Chapter 1

From Isolated Actions to True Muscle Function

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Introduction

In order to function properly for force and power production in locomotion, the skeletal muscle possesses structural elements, which make it very responsive to commands from the nervous system, both centrally and peripherally. It is not intended to go into the details of the nervous control of the muscle contraction in this chapter. However, certain important aspects are needed to clarify the role the nervous system plays in muscle function and movement control. For more specifics, the reader is referred to general textbooks of neurophysiology and motor control. In the simplest form of force generation, the central nervous system (CNS) triggers the chain of activation along the direct pathway (pyramidal or corticospinal tract) as shown in Figure 1.1. The signal can also come from the different brainstem motor areas along the indirect pathways labeled as extrapyramidal tract. The activation signal from the motor areas passes then through several stages before reaching the muscle fibers to activate events which include Ca\(^{2+}\) release from the sarcoplasmic reticulum (SR) and subsequent contraction (excitation–contraction coupling). In addition, and very importantly in motor control, the signal can be initiated in the various muscle, joint, skin receptors, etc. The nervous system operates as a controller being able to initiate action potentials, receive and integrate feedbacks from the higher brain centers and from the spinal cord levels. Consequently, even when the activating signal travels along the simplest and most direct pathway (corticospinal tract, CST) it is under the influence of

Figure 1.1 Control of muscle by the nervous system. Voluntary strength performance is determined not only by the quantity and quality of the involved muscle mass, the “engine”, but also by the ability of the nervous system, the engine controller, to effectively activate the muscles. (According to Sale 1992, with permission.)
of inputs from different sources and levels of the nervous system. All this information, regardless of the source, is received and integrated by the alpha motor neuron, which is called the “final common pathway of the motor system.” The type of muscle contraction is then determined by the frequency of action potentials coming from the alpha motor neuron. The alpha motor neuron can itself have different properties, as will be discussed shortly in connection with “fast” and “slow” motor units. Skeletal muscle contains all of the elements needed for force and movement production, but without the nervous control, the muscle is not capable of any force production above the passive tension. The passive tension (or resting tension) maybe due to the muscle’s structural elements, which offer resistance to stretch. Nonetheless, the muscle can be activated by impulses coming along the final common pathway, the alpha motor neuron. Upon activation, it then has a special ability to generate force, resulting in either shortening (concentric action) or resisting external loads (lengthening contraction or eccentric action). A complex integrative process involving the three components, the nervous system, skeletal muscle, and the external load, determines the final direction of movement as well as its velocity (or rate) and magnitude. It is the purpose of this chapter to characterize those factors that are important in understanding the basic interaction between the elements mentioned earlier. Greater emphasis will, however, be given to the important concepts of muscle mechanics as well as to the interaction between the contractile structures and tensile elements in the process of force production under varying movement conditions.

The Motor Unit and its Functional Significance

It is usually believed that human skeletal muscle fibers are innervated by only one motor neuron branch, but this branch maybe one from 10 to 1000 similar branches all having the same axon. Therefore, one axon innervates a number of muscle fibers and this functional unit is called a “motor unit.” Consequently, a motor unit is defined as a combination of an alpha motor neuron and all the muscle fibers innervated by that neuron. Motor unit size (muscle fibers per alpha motor neuron) varies within a muscle, and the number of motor units varies between muscles. As illustrated in Figure 1.2, the motor units have different structural and functional characteristics, which result in their differences with regard to rate of force development (RFD), peak force production, and maintenance of force level without loss of tension (fatigue). The fast, fatigable (FF) type unit develops tension quickly, but is also very easily fatigued. At the opposite end, the S-unit has a slow rate of force production but can produce the same tension (force) repeatedly for longer periods of time without signs of fatigue. It is therefore also called a “fatigue-resistant motor unit.” In addition to those events described in Figure 1.2, there are also other functional differences between motor unit types. One particular feature that illustrates such differences is the response of the motor units to tetanic stimulation. The FF type unit requires a high stimulation frequency to reach a state of tetanus. In contrast, the slower unit requires a much lower fusion frequency. When subjected to repetitive tetanic stimulation, the resulting difference in mechanical response between the two extreme types of motor units is remarkable. It is most probably the size of the alpha motor neuron that determines the specific type of the motor unit. Motor neurons supplying the faster motor units have larger cell bodies and axons. They also innervate larger number of individual muscle fibers. One important feature must be emphasized here: the type of alpha motor neuron determines the histochemical profile and biochemical performance of the individual muscle fibers in a motor unit. Consequently, all the fibers in the same unit have similar chemical profile. It is well known in the literature that muscles differ in their fiber composition (and thus in their motor unit profiles), and that there can be great variation among athletes with regard to the fiber structure in a specific muscle. For example, in the vastus lateralis (VL) muscle, sprinters may have a motor unit make up that causes most of the fibers in that muscle to be of a fast type, and thus capable of producing force at a high rate, but with low fatigue resistance. Endurance runners, on the other hand,
have primarily slow type fibers in the same muscle for the purpose of high resistance to fatigue, but at the same time the rate of force production is lower than in their sprinter counterparts. It has been reported from studies with monozygotic twins that genetic factors strongly influence the variation observed among individuals in muscle fiber composition (Komi et al., 1977) of a specific muscle. Differences in muscle fiber composition observed among athletes have thus raised the question as to whether the fiber composition of an individual athlete is an acquired phenomenon or is due to a genetically determined code.

As discussed in more detail in Chapter 13, the order of the motor unit recruitment follows the so-called “size principle” (Henneman, 1957). The influence of size on recruitment order is attributable to its effect on input resistance. The small motor neurons have a high input resistance, and they are the first to be recruited in response to an increase in depolarizing synaptic currents. As a consequence, smaller motor units are activated before larger units. Due to the relation between the size of the motor neuron and the properties of the muscle fibers it innervates, this recruitment sequence results in slow-contracting and fatigue-resistant motor units being recruited before fast-contracting and fatigable motor units. Although there is some variability in the recruitment order of motor units with similar thresholds, the recruitment order of motor

Figure 1.2 Schematic representation of the anatomic, physiologic, and histochemical properties of the three motor unit types. FF units (top) have large axons that innervate many large muscle fibers. The units generate large tensions but fatigue rapidly (tension record insets). FR units (middle) have moderately sized axons that innervate many muscle fibers. The units generate moderate tensions and do not fatigue a great deal. S units (bottom) are composed of small axons that innervate a few small fibers. The units generate low forces but maintain force for a long time. Reproduced with permission from Lieber R. L. (2003) Skeletal Muscle Structure, Function, & Plasticity, © Lippincott Williams and Wilkins (http://lww.com)
units is essentially the same for isometric and
dynamic contractions, including shortening and
lengthening contractions and during rapid (ballis-
tic) isometric and shortening contractions.

**Muscle–Tendon Mechanics**

Skeletal muscle has different properties, which
influence its functional characteristics. Based on
the earlier discussion about the different types of
motor units (e.g., fast versus slow), the property
of the alpha motor neurons should then be mostly
responsible for the final product of the function:
mechanical performance of the muscle. The human
skeletal muscle is not, however, only the muscle; it
contains an important element of the tendon, which
in its turn has special mechanical characteristics.
Consequently, the performance of skeletal muscle
is under the influence of the innervation, the his-
tochemical make-ups of the contractile elements
and the tendon, which connects the muscle to the
insertion sites on the bones. In human (or animal at
large) body, these elements and profiles must func-
tion together to produce a well-controlled move-
ment. In addition, a muscle in the body acts often
together with its synergist and antagonist muscle.
The final mechanical output is therefore a complex
phenomenon, and it is almost an impossible task
to predict the true movement from measurements
performed with individual components (activation
profile, contractile part, and tendon) only in an iso-
lated form. However, the contribution of the scient-
ists, who have done pioneering work with isolated
preparations, must not be forgotten. This work,
which started already in the early 1900s, has been
fundamental to understanding muscle mechan-
ics in vivo locomotion. Several steps needed to be
taken and the following paragraphs make attempts
to present this basic information.

**Twitch Characteristics of Isolated Muscles**

As already referred to, action potentials traveling
along the final common pathway (alpha motor
neuron) reach finally the t-tubule and release cal-
cium from its stores in the SR. Even a single action
potential results in calcium release with subsequent
binding with the troponin C and generation of
force in the actomyosin cross-bridges. Almost at the
same time the free calcium is taken back into SR.
During this short-lived “active” period when cal-
cium is attached to troponin C, the generated force
can be recorded, and it is called “twitch.” The rate
of rise of the twitch tension as well as its relaxation
are under influence of several factors, including the
availability of free calcium, the speed of the bind-
ing of the myosin heads, rate of the calcium uptake
back to SR, and the rate of the cross-bridge disso-
ciation. Both the rates of the force development and
relaxation are under influence of elastic properties
of the cross-bridge. Most importantly, however, it
is the activation profile that determines the twitch
properties of the motor unit or the entire muscle.

When the electrical stimulation is used for twitch
experiments, its strength must be strong enough to
depolarize the muscle fiber (or muscle) membrane.
Single stimuli of identical strength should then
produce exactly similar force records (twitches).
This indeed happens, if the two stimuli are sepa-
rated by suitable interval. However, when the sec-
ond stimulus is given before the first twitch is over,
the resulting second force peak is usually higher
than the first one (see Figure 1.3). The increase
of the compound force becomes more pronounced
the closer the consecutive twitches are brought
together. This is illustrated in Figure 1.3. If the
time interval between twitches is reduced so that
the train of shocks comes with the frequency of
30 Hz, the force records of the consecutive twitches
do not return to zero. If the stimulation frequency
is further increased, e.g., to 50 Hz, the compound
record may still increase and the curve looks like
an unfused tetanus. Further increase in stimulat-
ing frequency (until 100 Hz, corresponding to a
10 ms stimulus interval) will finally result in com-
plete fusion of the twitch responses. Thus as the
frequency is increased, the ripple over the force
record is reduced. Relationship between degree
of this oscillation and the mean (or sometimes
peak) force is used to imply the speed of muscle.
Fast twitch muscle usually has a higher tetanic
frequency as compared to the slower muscle. In
a particular muscle, however, the 50 Hz stimula-
tion is usually enough to reach almost the full
maximum isometric force level, and the additional
increase of frequency up to 100 Hz does not necessarily increase the peak force, but has considerable influence to increase the RFD (see Figure 1.4). This force–frequency relationship has given the basis for the force–time (F–T) relationships in the conditions of maximal voluntary activation. The fast type muscle can increase the force much faster than the slow type muscle, and this is primarily due to the faster rate of activation. This has subsequently been applied to strength and power training, in which the increase in the RFD indicates improvement in the explosive force production. As explained in Chapter 13, specificity of training calls for modification of the F–T curve, the changes of which take place in the different parts of the curve depending on the training intensities and loads.
There are also indications that young girls have much slower rates of force development as compared to their male counterparts of the same age category (Komi et al., 1977). This was interpreted to indicate that females may have slower activation profile as the boys in the explosive F–T test, where the force production is started with zero activation. This difference may not be so apparent in more normal locomotion, such as stretch-shortening cycle (SSC) type muscle function, in which the preactivity plays an important role in efficient force and power production (see Chapter 2). Further discussion of the importance of the F–T curve and its practical relevance is given in the following paragraphs.

**Basic Muscle Mechanics**

**Types of Muscle Action**

In order to understand the way that skeletal muscle functions in normal locomotion, the relation between stimulus and response needs to be examined in more isolated forms of muscle actions: isometric, concentric, and eccentric. The term “contraction” maybe thought of as the state of muscle when it is activated via its alpha motor neurons, and generates tension across a number of actin and myosin filaments. Depending on the external load, the direction and magnitude of action is different as shown in Table 1.1. In a concentric action, the muscle shortens (i.e., the net muscle moment is in the same direction as the change in joint angle and mechanical work is positive). An eccentric action, the muscle actively resists while it is being lengthened by some external force, such as gravity. In this case, the resulting muscle moment is in the opposite direction to the change in joint angle, and the mechanical work is negative. The use of the term “muscle contraction” is therefore sometimes confusing, and we would prefer to follow a suggestion made by Cavanagh (1988) that the term “contraction” should be replaced by “action.”

The muscle action most frequently used to characterize the performance of human skeletal muscle is the isometric action, which by definition refers to the activation of muscle (force production) while the length of the entire muscle–tendon unit (MTU) remains the same, and the mechanical work is zero. The use of isometric action in locomotion is not, however, meaningless; it plays a very important role in the process of preactivation of the muscle before the other actions take place.

Force production in all types of muscle actions can be seen in the internal rearrangements in length between the contractile and elastic elements. Figure 1.5 depicts these events for the isometric and concentric actions. For the isometric action, in this simplest model of the muscle, force is generated through the action of the contractile component (CC) on the series elastic component (SEC) which is stretched. The resulting S-shaped F–T curve is shown on the right side of Figure 1.5. Concentric action, where the load is attached to the end of the muscle, is always preceded by the isometric phase.

**Table 1.1 Classification of muscle action of exercise types**

<table>
<thead>
<tr>
<th>Type of action</th>
<th>Function</th>
<th>External mechanical work*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Concentric</td>
<td>Acceleration</td>
<td>Positive ($W = F(D)$)</td>
</tr>
<tr>
<td>Isometric</td>
<td>Fixation</td>
<td>Zero (no change in length)</td>
</tr>
<tr>
<td>Eccentric</td>
<td>Deceleration</td>
<td>Negative ($W = F(-D)$)</td>
</tr>
</tbody>
</table>

* $W$, work; $F$, force; $D$, distance.
with the rearrangement of the lengths of CC and SEC. The final movement begins when the pulling force of CC on the SEC equals, or slightly exceeds, that of the load. In eccentric action (not shown in Figure 1.5), some external force, e.g., gravity and antagonist muscles, forces the activated muscle to lengthen.

Of the two “dynamic” forms, eccentric action plays perhaps a more important role in locomotion. When the active MTU is lengthening—after the preactivation (isometric) phase—it forms the basis of an SSC, the natural form of muscle function in sports and normal daily life involving movement of the joints or the whole body. Before going into detail about SSC, the main mechanical attributes of muscle function need some consideration. This will help the reader to understand why SSC has such an important role in force and power production.

**Figure 1.5** Models of isometric (A) and concentric (B) muscle action. In isometric contraction, the total length of the muscle does not change, but activation (A–B) causes the contractile component (CC) to shorten and stretch the series elastic component (SEC). Concentric action begins with an isometric phase where CC first shortens and stretches SEC (A–B). Actual movement occurs when the pulling force of CC on SEC equals or slightly exceeds that of the load P (B–C). (From Braunwald et al., 1967, with permission.)

**Force–Time Characteristics**

As is evident from Figure 1.5, to perform movement at a joint requires time, as calculated from the first intentional “command” either from the CNS or via reflexes from, for example, proprioceptive feedback. This time delay has several components, including both neuronal conduction delays such as synaptic transmission, events for excitation–contraction coupling, as well as mechanical characteristics of the muscle fibers that receive the command signal. In this regard, isometric action is very convenient to describe the stimulus–response characteristics of human skeletal muscle. The first principle of muscle mechanics, the “F–T” relation, varies as a function of stimulus strength as well as between muscles and different species. As already discussed, the size of a single twitch response depends on the stimulus strength: a single shock, if strong enough, produces...
only a small twitch; a second repetitive shock adds to the force of the first stimulus, when it is given before complete recovery of the first response. If one imagines a real movement situation, in which the load is fixed to the end of the muscle, that load does not begin to move before the stimulus strength to the CC to pull the elastic component of the muscle equals or exceeds the total load. When stimulus frequency is increased, the force gradually reaches a tetanic state that ultimately describes the maximum F–T characteristics of a muscle in isometric actions. As already referred to, the isometric F–T relationships are different between muscles and species. The most fundamental feature for human locomotion is the difference between the fast type and endurance type muscles: muscles consisting of a majority of fast twitch fibers (and consequently innervated more heavily by fast conducting alpha motor neurons) have a faster RFD compared with muscles possessing a majority of slow (endurance) type fibers (Komi, 1984).

In spite of this rather clear difference that has been observed in isolated muscle preparations, the existing experimental evidence in humans does not always support the interrelationships (structure versus function) found in isolated muscles. For example, some studies (Viitasalo & Komi, 1978) have demonstrated a significant relationship between structure and function in the case of isometric force production, while the same authors (Viitasalo & Komi, 1981) have failed to do so in another study. Similar contradictions have been observed for the vertical jump test. Consequently, F–T characteristics of either isometric or dynamic origin seem to be under strong environmental influence. Effects of training, for example, on the F–T curve are probably of greater importance than the muscle structure itself. Voluntary explosive force production requires a well-controlled, synchronized activation process. Thus the experimental situation is very different from that of isolated preparations, which utilize constant electrical stimulation either on the muscle or its nerve. In normal human locomotion, the movement is seldom, if at all, initiated from zero activation. Preactivation is a natural way to prepare the muscle for fast force (and movement) production, and to set a zero electromyographic (EMG) activity as a required condition, may not be so successful in all individuals. The important role of preactivation will be discussed later.

Force–time curve has considerable practical interest. In sporting activities, the time to develop force is crucial, because the total action times for a specific muscle may vary between less than 100 ms to a few hundred ms. Thus, if the F–T curve is measured, for example, for the leg extensor muscles, the peak force is sometimes reached after 1000 ms, implying that a specific movement in a real life situation would already be over before these force values were reached. Consequently, training studies have recently concentrated on examining the F–T curve in its early rising phase (see Chapter 13). Several methods have thus been used in the literature to assess the RFD. As recently examined by Mirkov et al. (2004), most of these methods maybe considered as fairly reliable, but their “external validity” to evaluate the ability to perform rapid movements remain questionable. The F–T curve also reveals that if the movement begins at the point of zero EMG activity (the force is also zero), then the practical consequences would be catastrophic. This is naturally corrected by preactivating the muscles appropriately before the intended movement begins. Preactivation is preprogrammed (Melvill-Jones & Watt, 1977) and is introduced to take up all the slack within the muscle before the initiation of fast movements. The preactivation refers usually, but not always, to the isometric phase before the other forms of action take place. Its EMG magnitude is a function of an expected load to move or an impact load to receive, such as in running (Komi et al., 1987). This preactivity corresponds to the initial stimulation that is a necessary component in the measurement of concentric and isometric actions. This requirement is in agreement with the measurement techniques applied in isolated preparations (Hill, 1938; Edman, 1978).

Force–Length Relationship

The skeletal muscle is not only “muscle;” it contains several connective tissue structures, which are not under efferent nervous control. Contribution of these passive structures can be measured by
simply stretching the muscle without stimulation to a number of constant lengths. This procedure demonstrates that resting muscle is elastic and able to resist the force that stretches it. During this stretching, the muscle becomes more and more inextensible, i.e., the force curve becomes steeper with larger stretches. The resulting curve represents a passive force–length (F–L) relationship that is determined largely by the connective tissue structures such as endomysium, perimysium, epimysium, and tendon. Muscles differ especially in the form (and position) of the passive force curve. Figure 1.6 gives examples of three muscles, gastrocnemius (GAST), sartorius, and semitendinosus. From these the GAST muscle contains greater proportion of connective tissue, and consequently the passive force curve becomes steeper earlier than in the sartorius muscle. The active curve in Figure 1.6 constitutes the CC, whose form represents the contribution of the contractile material (fascicle or muscle fibers) to the total force curve, which is the sum of the active and passive forces at given muscle lengths. It must be emphasized that the active curve is not a continuous curve. It represents discrete data points observed when the muscle is held at different lengths and then stimulated maximally (or supramaximally) in each length position. The total F–L relationship differs between the muscles, and for this reason no definite F–L relationship can be described that would be applicable to all skeletal muscles. From these curves, as shown in Figure 1.6, the active component has received much more attention as it resembles the F–L curve of individual sarcomeres. As will be discussed later, the working range of the sarcomere F–L curve seems to be different depending on the activity. The form of the active F–L curve depends upon the number of cross-bridges that are formed at different sarcomere lengths. The sarcomere number is not fixed, even in adult muscles, being capable of either increase or decrease (for details see Goldspink & Harridge, 2003). For the entire MTU, however, exhaustive fatigue has been shown to shift the total F–L and torque–angle curve to the right (Komi & Rusko, 1974; Whitehead et al., 2001), and in severe eccentric exercise this shift has been considered to reliably indicate the degree of muscle damage (Jones et al., 1997). In addition to differences between muscles, the type of muscular exercise seems to determine the portion of the F–L curve (descending limb, plateau phase, or ascending limb) in which a particular muscle operates during locomotion.

It should be mentioned that until recently, it was very difficult to obtain anything other than
a measure of the torque–angle relationship in humans, leading to an estimate of the F–L changes. At present, accurate tensile force calculations can be performed in vivo by applying devices such as buckle transducers (Komi, 1990) or the optic fiber method (Komi et al., 1996) directly to human tendons. With the development of real-time ultrasonography (US), it is now possible to examine noninvasively and in vivo, the respective length changes of the fascicles and tendinous tissues (TT: aponeuroses and the free length of the in-series tendon) during exercise. In general, the obtained results highlight the complexity of interaction between fascicle and TT components (see Chapter 10).

**Force–Velocity Relationship**

It is a common experience that a muscle can shorten faster against a lighter load than it does against a heavier one. In sport an example can be given from shot put, where the lighter shot can be put much further than the heavier shot. The inertia of the weight (shot) is partly responsible for this difference, but the main cause can be found on the muscle level. The muscles can produce much less force when actively shortening against a lighter load. When the load (shot, in our example) is extremely heavy, it cannot be put or lifted. In fact the load that cannot be moved at all, despite the maximum voluntary effort, corresponds to the maximum isometric force of the muscle involved.

Work performed with the isolated muscle preparations has explained this phenomenon. Hill's classical paper (1938) describes this force–velocity (F–V) relationship of an isolated muscle preparation (Figure 1.7a).

This curve can be obtained with constant electrical stimulation against different mechanical loads. The muscle is maximally (or supramaximally) stimulated and when the isometric force reaches its maximum, the muscle is suddenly released, and depending on the magnitude of the extra load the resulting shortening speed can be determined. In this relationship, the maximum force decreases in the concentric mode in a curvilinear fashion, and as a function of the shortening speed. It must be emphasized that the obtained curve is not a continuous one, but a discrete relationship of distinct data points. This classical curve demonstrates the

![Figure 1.7](image-url)
fundamental properties of the skeletal muscle, and its form has also been confirmed in human experiments with maximal efforts against different loads (Wilkie, 1949) or with maximal efforts at different constant angular velocities (Komi, 1973). When the F–V measurements are extended to the eccentric side by allowing the muscle to actively resist the imposed stretch that begins after the maximum (isometric) force level has been reached, maximum force increases as a function of stretching velocity, as shown in Figure 1.7. An important prerequisite in the measurements of F–V curves is the strict control of the maximum preactivation before the movement begins. Although this principle is equally relevant to the measurements of both concentric and eccentric sides, the eccentric force measurements have not followed these principles carefully enough. Figure 1.8 gives this requirement of full preactivation in the eccentric force measurement performed with human knee extensors. The presentation is exactly similar to that used for isolated muscle fiber/sarcomere preparations (Edman et al., 1978).

In both cases, the muscle tissue is fully activated (electrically in the case of isolated muscle fiber and voluntarily in human knee extensors). The stretching of the fiber or muscle must not begin before the preactivation brings the force to full isometric maximum of the particular length of the fiber or the muscle. One can imagine that if the stretch phase begins when the muscle has zero activation (no preparatory activity), the performance of the muscle will be reduced and especially in fast stretch situations the peak force may not be reached at all during the entire stretching phase. As the full isometric activation in human skeletal muscle takes considerable time (sometimes up to 1 s), it is important to obtain the full preactivity in all velocity conditions of shortening (concentric) and lengthening (eccentric) actions. When human experiments have followed the methods of isolated models (Hill, 1938; Edman et al., 1978), the voluntary concentric and eccentric F–V relationships were rather similar to those of isolated preparations (Wilkie, 1949; Komi, 1973; Linnamo et al., 2006). This includes the finding of similar maximal EMG activities across all contraction modes (eccentric, isometric, and concentric) and velocities (Komi, 1973). The observation that voluntary eccentric force can sometimes be less than isometric force (Westing et al., 1991) may well be explained by the fundamental differences between experiments, especially when the preactivation was not maximal before recording the concentric and eccentric forces at different velocities of shortening and stretch, respectively. This possible reduction in eccentric force as compared to isometric force has also been suggested to be due to the inhibition of EMG activity. Again the differences

![Figure 1.8](image-url)
in protocol between these experiments and those from the classical model could be looked at as a possible source of reduced EMG and the respective force level in eccentric action. Consequently, it is quite clear that it is the eccentric mode in which the force and power characteristics of skeletal muscle are greatest. In normal nonfatigue situations, the difference between maximal eccentric and concentric forces can be seen in all muscle lengths (or elbow angles) (Figure 1.9).

Although the Hill curve was not introduced to describe the instantaneous F–V relationship as shown later in Chapter 2, it has been used successfully to follow specific training adaptations of human skeletal muscle. These adaptations deal with the concept of power training, especially for sporting activities requiring high levels of force and speed (see Chapter 13). From the Hill curve, it can be calculated that muscle mechanical power (the product of force and velocity) usually reaches its peak when the speed and forces that are involved represent about \( \frac{1}{3} \) to \( \frac{1}{2} \) of the discrete points in the F–V relationship. Figure 1.10 shows the mechanical power values for both concentric and eccentric sides. In the eccentric actions, the force increases (up to a certain point) as a function of increase in stretch velocity, and the resulting mechanical power values also increase in parallel, and reach values which are many times higher than in the concentric mode. The peak power in the concentric action is very sensitive to differences in muscle fiber composition. Faulkner (1986), among others, demonstrated in human skeletal muscle that the peak power output of fast twitch fibers was fourfold that of slow twitch fibers due to a greater velocity of shortening for a given afterload. In mixed muscle, the fast twitch fibers may contribute 2.5 times more than the slow twitch fibers to the total power production. In human experiments, it is difficult to utilize shortening (and also eccentric) velocities that
can load the muscles with a suitable protocol (as described earlier) across the entire range of physiological speeds. The maximum speed of most of the commercially available instruments can cover only 20–30% of the different physiological maxima. As Goldspink (1978) has demonstrated, the peak efficiencies of isolated fast and slow twitch fibers occur at completely different contraction speeds. Therefore, it is possible that in measurements of the F–V curve in humans, when the maximum angular velocity reaches a value of 3–4 rad/s, only the efficient contraction speeds of slow twitch fibers will be reached. The peak power of fast twitch fibers may occur at angular velocities more than 3 times greater than our present measurement systems allow. Notwithstanding, Tihanyi et al. (1982) were able to show clear differences in F–V and power–velocity (P–V) curves in leg extension movement between subject groups who differed in the fiber composition of their VL muscle. These measurements have been restricted to the concentric part of the F–V curve only. In human muscle, similar efforts have not been made to explore the effect of muscle fiber composition on the eccentric F–V and P–V curves.

If the F–V (and P–V) curve demonstrates the primary differences between concentric and eccentric actions, there are some additional features that stress the importance of the performance potential between these isolated forms of exercise. As already mentioned, the maximum EMG activity between concentric and eccentric actions should be approximately the same. However, it is well documented that the slopes representing EMG and force relationships are different in these two forms of exercise (Bigland & Lippold, 1954; Komi, 1973) (Figure 1.11). To attain a certain force level requires much less motor unit activation in eccentric than concentric action. Logically then, oxygen consumption is much lower during eccentric exercise than in comparable concentric exercise (Asmussen, 1953; Knuttgen, 1986). Furthermore, in relation to movement in general, these earlier findings, including the important reference to Margaria (1938), emphasize that mechanical efficiency (ME) can be very high during eccentric exercise as compared to concentric exercise. This information is then used to explain why the ME in normal locomotion can subsequently be high also in normal locomotion involving SSC exercise (for details see Chapter 7).

One additional and particularly relevant question is “what happens to the fascicle length (magnitude and change of length) during different muscle actions?” In our recent studies, we were able to demonstrate that during pure concentric actions the fascicles show normal shortening (Finni et al., 1998), the magnitude of which maybe intensity dependent (Reeves et al., 2003). In pure eccentric actions, fascicle lengthening (resistance to stretch while muscle fibers are active) should be expected and has indeed been well demonstrated by Finni et al. (2003) for the VL muscle. The fascicle lengths during eccentric action remained constant at all measured isokinetic speeds, but they were also shorter than those measured at higher concentric velocities. Although the latter finding does not directly imply the magnitude or even direction of shortening/lengthening they may stress an important point: the fascicle length change maybe dependent on the muscle and also on the specific movement. This notion becomes even more important, when the fascicle–tendon interaction is studied under conditions of different intensity SSC exercise. Both the chapter to follow (Chapter 2 on SSC) and Chapter 10 (on Ultrasound methodology) will discuss these issues in more detail and in situations of “true muscle function.”

![Figure 1.11 Electromyographic (EMG) force relationship in concentric and eccentric muscle action as measured with forearm flexors. (From Komi, 1973 with permission.)](image-url)
References


