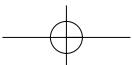
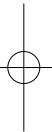
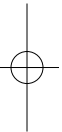
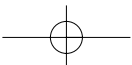
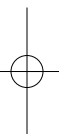
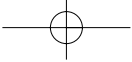


# Part 1

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## Physiology and Biochemistry





# Chapter 1

## Muscle: Producing Force and Movement

PAAVO V. KOMI AND MASAKI ISHIKAWA

The central nervous system (CNS) naturally plays a very important role in the initiation of force and movement. It also coordinates the final action, together with the information coming from the various receptors residing in skeletal muscles, joints, ears, eyes, etc. Skeletal muscle contains all of the elements needed for force and movement production, but without nervous control it is incapable of generating any force above that of passive tension. This may be due to the structural elements of skeletal muscle, 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 resistance to 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 the factors that are important in understanding the basic interaction between the elements mentioned above. 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.

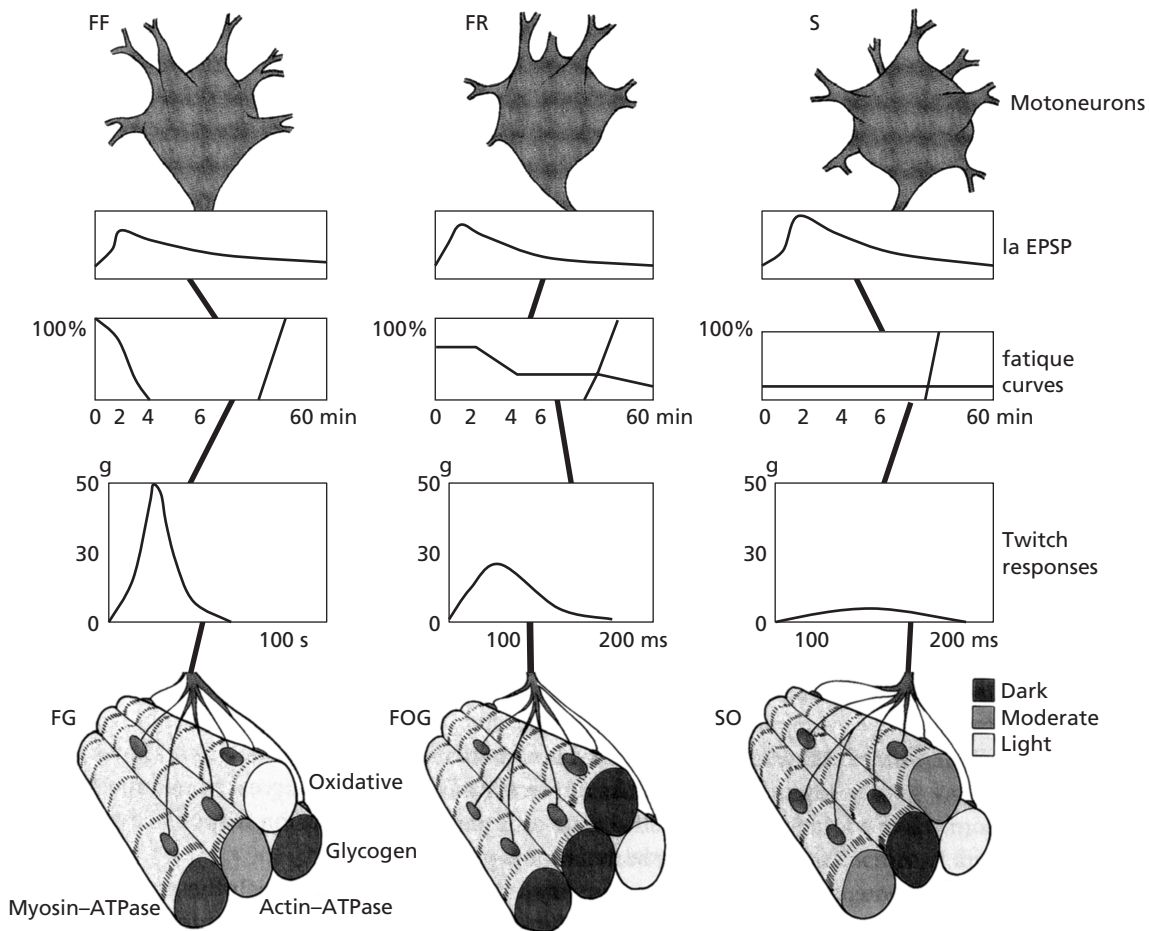
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### The motor unit and its functional significance

It is usually believed that human skeletal muscle fibers are innervated by only one motor neuron branch, but this branch may be one from between 10 and 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 Fig. 1.1, the motor units have different structural and functional characteristics, which result in their differences with regard to rate of force development, peak force production, and maintenance of force level without loss of tension (fatigue). The fast fatigable (FF) unit develops tension quickly, but is also very easily fatigued. At the opposite end, the slow oxidative (SO) 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 the events described in Fig. 1.1, 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

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**Fig. 1.1** An illustrative example of the functional interrelationship between a motor neuron and its muscle fibers within different types of motor units. Motor neurons may be phasic (fire rapidly but with sort bursts) or tonic (slow and continuous). Axon diameter size is directly related to conduction velocity. The muscle fibers have been stained to show: myosin-ATPase, acid-ATPase, succinate dehydrogenase (an oxidative enzyme), and glycogen. Note the differences in twitch tension for each motor unit. EPSP, excitatory post-synaptic potential; FF, fast-twitch and fatigable; FG, fast-twitch and glycolytic; FOG, fast-twitch oxidative and glycolytic; FR, fast-twitch and fatigue resistant; S, slow-twitch; SO, slow-twitch oxidative. (Reproduced with permission from Edgington & Edgerton 1976.)

stimulation, the resulting difference in mechanical response between the two extreme types of motor units is remarkable. 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 of the fibers in the same unit have a similar chemical profile. It is well known in the literature that muscles differ in their fiber composition (and thus in their motor unit pro-

files), 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 composition 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 of a specific muscle (e.g., see Komi *et al.* 1977). This raises the question of whether the fiber composition of an individual athlete is an acquired phenomenon or is due to a genetically-determined code. There is naturally no direct answer to this problem and further discussion of this particular topic is beyond the scope of this chapter.

## Basic muscle mechanics

### Types of muscle action

In order to understand the way that skeletal muscle functions during 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” may be thought of as the state of a muscle when it is activated via its alpha motor neurons, which 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). In 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 “contraction” should be replaced by “action.”

The muscle action most frequently used to characterize the performance of human skeletal muscle is 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 pre-activation of the muscle before other actions take place (Komi 2000).

Force production in all types of muscle actions can be seen in the internal rearrangements in length between the contractile and elastic elements. Figure 1.2 depicts these events for isometric and concentric actions. For the isometric action, the simplest muscle model, force is generated through the action of the contractile component (CC) on the series elastic component (SEC), which is stretched. The resulting S-shaped force-time (F-T) curve is shown on the right side of Fig. 1.2. Concentric action, where the load is attached to the end of the muscle, is always preceded by an isometric phase with a concomitant rearrangement in 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 some external force, for example gravity and antagonist muscles, forces the activated muscle to lengthen.

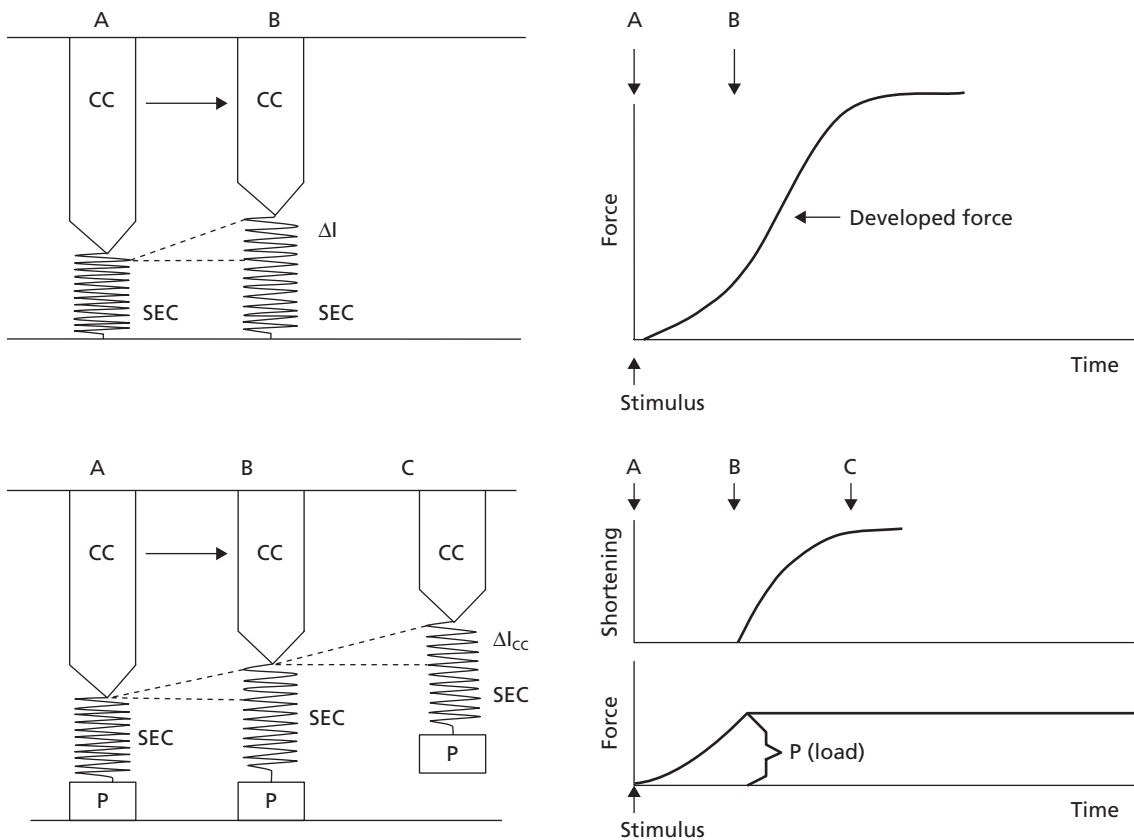
Of the two “dynamic” forms, eccentric action plays perhaps a more important role in locomotion. When the active MTU is lengthening – after the pre-activation (isometric) phase – it forms the basis of a stretch-shortening cycle (SSC), the natural form of muscle function in sports and normal daily life involving movement of the joints or the whole body. Before considering the SSC in more detail, the main mechanical attributes of muscle function need some consideration. This will help the reader

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

Type of action	Function	External mechanical work*
Concentric	Acceleration	Positive ( $W = F(+D)$ )
Isometric	Fixation	Zero (no change in length)
Eccentric	Deceleration	Negative ( $W = F(-D)$ )

\*D, distance; F, force; W, work.

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**Fig. 1.2** 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 hence stretch the series elastic component (SEC). Concentric action is then begun with a similar isometric phase as above (A→B), 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). (Adapted with permission from Sonnenblick 1966.)

to understand why the SSC has such an important role in force and power production.

### Force-time (F-T) characteristics

As is evident from Fig. 1.2, to perform movement at a joint requires time, which is 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 charac-

teristics of the muscle fibers that receive the command signal. In this regard, isometric action is a very convenient model for describing the stimulus-response characteristics of human skeletal muscle. The first principle of muscle mechanics, the “F-T” relationship, varies as a function of stimulus strength as well as between muscles and different species. The size of a single twitch response depends on the stimulus strength: a single shock, if sufficiently strong, will produce only a small twitch; a second repetitive shock adds to the force of the first stimulus when it is given before complete recovery from the first response. If one imagines a real movement

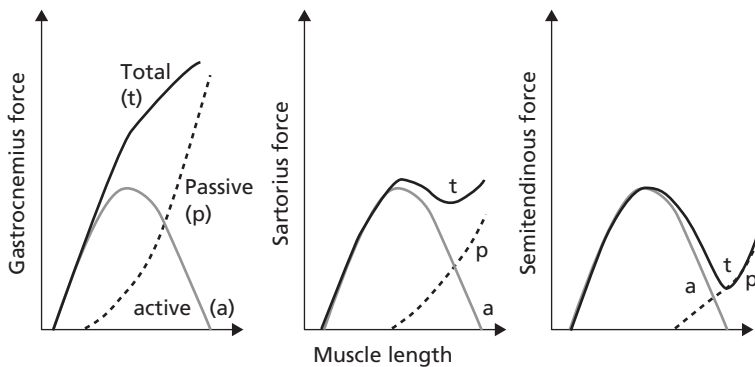
situation in which the load is fixed to the end of the muscle, that load does not begin to move before the stimulus strength to the contractile component to pull the elastic component of the muscle equals or exceeds the total load. When stimulus frequency is increased, the force gradually reaches a tetanic state that ultimately describes the maximum F-T characteristics of a muscle in isometric action. 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 rate of force development compared to muscles possessing a majority of slow (endurance)-type fibers (e.g., Komi 1984).

In spite of this clear difference, the existing experimental evidence in humans does not always support the interrelationships (structure vs. function) found in isolated muscle preparations. For example, some studies (Viitasalo & Komi 1978; Viitasalo & Bosco 1982) have demonstrated a significant relationship between structure and function in the case of isometric force production, while the same authors (e.g., Viitasalo & Komi 1981) 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. Pre-activation is a natural way to prepare the muscle for fast force (and movement) production; to set zero electromyographic (EMG) activity as a required condition may not be successful in all individuals. The important role of pre-activation will be discussed later.

The ability to modify the F-T curve for a specific muscle or muscle group has important implications for athlete training. 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. Several methods have been used in the literature to assess the rate of force development. As recently examined by Mirkov *et al.* (2004), most of these methods may be considered as fairly reliable but their "external validity," in terms of evaluating the ability to perform rapid movements, remains questionable. The F-T curve also reveals that if the movement begins at point zero EMG activity (the force is also zero) then the practical consequences would be catastrophic. This is naturally corrected by pre-activating the muscles appropriately before the intended movement begins. Pre-activation is pre-programmed (Melvill-Jones & Watt 1977) and is introduced to take up all of the slack within the muscle before the initiation of fast movements. This pre-activation corresponds 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 pre-activity corresponds to the initial stimulation, which 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 *et al.* 1978).

### Force-length (F-L) relationship

It is not a surprise that resting muscle is elastic and able to resist the force that stretches it. During this stretching, however, the muscle becomes more and more inextensible; i.e., the force curve becomes steeper with larger stretches (Fig. 1.3). This curve represents a passive force-length (F-L) relationship



**Fig. 1.3** Active (a), passive (p), and total (t) force-length relationships for tree frog muscles. Note that the passive force comes into play at distinctly different regions of the active force-length relationship.

that is determined largely by the connective tissue structures such as endomysium, perimysium, epimysium, and tendon. The active curve in Fig. 1.3 constitutes the contractile component, 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 one. Rather, 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. The active component of these curves (Fig. 1.3) has received significantly 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 increasing or decreasing (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 (see "Task (movement) specificity").

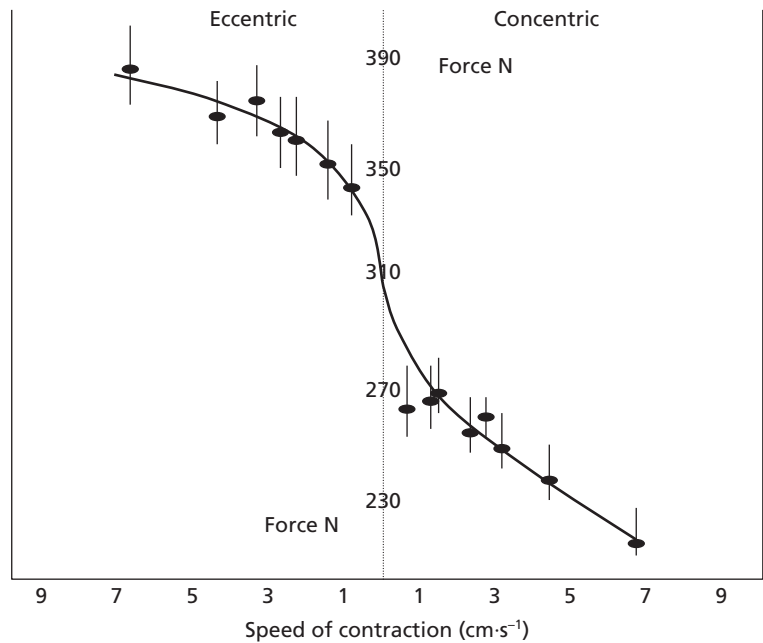
It should be mentioned that until recently it was very difficult to obtain anything other than a measure of the torque-angle relationship in humans, leading to an estimate of the F-L changes. At present, accurate tensile force calculations can be performed *in vivo* by applying devices such as buckle transducers (Komi 1990) or the optic fiber method (Komi *et al.* 1996) directly to human tendons. With the development of real-time ultrasonography it is now possible to examine, both non-invasively 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 "Task (movement) specificity").

### Force-velocity (F-V) relationship

Hill's classic paper (1938) describes the force-velocity (F-V) relationship of an isolated muscle preparation. This curve can be obtained with constant electrical stimulation against different mechanical loads. The muscle is maximally (or supramaximally) stimulated and when the isometric F-T curve 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



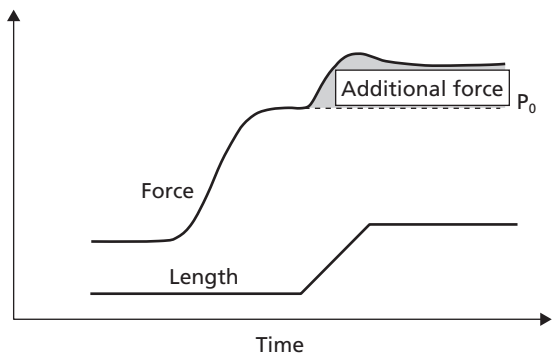
**Fig. 1.4** A force-velocity relationship in eccentric and concentric muscle action for elbow flexor muscle. The measurements were performed with an electromechanical dynamometer, which was designed to apply a constant velocity of shortening or lengthening for the biceps brachii muscle. (Reproduced with permission from Komi 1973 courtesy of S. Karger AG, Basel.)



as a function of the shortening speed. It must be emphasized that the obtained curve is not a continuous one, but a discrete relationship between distinct data points. This classic curve demonstrates the 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 Fig. 1.4. An important prerequisite in the measurements of eccentric and concentric F-V curves is the strict control of the maximum pre-activation before the movement begins. When human experiments have followed the methods of isolated models (Hill 1938; Edman 1978), the voluntary concentric and eccentric F-V relationships were similar to those obtained using isolated preparations (Wilkie 1949; Komi 1973; Linnamo *et al.* 2006). This includes the finding of similar maximal EMG activities across all contraction modes (eccen-

tric, isometric, and concentric) and velocities (e.g., 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 pre-activation 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 in protocols between these experiments and those of the classical model could be considered as a possible source of reduced EMG and respective force level in eccentric action. Consequently, it is quite clear that force and power characteristics of skeletal muscle are greatest in the eccentric mode. Figure 1.5 makes an additional note of the measurement of maximum eccentric force, and demonstrates force enhancement above the isometric level during the lengthening phase.

Although the Hill curve was not introduced to describe the instantaneous F-V relationship (see "Instantaneous F-V relationship during SSC"), it has been used successfully to follow specific training



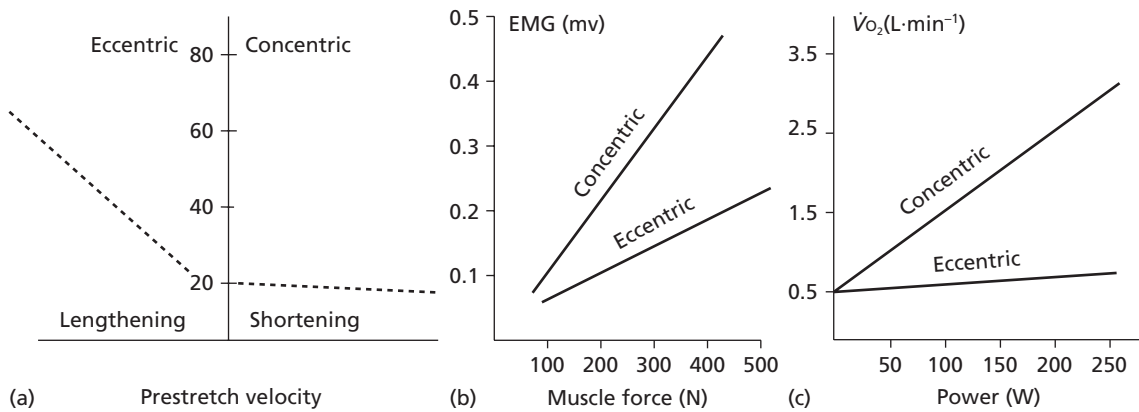
**Fig. 1.5** A schematic presentation to show that if human skeletal muscle is stretched (eccentric action) after maximal isometric force ( $P_0$ ) has been attained, then the force increases considerably. A similar phenomenon is seen in isolated sarcomeres.

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. 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 one-third to one-half of the discrete points in the F-V relationship. The peak power is very sensitive to differences in muscle fiber composition. Faulkner (1986), among others, demonstrated that the peak power output of fast-twitch fibers in human skeletal muscle was four-times 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 to the total power production than the slow-twitch fibers. In human experiments it is difficult to utilize shortening (and also eccentric) velocities that can load the muscles with a suitable protocol (as described above) across the entire range of physiological speeds. The maximum speed of most 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  $3\text{--}4\text{ rad}\cdot\text{s}^{-1}$ , 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 three-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 for leg extension movements between subject groups that differed in the fiber composition of their VL muscle.

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; Fig. 1.6). To attain a certain force level requires much less motor unit activation in eccentric than in 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 can be very high during eccentric exercise as compared to concentric exercise (Fig. 1.6c).

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 may be 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. In this study, the fascicle lengths remained constant during eccentric action at all measured isokinetic speeds, but they were also shorter than those measured at higher concentric velocities.



**Fig. 1.6** (a) Mechanical efficiency of negative work (eccentric exercise) is much higher than that on positive work (concentric exercise). The drawing in (a) is based on the EMG-force relationship (b) and the  $\dot{V}O_2$ -power relationship (c). Important references: (a) Aura and Komi 1987; (b) Asmussen 1953, Komi 1973; (c) Asmussen 1953.

Although the latter finding does not directly imply the magnitude or even direction of shortening/lengthening, it may indicate an important point; i.e., the fascicle length change may be 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.

### Stretch-shortening cycle (SSC) of muscle function

When the different isolated muscle actions were explained in the previous paragraphs, indications were given that they are often used successfully in describing the force transmission and related metabolic events in well-controlled experimental situations. In natural situations and environments, human (and animal in general) skeletal muscle produces force and movement by utilizing a combination of eccentric and concentric actions, and the isometric action plays more of a role in pre-activation; i.e., to prepare the muscle to take up the expected load. The function of the triceps surae muscle during the ground contact phase in running, hopping, and even walking can be used as a typical example to describe normal muscle action – the SSC. Before ground contact the muscle is pre-activated, the level

of which is a function of the expected impact load (or running velocity, for example; Komi *et al.* 1987). The pre-activated triceps surae muscle begins its eccentric action upon the initial ground contact, when the MTU lengthens and receives activation signals from the nervous system. This eccentric or braking phase is then followed, without much delay, by the shortening (concentric) action which, depending on the intensity of effort, can take place in many cases as a recoil phenomenon with relatively low EMG activity. Consequently, SSC has important functions in locomotion: (i) to minimize unnecessary delays in the F-T relationship by matching the pre-activated force level to the level required to meet the expected eccentric loading; and (ii) to make the final concentric action (push-off phase in running, for example) more powerful (in maximal effort) or to generate force more economically (sub-maximal conditions), as compared to the corresponding isolated concentric actions. Cavagna *et al.* (1965, 1968) were among the first to describe the mechanisms underlying this performance potentiation in SSC by using elegant control situations of force and stimulus in a device designed for the group's first experiments with isolated frog sartorius muscle (Cavagna *et al.* 1965), and later also with human forearm flexors (Cavagna *et al.* 1968). Based on these findings and some others (e.g., Aura & Komi 1986),

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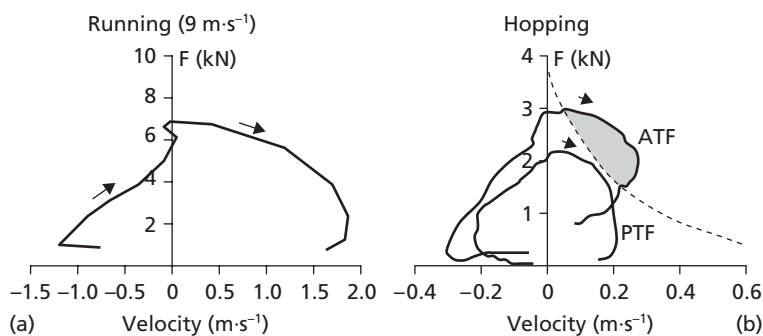
SSC power production is very likely to be dependent not only on the stretch velocity, but also on the time delay (coupling time) between the stretch (eccentric) and shortening (concentric) phases; performance enhancement of the force (and power) output takes place in the final concentric phase of SSC. Economy has subsequently been shown to improve in SSC movements with a shorter coupling time between the braking and push-off phase in more natural types of hopping movements (Aura & Komi 1986). The mechanisms of this performance potentiation involve the important parts of the entire MTU; i.e., the fascicles and TT.

### Instantaneous F-V relationship during SSC

The F-V relationship of the isolated muscle actions (Hill 1938) describes the fundamental mechanical properties of human skeletal muscle. However, its direct application to natural locomotion, such as SSC, is difficult to ascertain as the *in situ* preparations utilize constant electrical stimulation. The techniques available for measuring the instantaneous F-V relationship in human muscle include the buckle transducer and fine optic fiber (for details, see Komi 2000). When these techniques have been applied in human Achilles tendon (AT) and patella tendon during SSC movements, the F-V curve during the functional contact phase of running was completely

different from the classic F-V relationship (Komi *et al.* 1992; Fig. 1.7a). Characteristic of the natural instantaneous F-V curve is the considerable force potentiation in the final push-off (concentric) phase of ground contact. Figure 1.7b demonstrates two important aspects of human skeletal muscle function: first, in short-contact hopping the triceps surae muscle behaves in a bouncing ball type of fashion; second, when the hopping intensity is increased or changed from a hopping type of movement, the contribution of the patella tendon force increases and that of the AT may decrease (Finni *et al.* 2001). The classic type of curve obtained for concentric action with constant maximal activation is superimposed on Fig. 1.7b. The shaded area denotes remarkable performance potentiation, although the hopping effort was submaximal (Finni *et al.* 2001). Animal experiments performed by Gregor *et al.* (1988) have produced similar results. Such a difference between the instantaneous curve and the classic curve is partly due to a natural difference in muscle activation levels between the two conditions.

Natural locomotion utilizes primarily SSC actions and involves controlled release of high forces caused mainly by the eccentric action of the cycle. This high force favors the storage of elastic strain energy in MTU. A portion of this energy can be recovered during the subsequent shortening phase and used for performance potentiation. Thus, natural locomotion



**Fig. 1.7** Examples of instantaneous force-velocity curves measured in human running (a) and hopping (b). The records in (a) were obtained with a buckle transducer (reproduced with permission from Komi 1990) and those in (b) with an optic fiber (reproduced with permission from Finni 2001). Each record is for a functional (contact) phase on the ground. A record (b) demonstrates greater loading of the Achilles tendon (ATF) as compared to the patellar tendon (PTF). The left side of both figures represents eccentric action and the right side concentric action. The dashed line (b) signifies the force-velocity curve for plantar flexors, as measured in the classical way.

with SSC actions may produce efficient muscle outputs, which can be very different from the conditions of isolated preparations (where activation levels are kept constant and the storage of strain energy is limited). Another important point needs to be emphasized here: in SSC activity performed without fatigue, the muscle EMG activity usually peaks before the eccentric phase ends, thus confirming the important role that the eccentric part plays in the SSC action.

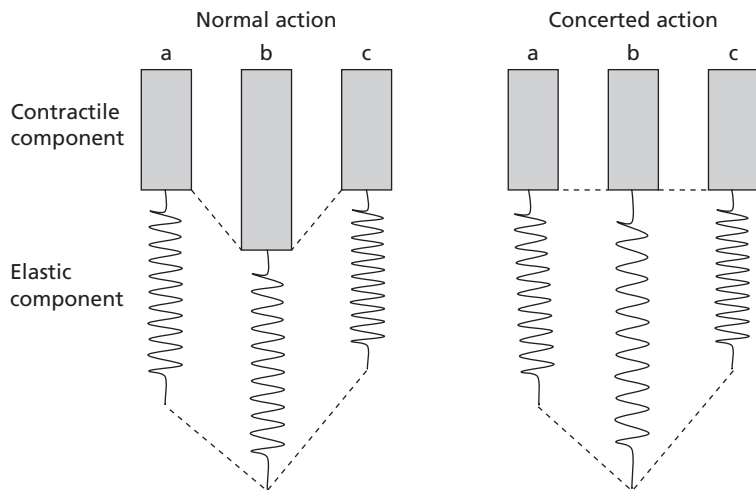
SSC muscle function has one additional, but very important characteristic. Due to the high stretch loads, it can efficiently utilize stretch reflex contributions to enhance force production. This has been clearly demonstrated in many studies (for a review see Komi & Gollhofer 1997), although its exact magnitude is almost impossible to quantify from global EMG measurements. Its role is also to make the impact in running, for example, take place smoothly. In marathon running, there is a parallelism between the changes in the amplitude of the short-latency stretch reflex component (SLC) and the impact force peak. When the fatigue progresses, the impact peak and subsequent immediate force reduction increase while the SLC decreases (Avela & Komi 1998), indicating a loss of reflex contribution to the force production of the respective muscles. The occurrence of the stretch reflex during running and hopping is easier to record in the soleus (SOL) than gastrocnemius (GA) muscle, although recent high speed ultrasound measurements have demonstrated a clear short duration stretching of the GA fascicles during the very early phase of ground contact (Ishikawa *et al.* 2006). In addition to the obvious role of gamma activation, stretching of the fascicles (extrafusal fibers) must be considered as a prerequisite for initiation of muscle spindle activation.

### Force potentiation

As has become evident from the previous discussions, SSC is intended to enhance the force or power output of the muscle over the pure concentric action. This additional force output can be called pre-stretch-induced force enhancement, which results in greater performance of the final push-off (concentric action) phase. This performance potentiation

naturally has several mechanisms, which are sometimes very complicated and remain contentious among researchers (e.g., see van Ingen Schenau *et al.* 1997). In the following discussion we make no attempt to illustrate all of the possibilities for force potentiation in SSC, but merely concentrate on the most obvious ones.

In addition to the reflex-induced force potentiation discussed above, the mechanical aspects associated with optimal coupling between stretch and shortening play an important role in increasing force, velocity, and power production during the final concentric phase. This is in contrast to the situation in which a pure concentric action is produced without pre-stretch of a pre-activated muscle; where the muscle performs normal shortening (concentric action), the potential to increase power or movement velocity in a step-like sequence of cross-bridge attachment, detachment, and reattachment is very limited. To overcome this limitation some sort of spring must be employed in order to store elastic energy and to utilize this energy to transform muscle action into movement more efficiently. The role of the whole MTU can be considered in this particular phenomenon. During human movements the energy stored during lengthening can amplify force production in the subsequent shortening phase and/or reduce the metabolic consumptions due to the decreased work of muscle fibers (Cavagna *et al.* 1968; Asmussen & Bonde-Petersen 1974; Komi & Bosco 1978). This ability of muscle to store and utilize elastic energy could be dependent on such factors as stretch velocity, muscle length, the force attained at the end of the pre-stretch, as well as the coupling time during the SSC action (Cavagna *et al.* 1965; Bosco *et al.* 1982). The elastic properties of MTU seem to be located mainly in TT, although muscle fibers also possess elastic properties in the cross-bridges (Huxley & Simmons 1971) and in the giant cytoskeletal protein called titin (Maruyama *et al.* 1977). Stretched tendons can recoil elastically much faster than any muscle can shorten. Alexander and Bennet-Clark (1977) proposed that tendon elasticity may be much more important than muscle elasticity and estimated the elastic strain energy stored in tendons to be 5–10-times higher than that stored in the muscle. This return of elastic energy in tendons has



**Fig. 1.8** A schematic diagram of a two-component Hill muscle model during a stretch (a → b)-shortening (b → c) cycle. During concerted action (right) the contractile component remains the same length when muscles are stretched and the elastic component can stretch more than during normal action (left). (Adapted with permission from Hof *et al.* 1983.)

been reported as approximately 93% of the work previously done during stretching it and as 7% of heat dissipation (Bennet *et al.* 1986). The work done during the recoil phase is almost independent of shortening velocity over a wide range of speeds.

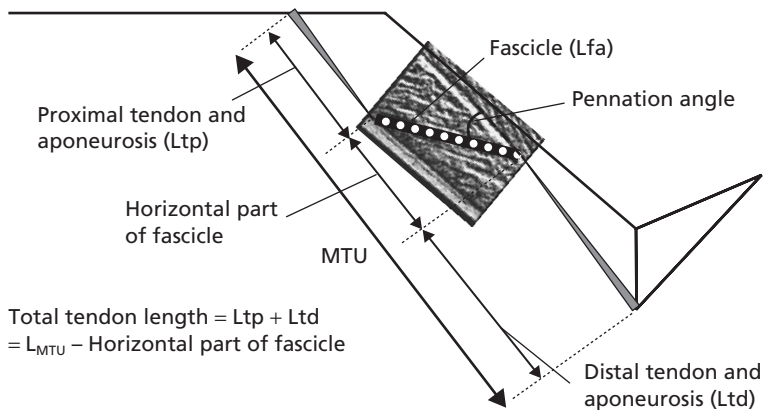
The idea of concerted action plays an important role in the utilization of tendon elasticity (Hof *et al.* 1983). In this concept, muscle activation is matched to maintain a constant length of the contractile components or even cause shortening of the muscle when the MTU is forced to lengthen during the braking phase of the SSC (Fig. 1.8). The negative work done on the muscle fibers, where the length is close to the optimum of the F-L relationship, can be converted into tendon elastic energy. Several studies have confirmed this behavior in GA muscle during human SSC movements (Fukunaga *et al.* 2001; Kawakami *et al.* 2002; Ishikawa *et al.* 2005a). Another concept is “catapult action,” in which the spring stretches slowly and recoils rapidly. In this action, power output can be amplified by the rapid positive work against the negative work done during the slow stretch, as demonstrated by an insect jumping (Bennet-Clark & Lucey 1967; Bennet-Clark 1975; Alexander & Bennet-Clark 1977). Ishikawa *et al.* (2005b) also reported this behavior during human walking. One may therefore ask which mechanism would be responsible for causing utilization of elastic energy during activities that involve different stretch and recoil patterns of the TT, such as

the ground contact phases of walking and running, which differ in terms of contact duration.

### Behavior of fascicle-tendon interactions during SSC movements

The role of muscle fibers and MTU in producing force and movement in experimental conditions seems clear. However, the manner in which fascicle-tendon interaction occurs during human SSC movements is not well recognized. The traditional geometric approximation treats the muscle fibers and tendons as an array of parallelograms. Non-invasive ultrasonographic techniques measure fascicle and tendon length changes directly during movements (Fukunaga *et al.* 2002; Fig. 1.9). This dynamic condition can reveal how the interaction between muscle fibers and tendons can be modified to utilize the tendon elasticity, for example. This modification is dependent on variable EMG activity including pre-activation and stretch reflex EMG. The final objective would be to capture the fascicle-tendon interaction in such a way that the roles of both tendon elasticity and the reflex contribution can be clarified to explain the power output and mechanical efficiency in SSC types of locomotion. This cannot be achieved with any available approximation methods, but the direct measurement approach utilizing moderate-speed ultrasound has revealed that the behavior of the overall MTU is not the same

**Fig. 1.9** A schematic model of the gastrocnemius muscle fascicle and tendon length measurements. This model requires that the total muscle-tendon unit (MTU) length is recorded continuously (e.g., kinematically) during locomotion. The rest of the measurements are calculated using continuous ultrasound records. (Important methodological references: Fukunaga *et al.* 2001; Zajac 1989.)



as that of the muscle fibers (Fukunaga *et al.* 2002). In fact, recent studies have indicated that the entire fascicle-tendon interaction is very complex and subject to adaptation including muscle, intensity, and task (movement) specificities.

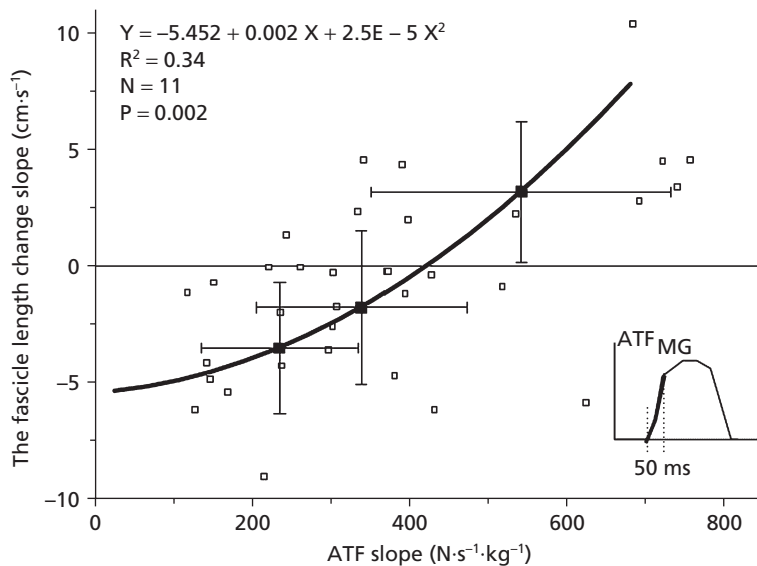
#### Muscle specificity

There are arguments in the literature suggesting that the fascicles can maintain a constant length (Fukunaga *et al.* 2001; Kawakami *et al.* 2002), shorten (Ishikawa *et al.* 2005a, 2006), or lengthen (Ishikawa & Komi 2004; Ishikawa *et al.* 2003, 2005a) during the braking phase of the ground contact of SSC exercises. These observations have come from conditions utilizing a single muscle method only. As the mechanical behavior of muscles may vary, these patterns may not apply when the muscles have different basic functions. For example, in contrast to the SOL muscle, the GA muscle is clearly bi-articular and has unique functions in conserving energy and power flow from one joint to another during locomotion. In addition, the force sharing (Herzog *et al.* 1994) and motor unit recruitment (Moritani *et al.* 1990) between synergistic muscles (GA and SOL) may occur differently. The GA muscle activity can also play an important role in generating forward propulsion in walking, whereas the SOL functions in stabilization and load bearing during the early stance phase (Gottschall & Kram 2003). Consequently, it is not surprising that fascicle-tendon interaction does not occur in a same manner in these two muscles in this particular movement condition. As already mentioned, the GA

fascicles can remain the same length, shorten, or be lengthened during the braking phase of SSC movements. In contrast, during the same movement, the VL and SOL fascicles are continuously lengthened prior to shortening (Ishikawa *et al.* 2005a; Sousa *et al.* 2007). The differences in fascicle behavior between GA and SOL support the idea that a bi-articular muscle can be involved in the fine regulation of the distribution of net torques over two joints, whereas mono-articular muscles may act mainly as force generators or load bearers (van Ingen Schenau *et al.* 1987).

#### Intensity specificity

As referred to earlier, the GA fascicles also behave differently from the SOL fascicles during drop jumps (DJ). In this activity, the GA shortening continues during the braking phase until the optimal stretch load condition has been achieved. When the dropping height exceeds the optimal stretch load, the GA fascicles shorten only initially but are suddenly stretched during the rest of the braking phase. In this extreme drop intensity condition, the estimated AT force (ATF) values were 10–12-times body weight. Consequently, the stretch load upon impact was so high that GA fascicles could only maintain a constant length during the initial braking phase. Thereafter they were forced to lengthen suddenly at 30–50 ms after contact. Thus, it appears that fascicle behavior in the GA muscle is, as an overall concept, dependent on the stretch load intensity. If we draw the length changes of the GA fascicle



**Fig. 1.10** Correlation between the slope of medial gastrocnemius (MG) fascicle length changes from 30 ms after contact to the end of the braking phase, and the averaged slope of Achilles tendon force (ATF) according to body weight. (Used with permission from Ishikawa *et al.* 2005a.)

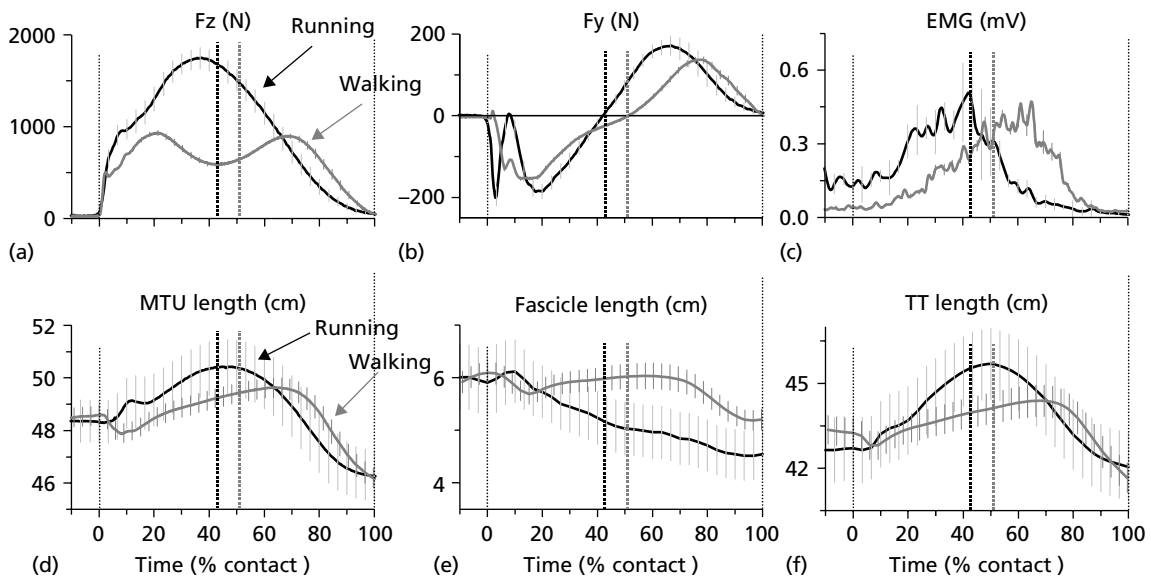
against the ATF slope measured during the braking phase of DJ, we obtain the relationship shown in Fig. 1.10. This quadratic relationship may be indicative of the critical stretch load for the GA ( $y$  axis = 0; Fig. 1.10) to maintain the concerted action effectively in the fascicle-TT interaction before being suddenly overstretched. On the other hand, in the SOL and VL muscles rapid stretching of the fascicles was not observed. Consequently, these muscles were still able to function “normally” without any additional rapid fascicle length changes (Ishikawa *et al.* 2005a; Sousa *et al.* 2007). These results clearly indicate the existence of intensity-specific interactions between fascicles and TT in a given muscle.

#### Task (movement) specificity

One question that may arise is whether the differences in movement types influence fascicle-tendon interactions. This problem has recently been investigated by comparing high intensity SSC exercises with different contact times. The rationale behind this comparison was that the contact time in the rapid SSC movements (cf. sprint running < 100 ms) may not be enough for the efficient storage and recoil of elastic energy. This is because the resonant oscillating frequency of the elastic component in the

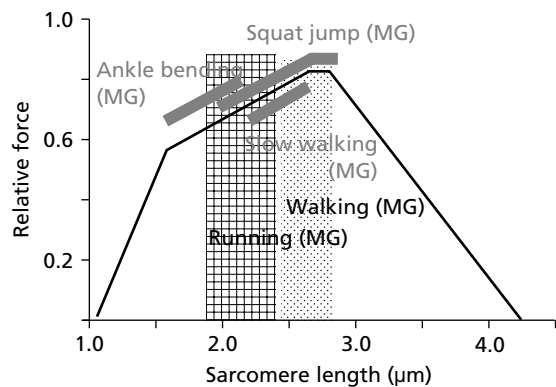
ankle extensors ( $3.33 \pm 0.15$  Hz; Bach *et al.* 1983) has a range of 2.6–4.3 Hz. This corresponds to a ground contact time between 233 and 385 ms (300 ms is 3.33 Hz). These values are well above those observed for running and hopping, for example. However, despite the strict theoretical oscillating frequencies for elastic components, TT can show lengthening before shortening during the contact phase of running (Ishikawa *et al.* 2006; Fig. 1.11). The same is true in the short contact DJ (Ishikawa *et al.* 2005a). One possible explanation for the elastic behavior during rapid movements is that the shortening of GA fascicles due to high muscle activation during pre-activation and braking phases of rapid SSC movements can increase TT strain rates. Viscoelastic material is stronger and becomes stiffer at increasing strain rates (Arnold 1974; Welsh *et al.* 1971). Consequently, during short-contact SSC movements, increased TT strain rates make the TT stiffer due to fascicle length regulation. This would not apply to walking where muscle activation during the pre-activation and braking phases is low and fascicles are lengthened during the long (> 500 ms) contact phase (Fig. 1.11). Consequently, it is very likely that differences in movements, especially in the contact times during running, hopping, and walking, are involved in fascicle and TT interactions, and in determining how TT viscoelasticity can be utilized.





**Fig. 1.11** Records of the measured and calculated parameters during the contact phase of running and walking showing: vertical (a;  $F_z$ ) and horizontal (b;  $F_y$ ) ground reaction forces; electromyographic (EMG) activities of the medial gastrocnemius (c; MG); and lengths of the muscle-tendon unit (d; MTU), fascicle (e) and tendinous tissues (f; TT). The contact period was normalized to 100%. Bars show SE values. The vertical lines denote the contact point, transition point from braking to push-off phases, and the take-off. (Used with permission from Ishikawa *et al.* 2006.)

In human movements the fascicles play an important role, not only to produce force by themselves but to regulate force and power production for TT. At the sarcomere level, fascicle contraction occurs around the plateau region of the F-L curve (Hof *et al.* 1983; Fukunaga *et al.* 2002). It is very likely that utilization of the specific points in the sarcomere F-L curve may vary depending on the type of movement. For example, the working range of active muscle fibers in the F-L relationship can shift more to a plateau (optimal) phase at normal walking speed ( $1.5 \pm 0.1 \text{ m}\cdot\text{s}^{-1}$ ) as compared to slow walking ( $0.8 \text{ m}\cdot\text{s}^{-1}$ , Fig. 1.12; Fukunaga *et al.* 2002). This would effectively favor the relatively larger force generation. This is not the case for rapid SSC movements; when the movement changes from walking to running the working range of muscle fibers can shift more towards an ascending limb (shorter length). This shift in running is suggested to make efficient use of greater TT stretching (Ishikawa *et al.* 2006). These assumptions further suggest that modulation of GA fascicle-TT interactions takes place in response to changes in mechanical demands



**Fig. 1.12** A proposed scheme for the human medial gastrocnemius (MG) muscle to utilize the various parts of the sarcomere force-length relationship during human movements. The shaded and meshed ranges for sarcomere length are shown during the contact phase of walking and running with same subject group, respectively. Please note that working length of sarcomeres shifts to the ascending limb when the activity changes from walking to running. (For further details see Fukunaga *et al.* 2002; Ishikawa *et al.* 2006.) (Used with permission from Ishikawa *et al.* 2006.)

associated with locomotor tasks in order to utilize the elasticity of TT effectively.

## Conclusion

In conclusion, nervous control is essential for force and power production in human movement. This activation is nicely integrated with the mechanical structure and function of the human skeletal muscle. The mechanical characteristics, such as F-T, F-L, and F-V relationships, are different depending on the motor unit make-up of the neuromuscular system. A skeletal muscle containing primarily fast motor units can produce greater force and power than the slower-type muscle whose motor unit composition has a greater proportion of slow motor units (and corresponding slow-type muscle fibers), which are meant to maintain force and power for a longer period of time.

In natural locomotion, some of these mechanical features cannot be applied directly. For example, the F-V relationships of MTU measured in isolated conditions are not applicable to natural locomotion where the F-V relationships is characterized by the so-called instantaneous F-V curve whose form is completely different to the classical one. This

difference is due to the ability of the human neuromuscular system to activate muscle in proper correspondence with external load and intended velocity of movement. A specific feature of this interaction is a well-controlled variability of the nervous input to the muscle as well as purposeful proprioceptive feedback. This makes force and movement production not only more difficult to understand but also more challenging to explore. In this regard, especially relevant is a recent new finding that the external load is not the only factor that determines the fascicle-TT interaction during human movement. When the measurements are performed during natural movements, called SSC action, movement specificity is complemented with differences in the fascicle-TT interactions that are also muscle, movement and intensity specific.

Consequently, it is not possible to understand the complexity of the mechanisms that contribute to the production of force and movement by human skeletal muscles by extrapolation from well-controlled studies of individual muscle actions or measurements made using isolated muscle preparations. This complexity also applies to the mechanisms of force and power potentiation that characterize natural SSC movements.

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