Muscle-Tendon Mechanics

Muscle Fiber Geometry

- Muscle fibers are linked together by collagenous connective tissue. Endomysium surrounds individual fibers, perimysium collects bundles of fibers into fascicles and epimysium ensheathes the entire muscle (Fig. 3.1).

- Muscle fibers do not attach directly to bone, but apply forces to the skeleton via aponeurosis and tendon, which arise from a specialized region called the myotendinous junction. Here myofibrils and collagen fibers overlap, forming longitudinal infoldings. Overlapping contact increases the strength of the junction compared to end-to-end contact since cell membranes support shear loads better than the tensile loads. Furthermore, the infolding serves to reduce the shear per unit area by increasing the area of surface contact between the myofibrils and the collagen fibers, thereby allowing larger shear loads to be supported.

- The proximal site of attachment of a muscle is known as its **origin** while the distal attachment site is its **insertion**. The origin and insertion sites are located on opposite sides of a joint. Muscle contraction produces rotation of the insertion site around the joint. Often a muscle or the muscle-tendon unit spans more than one joint. Contraction of such a muscle will produce rotation of all of the spanned joints.

- The geometrical arrangement of the fibers and connective tissue plays an important role in determining muscle force and mechanical behavior. Tendons vary considerably in shape, ranging from flat bands to cylindrical cords. They may be short and thick or long and thin. The shape of the tendon affects its physical properties and also determines how the muscle fibers can be geometrically arranged. Muscle fibers generally attach to aponeurosis or tendon in parallel arrays (Fig. 3.2).

- Surfaces of attachment are increased by the attachment of muscle fibers along the sides of tendons and aponeuroses. In almost all cases, the muscle fibers attach at a slight angle with respect to the line of pull of the tendon. This angle is called the pennation angle (Fig. 3.2).

- The pennation angle of a muscle at rest length can vary considerably among muscles. For example, muscles such as brachialis, tibialis anterior and lateral gastrocnemius have been shown to have pennation angles as small as 10° under resting conditions at neutral joint angles. However, under the same conditions, muscles such as soleus or medial gastrocnemius may have pennation angles as large as 20-25°.

- Pennation angle increases as the length of the muscle-tendon unit is shortened by rotation of the joint. For example, under resting conditions the pennation angle of soleus increases from about 20° to 35° when the ankle is plantarflexed from 90° to 150°.

- If a muscle contracts or if its length is changed while it is contracting there can be even greater variations in pennation angle. In the brachialis muscle the pennation angle can go from 10° in
the relaxed state to about 25° when contracting at a short length (Fig. 3.3). The medial gastrocnemius and soleus muscles can undergo even larger changes, with pennation angles as large as 50° when the muscles are contracting maximally at short lengths (e.g., 90° knee angle, 140° ankle angle). On the other hand, the pennation angle of tibialis anterior increases by only 2° from rest to maximal contraction at an ankle angle of 130°.

- The force vector generated by a pennate array of muscle fibers has a component that lies along the line of action of the tendon that contributes to force and motion at the origin or insertion sites. The other component is perpendicular to the line of action of the tendon and makes no contribution to force along the line of action of the tendon (Fig. 3.2). The greater the pennation angle, the less force a muscle fiber contributes along the line of action.

- The component of the muscle fiber force perpendicular to the line of action of the tendon causes muscle fibers to push against each other, against other soft tissue or against bone. This leads to changes in the shape of the muscle during contraction. These changes in shape may cause the tendon to shift position, leading to a change in the direction of the line of action with respect to the site of origin or insertion during contraction.

- Muscle fibers can be arranged in a variety of geometrical configurations (Fig. 3.4). When all of the muscle fibers are approximately parallel to one another the muscle is called a unipennate muscle. If there are two sets of parallel fibers, oriented in different planes, but inserting on a common aponeurosis or tendon, the muscle is called a bipennate muscle.

- In fusiform muscles such as the biceps, fibers run parallel to one another along the entire length of the muscle. Midway between origin and insertion, the fibers form a cylinder. However, since the cross-sectional area of the tendon is much less than the cross-sectional area of the central region of the muscle, the fibers must taper considerably as they approach the tendon junction. Consequently, the outer fibers will follow a curved path from origin to insertion. When the fibers in the center of the muscle are activated, they tend to shorten and bulge. This displaces adjacent fibers laterally, causing the peripheral fibers to curve farther from the central axis of the muscle. Thus, the most peripheral fibers can have large differences in their pulling directions from one end of the fiber to the other.

- In multi-pennate muscles the fibers may have a complex geometrical arrangement with sheets of fibers oriented in different planes. During contraction local rotations and deformations of sets of fibers will occur in each plane, leading to complex changes in shape. With such complex arrangements of aponeuroses, muscle fiber lengths may vary from one region of the muscle to another in addition to being oriented in different planes. This may lead to different sarcomere lengths for muscle fibers in different regions of the muscle. Since the length-tension relation for the whole muscle is an average of the length-tension relations of all of its fibers, the shape of the length-tension curve for the whole muscle will generally be different than that of a single fiber.

- Although muscle fibers frequently span the entire distance between origin and insertion, they sometimes span only part of this distance. Two or more sets of shorter fibers may be interdigitated between origin and insertion or there may be short bands of tendon, known as
inscriptions, that link the fibers. The advantage of shorter fibers is that they can be activated more quickly than a single fiber of the same length. This is because each fiber is separately innervated, resulting in a shorter distance for action potential propagation along the fiber.

- Different geometrical configurations of muscle fibers permit optimization of different variables such as force, displacement or velocity, according to the number of fibers and their relative lengths.

  - Pennation facilitates a variety of packing arrangements for muscle fibers in a fixed space without the need for modification of fiber length. It is possible to place more fibers in parallel (between the origin and insertion) in a pennate muscle than in a fusiform muscle. This increases the force generated by a given volume of muscle, although each fiber loses a small fraction of its force and the total displacement and velocity achievable at the tendon by contraction of these shorter fibers may be much less.

  - In pennate muscles, the changing angle of pennation during muscle fiber contraction results in movement of the tendon that is greater than the shortening in any single fiber (Fig. 3.2). This effect reduces the sarcomere shortening velocity without necessarily reducing the muscle shortening velocity. Hence, a greater muscle force can be produced for a given shortening velocity of the muscle. Increasing the pennation angle increases the linear excursion of the entire muscle relative to that of individual fibers.

  - If sarcomere length is approximately constant in all muscle fibers, then increasing the length of a muscle fiber implies the addition of more sarcomeres in series. The result is that for a given change in length of a long muscle fiber, each sarcomere will go through a smaller change in length than in a short muscle fiber. Consequently, sarcomeres in long muscle fibers will operate over a smaller range of their length-tension curve than sarcomeres in short muscle fibers. This reduces the variation in force due to length-tension characteristics.

  - The maximum velocity of muscle fiber shortening could be increased by increasing the number of sarcomeres or by increasing the maximum shortening velocity of each sarcomere. The former has the advantage of minimizing reductions in force due to the force-length and force-velocity relations, while the latter has the advantage of minimizing muscle mass.

  - Some muscles, such as the trapezius, the deltoid and the latissimus dorsi have triangular arrangements of muscle fibers. In this case, muscle fibers radiate in different directions from the origin to insertion sites. Muscle fibers originate from a small area from which they fan out to a broad insertion region. The lines of action of such muscles can be modified by activating different populations of muscle fibers, permitting the same muscle to apply force and produce movements through a range of directions.

- The relevant parameter for determining the force-generating capacity of a muscle is its physiological cross-sectional area (PCSA). The PCSA is the cross-sectional area measured perpendicular to the long axes of the muscle fibers. It is not the same as the anatomical cross-
sectional area which is perpendicular to the muscle. The PCSA is a measure of the number of sarcomeres working in parallel within a muscle.

- Note that the volume or mass of a muscle is not a good indicator of its relative force-generating capacity. Muscles can differ in fiber length and PCSA and yet have equal volume (and therefore equal mass) because the volume of a muscle equals its PCSA multiplied by its fiber length. Of two muscles with equal volume, the muscle with the longer fiber length will have the smaller PCSA. The muscle with the longer fibers will be able to shorten faster and will have a larger range of motion, but will have a smaller force potential.

**Tendon Mechanics**

- Muscle fibers are anchored to bone or to other muscles through tendons or tough, flat fascial sheets called aponeuroses (Fig. 3.5). Tendon and aponeurosis have elastic and dissipative properties, but unlike muscle, tendon has no active elements so its elasticity is purely passive.

- The mechanical properties of tendon have usually been determined by means of tensile tests in which the tendon is elongated to failure at a fixed rate while the changes in force are recorded. However, recently, it has been possible to use ultrasound images of muscle and tendon to perform these measurements *in vivo* under true physiological conditions.

- The elongation produced by tensile loads is usually referenced with respect to a length, $l_0$, at which the tissue first bears the load, i.e., when it begins to resist elongation. The elongation, $\Delta l$, divided by $l_0$ is called the tensile strain, $\varepsilon$:

  $$\varepsilon = \frac{\Delta l}{l_0}$$

  Strain is usually expressed as a percentage since it is a dimensionless quantity.

- When tendon is stretched from a relaxed (unloaded) state, there is initially very little resistance to stretch. This is indicated by a concave region in the curve of force plotted against elongation, termed the toe region. Continued elongation within the toe region produces an increase in the stiffness of the tendon, necessitating greater forces for equivalent elongation. Elongation beyond the toe region produces a linear increase in force up to the point of tendon failure (Fig. 3.6).

- Tendon stiffness is very low below about 1% strain, then begins to increase until the strain reaches about 4%, beyond which it remains relatively constant. Tendon failure occurs at about 8-10% strain. Estimates of tendon strain with *in vivo* techniques are subject to error because accurate determination of the length at which tendon first begins to bear load is not possible. However, it would appear that even at maximum contraction, tendon strain is less than 4%, i.e., the tendon may always be operating in the toe region. Aponeurosis, which is more compliant
than tendon, may reach strains of up to 9%. The greater compliance of aponeurosis allows it to be stretched more than tendon before catastrophic failure.

- Tendon stiffness increases as the tendon is stretched. In some muscles it would appear that the stiffness continues to increase over the entire range of force, while in others it remain fairly constant beyond 50% of maximal isometric force. *In vivo* estimates of the elastic modulus, $E$, of tendon suggest that it varies from 0.45-1.2 GPa (1 GPa=$10^9$ N/m$^2$) as stress increases. The tendon stiffness can be calculated from the cross-sectional area, $A$, and tendon length, $l$.

$$K = \frac{AE}{l}$$

- Tendon stiffness increases with thickness and decreases with length. Thicker tendons are stiffer and longer tendons are more compliant.

- Tendon behaves much like muscle when it is stretched. Peak tendon force depends on the rate of stretch, increasing with faster rates of stretch. Once the stretch is complete, force drops to a new steady-state level that depends only on the final length (Fig. 3.8).

- If a constant load is applied to a tendon for an extended period of time, the tendon will slowly lengthen, a phenomenon known as creep (Fig. 3.8). The amount of creep for a given load will depend on the past loading history, i.e., the peak force and rate of loading. Creep indicates that tendon has dissipative as well as elastic properties. When the tendon lengthens without changing force, it does work against dissipative forces and consequently loses stored energy.

- When a tendon is stretched and then brought back to its original length, the force-displacement curve follows a different path during relaxation than it does during stretch. The shape of the curve is similar, but it is displaced slightly towards lower forces, i.e., for the same tendon length (or strain), the force is lower (Fig. 3.9). This is due to dissipative forces in the tendon. The separation between these two curves is known as hysteresis. The area contained between the boundaries of the elongation and relaxation curves represents the energy put into the tendon, which is not returned on recoil. The greater the hysteresis the greater the loss of stored energy.

- The energy loss in a tendon due to hysteresis is typically less than 10%, indicating that its elastic properties dominate over its dissipative properties.

**Muscle-Tendon Unit**

- Tendon must be sufficiently stiff to transmit muscle forces to bone without undergoing significant deformation itself. Some muscles have tendons which are considerably shorter than the length of the muscle fibers, while others have tendons that can be several times longer than the muscle fiber length.

- The greater the relative length of tendon compared to muscle, the fewer sarcomeres in series and the more each sarcomere must shorten to move a given distance or to achieve a given velocity. Increasing the relative length of the tendon tends to increase the variation in force of a muscle due to the greater range of the length-tension curve over which the sarcomeres must
operate. However, an advantage is gained by reducing inertia when the muscle mass is located relatively far from the moving segments, as in the case of the wrist and fingers.

- Because tendon and aponeurosis are elastic elements in series with muscle, the relative stiffness of the tendon or aponeurosis compared to muscle can profoundly affect the mechanical behavior of the muscle-tendon unit.
  - Increasing the tendon length reduces the relative stiffness of the tendon compared to the muscle fibers, while increasing tendon thickness increases it.
  - The static length-tension curve of the muscle-tendon unit undergoes distortion as the tendon or aponeurosis become less stiff compared to the muscle fibers. The slope of the ascending limb of the length-tension curve becomes more gradual. The plateau is shifted to longer lengths, although its width does not change appreciably because force produced by parallel elastic structures compensates for dropping contractile force at long sarcomere lengths (Fig. 3.10). The ascending portion of the length-tension curve of the muscle-tendon unit becomes stretched out because the force is low and, therefore, the tendon is most compliant in this region. Due to the high tendon compliance, a greater length change of the muscle-tendon unit is required to move the sarcomeres along their length-tension curve. Sarcomere length changes more gradually with a compliant tendon than with a stiff tendon, reducing the slope of the length-tension curve by stretching it out over greater lengths.
  - Under resting conditions when no force is being applied to the tendon, tendon, aponeurosis and muscle fibers may all be relatively compliant. When the muscle contracts, the force on the tendon and aponeurosis will increase and they will become stiffer. At the same time, the muscle fibers will become stiffer because the number of attached cross-bridges increases with activation. With increased activation, muscle fiber stiffness can increase to the point where the muscle becomes stiffer than the tendon.
  - As the muscle stiffness increases relative to the tendon stiffness, the amount of tendon stretch during muscle contraction will increase. This means that at higher muscle activation levels, muscle fibers must shorten more to produce the same angular displacement of the joint and must shorten faster to produce the same angular velocity of the joint.
  - Similarly, if an external perturbation is applied which produces motion of the joint, a smaller proportion of the length change will be taken up by the muscle fibers as the muscle stiffness increases with respect to the tendon stiffness.
Figure 3.1 Organization of muscle fibers into fascicles. Termination of fibers at aponeurosis is shown on right.

Relation among muscle fibers and tendon in a pennated muscle. Muscle fibers (lightly shaded region) lie in parallel, have the same length, and are oriented at some angle $\alpha$ to the tendon axis of pull. Functionally, tendon can be considered to consist of an internal portion (i.e., the aponeurosis of muscle origin and insertion; darkly shaded region) and an external portion. As muscle fibers shorten, muscle is assumed to maintain isovolume, tendon to move only along its axis, and fibers to become more pennated (i.e., $\alpha$ increases). Notice that the fiber and tendon shortening are not colinear (compare the "arrows").

(a) Sketches showing a single fiber layer of a loosely placed pinnate muscle and its change with contraction. Assuming that the surfaces of origin and insertion of the fibers do not approach each other during shortening, the force produced at the tendon will be less than the sum of the forces of the individual fibers, but the displacement of the tendon of insertion will be greater than the absolute shortening of any fiber.

(b) the effect of pennation on the contribution of each muscle fiber to whole-muscle force and velocity of shortening. $\beta$ = angle of pennation; $F_m$ = muscle force or velocity vector; $F_{m,n}$ = normal component; $F_{m,t}$ = tangential component.

Figure 3.2 Geometry of muscle fiber attachment to aponeurosis and tendon.
Sonograph of the brachialis muscle

A, actual and schematic pictures of a sagittal slice of the muscle at rest and at 90 deg. The most superficial part of the muscle is to the top, and distal is to the right: a, brachialis pennation. B, actual and schematic pictures of the muscle during a maximal contraction at 90 deg. In the sonograph, the major division marks on the scale are equivalent to 1 cm.

**Effect of torque on pennation during a “fixed-end” contraction**
Brachialis pennation of one subject during a single contraction and relaxation with the elbow fixed at 120 deg. A, elbow flexor torque (line) and pennation (circles) versus time. B, pennation versus elbow flexor torque. O, pennation for increasing torques; ●, pennation for decreasing torques.

**Effect of joint angle on pennation during a shortening and lengthening contraction**
Brachialis pennation of one subject during flexion and extension of the elbow against a constant torque. Upper panel, with a load of 24% of the maximal voluntary flexor torque; lower panel, zero torque or passive condition. O, increasing elbow angles (extension); ●, decreasing elbow angles (flexion). Lines are linear regressions.

Figure 3.3 Effect of contraction and joint angle (muscle length) on pennation angle.
Figure 3.4 Different possible geometrical arrangements of muscle fibers.

(A) Schematic diagram of the frog semitendinosus muscle-tendon unit drawn to scale. Values shown at the top of the figure are lengths in mm (mean ± S.D. for 14 specimens) of the muscle fiber, aponeurosis, tendon, and bone-tendon junction (BTJ). Note that the ratio of muscle fiber to connective tissue is 1.5 (calculated based on relative lengths as $5.5 \times 2 + 2.1 \times 2 = 13.2$; rendering this system relatively "stiff" as defined by Zajac, 1989). (B) Mechanical analog representing theoretical model. Muscle contractile component with ideal length-tension and force-velocity properties is represented by a schematic sarcomere.

Figure 3.5 Attachment of muscle to bone at bone-tendon junction.
Oscillograph record of force vs time for a tension test to failure of a rhesus femur—anterior-cruciate—tibia preparation. A constant distraction rate was used so that the time axis was proportional to specimen elongation. The photographs, obtained from high-speed movies taken during the test, show the preparation at four stages in the test. (From Grood, Noyes and Butler, Note 8. With permission).

Figure 3.6 Relation between force and elongation of tendon. If the force is divided by the cross-sectional area of the tendon and the elongation is divided by the initial tendon length then this becomes the stress-strain curve for the tendon.

Figure 4. Tendon mechanical properties
A, tendon force—displacement relationship; B, stress—strain relationship; C, stiffness—force relationship; D, Young's modulus—stress relationship. Data from one subject are presented.

Figure 3.7 In vivo tendon properties.
Input loading curves for (a) force relaxation and (b) creep tests. Typical output force relaxation and creep curves appear at the right. Note that when the input displacement rate is increased in force relaxation testing, the output peak force increases. After the length change is accomplished, the force relaxes until an equilibrium value is achieved. (From Butler, Noyes and Grood, 1978, in press. With permission).

**Figure 3.8** Dynamic mechanical behavior of tendon during loading.
Figure 3.9 Dynamic mechanical behavior of tendon during loading and unloading, showing hysteresis.

Figure 3.10 Effect of tendon compliance on the force-length relation of the muscle-tendon unit.