Morphological and functional characteristics of the muscle-tendon unit

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Abstract The biomechanical features of skeletal muscles are reviewed, with regard to their form and function and anatomical components (fascicles and tendinous tissues). 1) Studies on fascicle architecture are reviewed, highlighting its importance in the force and velocity potentials of the muscle along with its plasticity and muscle-size dependence. 2) The elastic properties of the muscle-tendon unit are described, pointing out the contribution of tendinous tissues as a spring. Functional consequences of tendon elasticity are summarized with respect to exercise performance under mechanically and neurally controlled joint actions, which lead to energy saving of muscle fibers and enhancing the positive work of the muscle. 3) The task-specificity of the muscle as an actuator or a spring and its position dependence (proximal to distal trend of functional divergence) are mentioned. Literature shows that proximal muscles are architecturally designed for actuation and distal muscles are more suited for a spring function. 4) Unique but strange behavior of tendinous tissues, that is seen in stretch-shortening types of movement, is described, suggesting variable elasticity of tendinous tissues that is modulated by muscle activation. 5) Finally, a need to consider multiple muscle-tendon units as a system is introduced to reasonably understand recent findings that otherwise cannot be accounted for. Collectively, it is suggested that the muscle-tendon unit is not only a simple combination of muscle fiber and tendinous tissues acting as actuator and spring, respectively, but also a unit that acts both anatomically and functionally.

Keywords : tendon and aponeurosis, fascicle, muscle architecture, muscle-tendon interaction, viscoelasticity

Introduction

A skeletal muscle is an organ that provides mechanical work to generate human movements. Production of mechanical work by a skeletal muscle is done through power generation by muscle fibers that exert contractile forces under various shortening velocities. These mechanical parameters feature the function of a skeletal muscle as an actuator. In this article, some unique biomechanical features of skeletal muscles are described, with regard to form and function and the anatomical components that operate in perfect unison as a functional unit.

Muscle architecture — design for force and speed production

In a skeletal muscle, muscle fibers are packed in bundles (fascicles) extending in many cases from proximal to distal tendinous tissues (tendons and aponeuroses). A skeletal muscle, therefore, should be regarded as a muscle-tendon unit (MTU). The way that fascicles and tendons are arranged in an MTU is termed “muscle architecture”¹⁾. Muscle architecture is a major determinant of the

capacity of skeletal muscle as an actuator, and its impact can be greater than that of the physiological properties of the muscle such as fiber types²⁾.

Skeletal muscles have various types of architecture. Some muscles have very short fascicles while others have longer fascicles. Given the condition of identical muscle volume, fascicles that are shorter in length are larger in number and vice versa. The former type of architecture is suited for force production and the latter for velocity, since the maximal muscle force is a function of the total number (and the average cross-sectional area) of muscle fibers; and the maximal shortening velocity is related to muscle fiber length or the number of sarcomeres in series within a fiber³⁾. For instance, the medial gastrocnemius has more than 1 million fibers while the sartorius has fibers with a quantity of only 1/10 of the gastrocnemius⁴⁾. A muscle with fascicles shorter than the muscle belly typically takes a pennate shape where fascicles are arranged obliquely (at an angle known as the pennation angle) from the line of action of the muscle. This shape is in contrast to the parallel-fibered architecture of a muscle with fascicles running parallel to and spanning the whole muscle belly (the long axis of the muscle) (Fig. 1)⁵⁾. For reasons described above, pennate muscles are suited for higher force production while parallel-fibered muscles are for

the range of motion and speed^{3,6}). But recently, pennate muscles have been shown to possess prominent power (force $\times$ speed) potential owing to the muscle-tendon interaction⁷) as described later in detail.

The pennation angle however acts to reduce the amount of muscle fiber force effectively transmitted to the tendon^{8,9}). Kawakami et al.¹⁰) found a positive correlation between the degree of muscle hypertrophy and pennation angle for the triceps brachii muscles, indicating that in individuals with hypertrophied muscles the adverse effect of the pennation angle on muscle fiber force transmission can be substantial. In fact, a negative correlation was found between pennation angle and the muscle force/cross-sectional area ratios of the triceps brachii muscles¹¹). Due to the muscle-tendon interaction, fascicles, during isometric contraction, shorten and increase their pennation angles, reaching up to 70° in the medial gastrocnemius even in normal individuals¹²). Thus the effect of the pennation angle on muscle force production should be much greater than previously thought¹³). Size-dependence of the pennation angle for the three different pennate muscles (triceps brachii, vastus lateralis and gastrocnemius medialis) was further confirmed¹⁴). Interestingly, the variability of the pennation angle and muscle thickness was different between muscles, with the triceps brachii showing the largest variability and the gastrocnemius the smallest (Fig. 2). This difference may be related to their architectural features (relative muscle fiber length).¹⁴)

Tendon elasticity and muscle-tendon interaction

The tendinous tissues in MTU are known to possess elastic properties and are elongated when a load is ap-

plied to them; and then shorten to the original length after the applied load is removed¹⁵⁻¹⁷). As an actuator of MTU, fascicles stretch the tendinous tissues during contraction; thus even during an isometric contraction, fascicle shortening occurs (Fig. 3)¹³). Such a muscle-tendon interaction is also seen in dynamic contractions. During isokinetic joint action, where the joint angular velocity is kept constant by a dynamometer, a divergence occurs in velocities of the fascicles from those of MTU¹⁸). Chino et al.¹⁸) found for the medial gastrocnemius and soleus muscles that the contribution of tendinous tissues to MTU velocities during isokinetic concentric and eccentric plantar flexions, was comparable to, and sometimes greater than, that of the fascicles. Such a large amount of tendinous

Fig. 2 The relationships between pennation angle and muscle thickness (normalized to the limb length in which each muscle is located) of the triceps brachii (filled circles), vastus lateralis (open circles), and medial gastrocnemius (open squares) muscles (14).

Fig. 1 Schematic illustrations of parallel-fibered (left) and pennate (right) muscles. Pictures of exemplar muscles (left: sartorius, right: gastrocnemii) are also shown (adapted from ref. 5).

Fig. 3 Longitudinal ultrasonogram of the human medial gastrocnemius muscle at rest and during maximal voluntary isometric plantar flexion (MVC) (13).

Fig. 4 Recordings of force, electromyogram, and fascicle length of the plantaris and gastrocnemius MTUs for two strides of wallaby hopping (A) and the relationship between force and relative length change of a single cycle for each muscle (B). Panel (C) illustrates how the fascicle length and tendon force were measured (23).

tissue lengthening and shortening would be due to the highly pennated architecture of these muscles with long tendinous tissues that allows substantial muscle-tendon interaction. Kawakami et al.¹⁹⁾ showed that the different magnitudes of tendinous tissue lengthening among changing velocities during isokinetic concentric knee extensions was the reason for the shape of the torque-velocity curve that deviates from the hyperbolic curve of the force-velocity relationship of isolated muscles²⁰⁾. They proposed that the force-velocity relationships of knee extensor muscles should be evaluated with the peak torque rather than an angle-specific torque in that the former can control fascicle lengths of knee extensors more than the latter. In vivo fascicle behavior also accounted for the joint-angle dependence of eccentric joint torque development²¹⁾.

During animal gait, a spring-like function of the limb allows the storage and return of elastic energy to reduce muscle work²²⁾. Biewener and Roberts²³⁾ identified the limb spring in the case of wallaby hopping and turkey running as the tendinous tissues of lower leg muscles

(Fig. 4). For their study they used sonomicrometry (using miniature ultrasonic crystals embedded in the muscle) to measure fascicle length changes. Although the fascicles of each muscle underwent considerable length change during the swing (aerial) phase when force was low, they developed substantial forces under nearly isometric conditions during the stance phase of the hop, which facilitated elastic energy recovery from the tendinous tissues²²⁾. In humans, Fukunaga et al.²⁴⁾ employed B-mode ultrasonography to track length changes of gastrocnemius fascicles during human walking, and showed that the fascicles contracted isometrically in the stance phase while the tendinous tissues were elongated, and the two structures then shortened just before toe-off (Fig. 5), which was similar to the findings of Biewener and Roberts²³⁾. These results indicate that the tendinous tissues play a major role in leg spring during locomotory movement regardless of intensity. Studies that followed on animals as well as humans showed similar fascicle behavior (much smaller length changes than those of MTU) during walking and running, although there were some differences depending on the

Fig. 5 Recordings of length change of fascicle (thick line), tendinous tissue (thin line [estimated]), and MTU (dashed line) (a), electromyogram of gastrocnemius (b), ankle (thick line) and knee (thin line) joint angle (c), and ground reaction force (d) during one stride of human walking (24).

task (walking and running, inclined, level, and declined surfaces)²⁵⁻²⁸. In some cases, there were changes in fascicle length (shortening and/or lengthening); but a message common to all studies is that muscle length change is dampened to a sizable amount, by the compliance of the tendinous tissues, allowing efficient muscle force exertion.

Kawakami et al.²⁹ showed that fascicle behavior (changes in both length and activation level) of the gastrocnemius MTU during a maximal ankle hopping exercise, was different when performed with and without counter-movement (Fig. 6, top). Estimated muscle power during the shortening phase of MTU was greater in the former compared to the latter (Fig. 6, bottom). This was likely due to 1) greater force owing to the sarcomere length that was closer to the optimal length at the onset of shortening, 2) slower fiber shortening velocity and hence greater force owing to the force-velocity relationship of muscle fibers, and 3) increased tendon shortening velocity through a “catapult action” (rapid shortening from a state of being stretched like a catapult) that was once

Fig. 6 The relationships between estimated Achilles tendon force and gastrocnemius fascicle length (top) and between estimated muscle power and ankle joint angle (bottom) during an ankle hopping exercise without (filled circles) and with (filled diamonds) counter-movement. Arrows indicate directions of the movements. The shaded area in the top panel indicates “isometric” force development during the lengthening phase of MTU. In the bottom panel, changes in positive muscle power are fitted by solid lines (29).

predicted by Hof and van den Berg (1986)^{13,30}. This study clearly shows that with a counter-movement, MTU works in such a way that fascicles are responsible for force and tendinous tissues for speed¹³. Sugisaki et al.³¹ showed that as the intensity of rebound action of the ankle was increased by a drop jump, lengthening of the fascicles in the gastrocnemius increased; and with the eccentrically increased fascicle force, tendinous tissues were further stretched and provided greater speed when shortened, thereby enhancing MTU positive power.

Kawakami et al.²⁹ further showed that there is large inter-individual variation in movement performance as well as fascicle behavior, under conditions with and without counter-movement (Fig. 7). This result suggests how the interaction of muscle fibers with tendinous tissues changes from individual to individual, and is associated with the ability to utilize the spring properties of MTU. The authors’ recent study further demonstrated that one learns to effectively use this muscle-tendon interaction for greater work generation, by modulating the activation

Fig. 7 The relationships between plantar flexion torque and gastrocnemius fascicle length during an ankle hopping exercise without (filled diamonds) and with (filled circles) counter movement for the six subjects. Arrows indicate directions of the movements (29).

strategy of muscle fibers through practice³²).

Task specificity of MTUs — actuator or spring

There is a tendency, both in animals and humans, for the fascicle length (relative to that of MTU) to increase as the MTU is located proximally^{33,34}. Proximal muscles also tend to have larger mass³⁴. A tendency in the opposite direction is seen for tendinous tissue length³³. Theoretically, a large muscle with long fascicles can exert greater work when it shortens³⁴, while a muscle with a small fascicle length/tendinous tissue length ratio can utilize tendon elasticity more effectively^{17,35}. Thus the above proximal-to-distal trend of MTU architecture is likely to be associated with different functional roles imposed on respective muscles, i.e., proximal MTUs generate work through actuation (fascicle shortening) while distal MTUs act as springs.

Some evidence has been provided to support the above notion. Smith et al.³⁶ suggested this task specificity through anatomical observation of pelvic and limb muscles of an ostrich. Gillis and Biewener³⁷ showed

that the rat hip and knee extensors exhibited substantial length change of their fascicles during walking, trotting, and galloping, unlike the fascicle behavior seen in the gastrocnemius muscle. Lee et al.³³ modeled the forelimb and hindlimb of a goat as combinations of actuators and springs (Fig. 8) to reasonably explain the above proximal-to-distal trend of task specificity. McGuigan et al.³⁸ actually showed, in the case of the goat muscles, that distal muscle-tendon architecture favors economic force production of muscle fibers and elastic energy recovery of tendinous tissues, and that the majority of limb work during incline or decline running was performed by larger proximal muscles. Considering the close similarity of MTU architecture, it is quite likely that such task specificity also exists in human lower limb muscles. Such task divergence could be linked to the known function of the biarticular muscles (rectus femoris and gastrocnemius) of contributing to a net transfer of power from proximal to distal joints (hip to knee and knee to ankle) during explosive leg extensions³⁹.

It is of interest to note that some MTUs are designed exclusively for actuation by fascicles where negative work

Fig. 8 Schematic representation of the leg joint and MTUs of the goat fore- and hind-limb. Black rectangles represent muscles and gray-notched lines represent tendinous tissues. MCP and MTP refer to the metacarpophalangeal joint and metatarsophalangeal joint, respectively (adapted from ref 33).

is not provided from outside the body. Typical examples can be seen in the pectoralis muscle of a bird that flies, and the gastrocnemius muscle of a duck that swims²³, both of which demonstrate a muscle ‘work loop’ pattern of the force-length behavior of fascicles in a manner to exert positive work in the stroke phase.

Tendinous tissues as spring and actuator

As illustrated in Fig. 1, pennate muscles have large aponeuroses onto which fascicles are attached to form a muscle belly. There are studies showing the compliant nature of the aponeurosis^{40–42}, which can be a reason for the substantial amount of muscle-tendon interaction of the pennate muscles. But recent studies have brought to light the strange nature of this structure, suggesting that the tendinous tissue is not a simple linear spring that is serially connected to fascicles.

Studies have suggested that the mechanical properties of tendinous tissues (especially that of the aponeuroses) vary depending on the contractile status (passive or active, static or dynamic) of fascicles^{31,43–47}. Sugisaki et al.⁴⁵ revealed that the load-deformation curve of the human Achilles tendon shifted in an upper-right direction (toward higher tendon stiffness) as contraction intensity increased (Fig. 9).

Tendinous tissues are viscoelastic structures, and the load-deformation curve of isolated tendinous tissues typically forms a hysteresis loop in the clockwise direction: when the applied load is reduced after being increased, tissue length becomes longer for the same load⁴⁸. But

Fig. 9 The relationships between Achilles tendon force and its longitudinal deformation from at rest. Closed circles, open circles, and closed rhomboids indicate the maximal intensity, 60%, and 40% of eccentric contraction, and open rhomboids indicate passive lengthening, respectively (values are means and SEM of seven subjects). The Achilles tendon force corresponding to the elongation of 10 mm (vertical line with an asterisk) was significantly different between the maximal intensity and other conditions, and between the passive condition and others (45).

in *in vivo* (41 turkey gastrocnemius tendon during running, 49 human vastus lateralis tendon during drop jump, 50 and human gastrocnemius and soleus tendons during ankle bending) and *in situ*^{43,51} conditions where MTU is stretched before shortening, the load-deformation curve forms a counter-clockwise loop. The counter-clockwise loop of tendinous tissues means that the tendon exerts greater force during shortening than it stores during lengthening, which is not physically reasonable. Ettema and Huijing⁴³ discussed that the phenomenon may be related to “unidentified energy uptake by the aponeurosis, which is not detected by means of force and length changes,” and that “the origin of extra energy release is as yet obscure, but could be related to changes in the myotendinous junction.”

Recently, Sakuma et al.⁵⁰ showed that the size of the tendon counter-clockwise loop increased as movement speed increased, while the fascicle length-force curve formed a clockwise loop of a corresponding size (Fig. 10). The MTU did not make a work loop and behaved purely elastically (being lengthened then shortened to the same amount). This result hints at the hypothesis that the tendinous tissue receives mechanical energy from fascicles when the two components shorten. If this ever happens it should be at the myotendinous junction of the aponeurosis where muscle fibers terminate within the tendinous tissue⁴⁷. This possibility was mentioned by Lieber

Fig. 10 The relationships between estimated tendon force and fascicle length of the medial gastrocnemius (MG) and soleus (SOL) muscles (top) and the relationships between tendon force and estimated tendon length of the two muscles (bottom), during ankle bending at 4 frequencies. Arrows indicate directions of the movements (50).

et al.⁴⁴) and Zuurbier et al.⁴⁷) in the context of the “anchor effect” that states that muscle fibers are mechanically anchored within the aponeurosis. Other factors that might explain the variable aponeurosis mechanical characteristics include deformation of the aponeurosis both longitudinally and transversely^{52–55}) and a spring-like function that the foot arch can have^{56,57}). Azizi and Roberts⁵²) suggested that biaxial loading of the aponeurosis during muscle contractions increases longitudinal stiffness, causing the difference between active and passive conditions in the load-deformation relationship of tendon tissues. This might be operative during the stretch-shortening cycle of MTU where muscle fibers contract in a large spectrum of activation levels⁵⁸). In any case, it is likely that tendinous tissues cannot be regarded as a simple linear spring in series with the fascicles.

Multiple muscle — tendon units as a system

Finally, a need for considering different MTUs as a system is worth mentioning. This idea needs to be taken into consideration to rationalize our recent findings with the triceps surae MTUs.

In the human triceps surae muscles, the gastrocnemius and soleus muscles are located adjacent to each other, and their aponeuroses are anatomically separated proximally while sharing the same tendon distally⁵⁹). It is therefore expected that a change in the contribution of gastrocnemius and soleus muscle force to a different balance results in their respective tendon elongation to alter accordingly, provided that the two muscle-tendon units are mechanically independent proximally. This hypothesis was tested through *in vivo* measurement of tendinous tis-

sue elongation of the two muscles that were fatigued by repeated maximal voluntary isometric plantar flexions⁶⁰. Tendon elongation of the medial gastrocnemius significantly decreased over repeated plantar flexions, while that of the soleus did not. As the gastrocnemius is presumably more susceptible to fatigue than the soleus⁶¹, this result should suggest that changes in the exerted force of the two muscles is reflected in respective tendon elongation. It was expected that the tendon elongation of the soleus for the same relative torque would increase to compensate for the decreased maximal force of the gastrocnemius. However, tendinous tissue elongation of the soleus, for a given submaximal torque output, did not change after the fatigue task while that of the gastrocnemius decreased. This observation obviously violates the idea of assuming each tendinous tissue elongation as a function of the respective muscle force.

In a subsequent study⁶², the medial gastrocnemius muscle was selectively fatigued by repeated electrical stimulation until finally the evoked twitch torque of the medial gastrocnemius nearly dropped to zero. Tendinous tissue elongation, as a function of relative plantar flexion torque, decreased both for the medial gastrocnemius and soleus muscles after the fatigue test, while that of the lateral gastrocnemius was unchanged. These results not only contradict the notion of mechanical independence of the triceps surae muscle-tendon units, but could also jeopardize the assumption of an in-series connection of tendinous tissues and muscle fibers. Collectively, it is suggested that tendinous tissue elongation of the triceps surae muscles does not accurately represent their force. It is speculated that the tendons of the triceps surae muscles are mechanically linked in a whole continuum of fascial networks⁶³.

Final remarks — new insights into muscle tendon unit functions

Just as the fascicles are compared to an actuator, tendinous tissues can be regarded as a (positive) power amplifier. This idea explains the movement performance of animals, as well as humans. The available literature, however, suggests that this duality does not necessarily hold in the *in vivo* situation. We may need to consider MTU as a real 'unit', with components interacting in a complicated manner both anatomically and functionally. In this review many hypotheses were formulated, which will need verification in future studies.

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