-tropomyosin (Tn-Tm) complex. This complex is important in the regulation of muscle fiber contraction. It is arranged in a very specific way along the actin backbone of the thin filament. Recall that myosin and actin normally have an affinity for each other. Therefore, unless something prevents it, myosin tends to bind to actin and force is generated. Under resting, relaxed conditions, the Tn-Tm complex is in a position on the thin filament that interferes with actin and myosin binding. For contraction to occur, the Tn-Tm complex must move out of the way. This involves a change in conformation of the troponin, and sliding of the entire complex to a different position on the thin filament.

What controls this? Calcium is the key. When the concentration of the calcium ion (Ca$^{++}$) is high in the myoplasm, calcium tends to bind to troponin. This causes the changes in the Tn-Tm complex that allow myosin-actin binding, that is, contraction. When myoplasmic [Ca$^{++}$] is low, troponin gives up calcium; this causes the changes in the Tn-Tm complex that inhibit myosin-actin binding, and contraction stops.

So, high myoplasmic [Ca$^{++}$] leads to contraction and low myoplasmic [Ca$^{++}$] leads to relaxation.
### Functional Anatomy of Skeletal Muscle Tissue (cont.)

(Ref. Fig. 8.3 in Powers & Howley.)

What controls the myoplasmic $[\text{Ca}^{++}]$?

This is the function of the SR, the sarcoplasmic reticulum. A reticulum is a network. The SR is a network of membrane-bound tubes and sacs surrounding each myofibril. The SR membrane is made up especially of protein and lipid molecules. Inside the SR is fluid that contains a relatively high concentration of calcium. Imbedded in the SR membrane are specific proteins that pump calcium ions from the myoplasm into the SR. This calcium pumping requires energy from the breakdown of ATP. These pumps are constantly active, trying to keep myoplasmic $[\text{Ca}^{++}]$ low. Normally, calcium passes out of the SR into the myoplasm very slowly, so the pumps can easily stay ahead of calcium release. However, electrical stimulation of the muscle fiber causes the SR membrane to become much more permeable to calcium, so calcium passes easily from the SR into the myoplasm surrounding the myofilaments. This raises myoplasmic $[\text{Ca}^{++}]$ and leads to myosin-actin binding (i.e., contraction). This binding continues until myoplasmic $[\text{Ca}^{++}]$ is lowered, which depends on the calcium pumps of the SR.

I hope you recognize the critical role the SR plays in regulating contraction of a muscle fiber by regulating myoplasmic $[\text{Ca}^{++}]$. In the formation of a fiber or segment of fiber, the molecules of the SR membrane must also be synthesized and arranged properly in relation to the contractile elements.
There is one more structure of a skeletal muscle fiber that is essential for contraction, the sarcolemma. The sarcolemma is the specialized outer cell membrane of a muscle fiber. It has many functions. One is the obvious function of defining the outer limits of the fiber. Another is to separate the intracellular environment from the extracellular environment, regulating the passage of substances from one side of the membrane to the other. We referred to this function in the study of metabolism, referring, for example, to glucose and lactic acid transport across the sarcolemma. In this section, our interest is in the sarcolemma’s ability to be electrically stimulated by a neuron and to conduct an electrical impulse down the length of the fiber.

The main structure of the sarcolemma is the same as the structure of most membranes, consisting of a double layer of phospholipids (a lipid bilayer). This lipid membrane is impermeable to nearly all substances, so it provides excellent protection of the fiber’s internal environment. Embedded in the membrane are many different proteins that serve as channels through which specific substances can pass. Whether these channels are open or closed is controlled, and this controls entrance and exit of substances through the sarcolemma. For example, certain proteins are sodium channels and others are potassium channels. These control the passage of these ions across the sarcolemma, and this is critical in controlling electrical stimulation of the fiber.

Another protein in the sarcolemma is a sodium-potassium pump. This protein pumps sodium from inside the fiber to the outside in exchange for potassium going the other direction. This process requires energy from ATP hydrolysis. Sodium-potassium pumps are active all the time, but most active during periods of repeated fiber contractions. During stimulation of a fiber, sodium tends to move inward and potassium outward. If the pump did not counteract these ion movements, there would quickly be abnormal levels of extracellular potassium and intracellular sodium.
Under normal circumstances, a skeletal muscle fiber will contract only if it is electrically stimulated by an impulse from the central nervous system via an alpha motor neuron. The sarcolemma has a specialized area, usually near the midpoint of the fiber, known as the motor endplate. This is where the motor neuron synapses with the muscle fiber. The axon of the alpha motor neuron ends in close proximity to the motor endplate of the sarcolemma. (This is sometimes referred to as the myoneural junction.) An electrical impulse (action potential) that reaches the end of the axon causes release of the chemical substance acetylcholine from the axon into the synaptic area. The sarcolemma of the motor endplate is specially designed to bind acetylcholine briefly and then to release it again. This brief binding results in initiation of a single electrical impulse that is normally conducted over the entire sarcolemma.

Individual skeletal muscle fibers are organized into functional units known as motor units. A motor unit is a single alpha motor neuron and all of the skeletal muscle fibers innervated by the neuron. The cell body (soma) of each alpha motor neuron is located in the spinal cord. An axon extends out from the cell body, carrying impulses from the central nervous system to muscle fibers. Each axon branches to synapse with many skeletal muscle fibers.

Motor unit size refers to the number of muscle fibers in the particular motor unit. Motor units vary greatly in size. The largest motor units have more than 1,000 muscle fibers and the smallest have fewer than 100 muscle fibers. Although the muscle fibers in a motor unit are structurally distinct, they function as a unit. This is because electrical impulses in the motor neuron will go to every muscle fiber in the motor unit, and each of these muscle fibers will be electrically stimulated.
Functional Anatomy of Skeletal Muscle Tissue (cont.)

As mentioned earlier, skeletal muscle fibers are organized into bundles or fascicles, each surrounded by perimysium. In some muscles, fibers and fascicles are arranged in parallel to the long axis of the muscle organ. This is referred to as a fusiform arrangement. In other muscles, fibers and fascicles are arranged at an angle to the long axis of the muscle. This is referred to as a pennate or pinnate arrangement. Each of these arrangements has a functional advantage and disadvantage. The fusiform arrangement permits more sarcomeres in series and therefore longer fibers. Such fibers favor velocity of shortening when they contract. The pennate arrangement permits more sarcomeres in parallel with each other. This favors force development.

For the most part, these arrangements of fibers within various muscles are genetically fixed. However, when pennate muscles hypertrophy or atrophy, the angle of orientation of the fibers and fascicles may change, which can affect the muscle’s functional capacity.

Review of lesson

You have come to the end of the online content of Unit 3 - Lesson 1. When you want to review the concepts in this lesson, use the Learning Objectives on Page 1 of this lesson and the Review Question below. These should be a good study guide. If you can correctly do what the Objectives and Review Question ask, you will have mastered the most important concepts in this lesson. Please realize, however, that these do not exhaustively cover all the information in the lesson.

If you are uncertain about any Objective or Review Question, or if you want clarification or expansion of any point in the lesson, I urge you to start a threaded conference discussion on WebBoard. Other students may have the same concerns, will probably benefit from the discussion, and may have the information you seek. And, of course, feel free to contact me (Dr. Eldridge) for assistance.

Be sure to check the Announcements Page to see whether there is a specific WebBoard or other assignment associated with this lesson.

Review Question

Analyze the types of muscle contractions of the knee extensor muscles (e.g., quadriceps femoris m.) and the ankle plantar flexors (e.g., gastrocnemius and soleus m.) of both legs during one cycle of a step test. The person faces the same direction throughout the test, stepping up onto a step and stepping back down again always leading with the same foot (right foot leads first).
down again always leading with the same foot: right foot up, left foot up, right foot down, left foot down.