

Review Article

Force Transmission between Synergistic Skeletal Muscles through Connective Tissue Linkages

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The classic view of skeletal muscle is that force is generated within its muscle fibers and then directly transmitted in-series, usually via tendon, onto the skeleton. In contrast, recent results suggest that muscles are mechanically connected to surrounding structures and cannot be considered as independent actuators. This article will review experiments on mechanical interactions between muscles mediated by such epimuscular myofascial force transmission in physiological and pathological muscle conditions. In a reduced preparation, involving supraphysiological muscle conditions, it is shown that connective tissues surrounding muscles are capable of transmitting substantial force. In more physiologically relevant conditions of intact muscles, however, it appears that the role of this myofascial pathway is small. In addition, it is hypothesized that connective tissues can serve as a safety net for traumatic events in muscle or tendon. Future studies are needed to investigate the importance of intermuscular force transmission during movement in health and disease.

1. Introduction

When skeletal muscle fibers are excited, a cascade of events is triggered, which ultimately leads to forces exerted on the skeleton. Muscle forces are needed for movements, such as locomotion, and the maintenance of body balance. There are many structures involved at several levels organization: from actin, myosin, and titin of the sarcomeric cytoskeleton, desmin of the intermyofibrillar cytoskeleton, transsarcolemmal proteins such as dystrophin and integrin of the subsarcolemmal cytoskeleton, endo-, peri-, and epimysium, as well as tendon and aponeurosis at the muscle level to inter- and extramuscular connective tissues (e.g., the neurovascular tract, fascia) at the compartmental level. For understanding how forces are transmitted from sarcomere to the bony skeleton in normal and diseased muscle, it is necessary to investigate the role of each of these structural elements as well as their interaction. The present review focuses on the connective tissues that are found in the direct environment of skeletal muscles and their potential effects in muscle function during movement.

The most recognized pathway of force transmission from muscle fibers to bone is via the specialized myotendinous junction [1] and tendon, named myotendinous force transmission. Classical anatomy has defined each muscle as a separate entity with a unique function at the joint(s) it spans. Therefore, it has long been common to view muscles as mechanically independent actuators. This is readily apparent from biomechanical models of the musculoskeletal system in which muscles are connected to the skeleton at their origin and insertion [2, 3]. However, many scientists from the last century were aware of mechanical interactions between muscles (for a historical overview see [4]). For example, during measurements of soleus muscle forces in the cat, upon stimulation of the lateral gastrocnemius-soleus nerve branch Denny-Brown [5] noticed that "...it is found to be extremely difficult to avoid a slight early rise of tension, and fall in the plateau, due to the vibration or pull of gastrocnemius." More recently, Nichols [6] stated "Mechanical artifacts due to direct mechanical action of the stretched muscle on those isometrically constrained were indicated by essentially instantaneous latencies or by effects

observed after pharmacological block of heterogenic reflexes." Note that in these experiments the tendons are severed from their insertion site and individually connected to force transducers. This means that the mechanical linkage was provided by structures at the muscle belly boundary (i.e., the epimusculum).

The purpose of this article is first to review the initial series of systematic experiments on mechanical interactions between synergistic muscles (i.e., neighboring muscles which produce the same movement at the joint) via connective tissue linkages (named epimuscular myofascial pathways) that revealed the presence and capacity of this phenomenon (mechanical interactions between antagonistic muscles have been reviewed elsewhere; see [7]); second, to discuss the current debate on the importance of epimuscular myofascial force transmission during normal movements; and third, to discuss the potential functions of inter- and extramuscular connective tissues for pathological muscle-tendon conditions.

2. Mechanical Interaction between Muscles through Connective Tissue Structures

2.1. Epimuscular Myofascial Pathways. Epimuscular myofascial force transmission is defined as transmission of muscle forces to the skeleton via pathways other than the muscular origin and insertion. A direct proof of epimuscular myofascial force transmission is a difference in force exerted at the origin (proximal) and insertion (distal) of a muscle. Another feature of this phenomenon is that length changes in one muscle can affect forces exerted at the tendons of muscles that are kept at a constant length.

Two epimuscular pathways are distinguished (Figure 1): (i) *intermuscular*, if force is transmitted between two neighboring muscles via the continuous connective tissue at their muscle belly interface, and (ii) *extramuscular*, if force is transmitted between the epimusculum of a muscle and an adjacent nonmuscular structure. The direct intermuscular pathway is provided by an areolar connective tissue layer at the interface between muscle bellies (for images see [8]). Several structures provide an anatomical substrate for the extramuscular myofascial pathway: (i) the matrix supporting nerves and blood vessels, that is, the neurovascular tract (see [8, 9]) (Note that the neurovascular tract is continuous with the extensive intramuscular connective tissue network, which reinforces the nerves innervating muscle fibers and the blood vessels entering the muscle.), (ii) fascia layers forming the borders of synergistic muscle groups that are continuous with more superficial layers (e.g., subcutaneous connective tissue), and (iii) connective tissue around tendons (for images the reader is referred to previous publications, e.g., [10–13]).

Dissection of a limb shows a vast network of collagen-based structures linking muscles together. Clearly muscles are connected by fascial sheets, loose areolar tissue, vascular links, nerves, and supporting collagen. Sometimes muscle fibers originate from neighboring muscle (e.g., in the cat there are some LG fibers that seem to terminate in MG

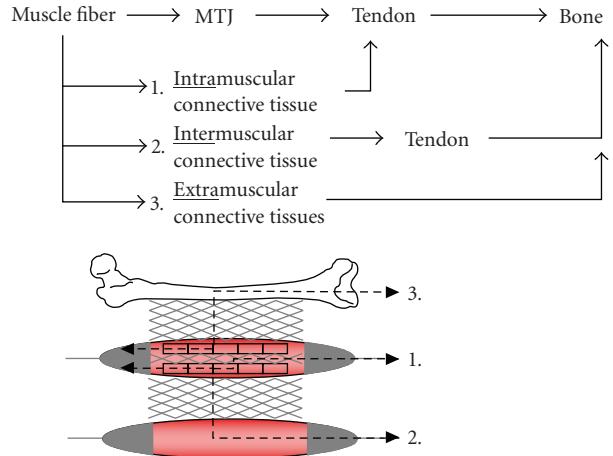


FIGURE 1: The different pathways via which force generated within muscle fibers can leave the muscle to be transmitted to the skeleton. Two epimuscular pathways are distinguished. (i) Intermuscular: force transmission between two neighboring muscles via the continuous connective tissue at their muscle belly interface. (ii) Extramuscular: force transmission between a muscle and adjacent nonmuscular structures. The term epimuscular myofascial force transmission is used to indicate transmission via inter- or extramuscular pathways.

muscle). Tendons appear to run together. Pushing or pulling on one muscle leads to movement of a neighbor. Thus, muscles are unquestionably linked. The question is how significant these links are to the normal function of muscle.

2.2. Mechanical Interactions between Muscles in the Anterior Crural Compartment. An in-depth analysis of transmission of extensor digitorum longus (EDL) muscle force in the rat, which is embedded within the anterior crural compartment together with extensor hallucis longus (EHL) and tibialis anterior (TA) muscles, has been performed. Because both the proximal and distal tendons of EDL can be attached to force transducers, EDL is a very suitable muscle for the assessment of epimuscular myofascial effects. Isometric forces were measured simultaneously at the proximal and distal tendons of EDL muscle as well as at the tied distal tendons of TA, and EHL muscles. These tendons can all be dissected with minimal disruption of the compartment, leaving epimuscular myofascial pathways mostly intact. By manipulating the position of the force transducers, the muscle-tendon complex length of one or all muscles as well as muscle relative position were changed.

Mechanical interactions between EDL and TA + EHL were found for various experimental conditions. Length changes of the TA + EHL complex affected the forces exerted at the proximal and distal tendons of EDL, which was kept at a constant length [9]. More specifically, lengthening TA + EHL distally increased proximal EDL force (by 37%), but decreased distal EDL force (by 39%). The mechanical interactions between synergistic muscles can be ascribed to changes in the position of one muscle relative to the other [15] and, consequently, changes in the configuration

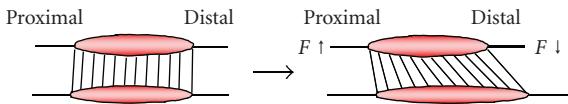


FIGURE 2: Schematic drawing to illustrate changes in the configuration of connective tissue between two muscles if one muscle is lengthened. Modified from Maas et al. [14].

(length and angle) of inter- and extramuscular connective tissues (Figure 2). It may appear obvious to explain these results by mechanical effects of intermuscular connective tissue. However, EDL, TA and EHL are also linked to each other via extramuscular structures. A clear example is the neurovascular tract that runs in between the muscles while giving off branches of nerves and blood vessels which enter the endo-perimysial network of the muscle [8, 9]. Therefore, we conducted a followup study to investigate the contribution of each pathway [16]. Equal experimental conditions were imposed before and after disruption of the connective tissue layer between EDL and TA + EHL, thereby eliminating force transmission via intermuscular myofascial pathways. This significantly decreased the effects of TA + EHL length on force exerted at the distal tendon of EDL. However, the interaction between TA + EHL and proximal EDL force did not change. Therefore, we concluded that mechanical interactions between synergistic muscles originate from both inter- and extramuscular connective tissues. Besides the above-described study [16], there is only one other study [10] that reports data indicating that the areolar connective tissues are stiff and strong enough to transmit force. Changes in the length-force characteristics were found following disruption of the intermuscular myofascial pathway [10].

In the above-described studies, relative displacements of muscle bellies were the result of length changes in a single muscle group. To distinguish between effects of muscle length and relative position, isolated effects of muscle relative position were studied [14]. The muscle-tendon complex length of EDL and TA + EHL was kept constant. The position of EDL muscle relative to its surroundings was changed by moving both the proximal and the distal tendons to an equal extent and in the same direction. Displacements of EDL in distal direction decreased force exerted at the distal tendons of TA + EHL. Simultaneously, distal EDL force increased and proximal EDL force decreased. Force changes in opposite direction were found if EDL muscle was repositioned more proximally. Each movement affected the proximo-distal force difference and, thus, the magnitude of net epimuscular myofascial force transmission. In addition, the sign of the force difference between proximal and distal EDL forces changed. Similar effects of muscle relative position were reported for slightly different experimental conditions [17]. Length-force characteristics of EDL muscle obtained by movements of the distal tendon were significantly different from its length-force characteristics if EDL muscle was lengthened by moving its proximal tendon.

In conclusion, the position of a muscle relative to surrounding tissues codetermines isometric muscle force.

Position effects can be explained by changes in the configuration of the tissues representing the epimuscular myofascial pathways (Figure 2). In general, the muscle end that is positioned farthest in a particular direction (e.g., distal) will draw force from neighboring muscles.

2.3. Do Mechanical Interactions between Muscles Occur *In Vivo*? The above *in situ* studies have shown the potential of force transmission between skeletal muscles via inter- and extramuscular connective tissues. The functional relevance of this phenomenon is dependent on the magnitude of the effects found in physiological muscle conditions. However, this mode of force transmission may be small in normal muscles during physiological conditions, because (1) the above studies all used tetanic stimulation. This rarely occurs during voluntary movement, so observations may be relevant only to lab conditions; (2) the muscle-tendon complex length of a single muscle was changed while the length of its synergists was kept constant, compared to simultaneous length changes in synergistic muscles during normal movements; (3) when individual muscles are stimulated alone and together, the force sums linearly which is surprising if the epimuscular pathway is used; and (4) a recent experiment studying force transmission between cat soleus (SO) and its synergistic muscles in an intact animal showed little epimuscular force transmission. Each of these points will be discussed below.

In the studies described up to this point, the effects of epimuscular pathways on muscular force transmission were tested predominantly during simultaneous maximal activation of both synergistic and antagonistic muscles. Coactivation of synergistic and antagonistic muscles has been observed in the awake, freely moving animal (e.g., [18]), but in most cases at submaximal levels of activation (e.g., [19]). Recently, using the *in situ* setup described above, substantial proximo-distal EDL force differences (up to 30% of maximal force at each frequency) as well as mechanical interactions with TA + EHL were found during nerve stimulation at submaximal frequencies (10–30 Hz) [20]. This suggests that also at firing frequencies encountered *in vivo* muscle forces can be transmitted via epimuscular myofascial pathways.

Another experimental condition of the studies described in Section 2.2 that was different from the conditions under which muscles function *in vivo* was changing the length of only one muscle. Due to differences in moment arms between synergists [21, 22], the change in length of one muscle can be different from that of its neighbor, but the relative movements imposed during lengthening a single muscle were beyond the physiological range. Recently, this issue was addressed by investigating proximal-distal force differences in EDL muscle while lengthening EDL, TA, and EHL simultaneously, as is the case during ankle movements [23]. Also in these experimental conditions, a large force difference (up to 30% of maximal force) was found. At submaximal stimulation frequencies, however, the difference (5%) and, hence, net epimuscular myofascial force transmission became small [23]. It should be noted that different myofascial pathways can be arranged in such a way that

they exert forces on a muscle in opposite direction (see [9, Figure 8]) and that the proximo-distal force difference is the net result of all myofascial loads [7]. A small difference can thus be explained by limited epimuscular myofascial force transmission or opposing myofascial loads of similar magnitude.

If force transmission through epimuscular pathways is substantial, then nonlinear summation of force is expected when different muscles are activated alone and together. Nonlinear force summation is defined as the difference between the force exerted when two muscle parts are excited simultaneously and the sum of the forces exerted when each muscle part is excited individually [24]. Force transmission between the medial gastrocnemius (MG) and lateral gastrocnemius/soleus muscles (LG/SO) was studied in the cat hindlimb [25, 26]. The muscles were activated by stimulation of the nerve branches to each of the muscle groups. LG and SO muscles were stimulated together because of the difficult surgery required to separate their nerves (see [27]). The cat hindlimb was left intact and the foot attached to a 6-degree-of-freedom (dof) load cell to measure force and torque. The femur was fixed to a rigid frame. MG was stimulated alone, LG/SO alone, and then both together. When both muscles were stimulated together, the resulting forces and torques (all 6 dof) were less than the sum of the individual forces. The peak error occurred during the onset of activation where force was about 9% less compared to the plateau where steady state force was about 2% less. There was no evidence that the direction of the forces changed during simultaneous activation of the muscles compared to activation of the muscles independently. These results suggest that when both muscle groups were activated together there was increased shortening of the muscle fibers, and hence less force due to a higher velocity of shortening during force onset. Thus, there is some interaction, either between the muscle bellies or between their tendons. However, the interaction was small, and during steady state, it was almost immeasurable. Similar experiments were performed on the vastus medialis and rectus femoris in cat. Both muscles are knee extensors. They share a border and a tendon and thus may be expected to show nonlinear summation. Nonlinear summation error was small in all 6 degrees of freedom. The average peak error was 8.4% and the mean average error during the contraction was 1.3% (unpublished observations). Note that these experiments do not preclude epimuscular force transmission, but rather suggest that in normal muscle it has little functional effect on the overall force delivered to the skeleton.

To tackle some of the concerns of previous studies, a new experimental approach was developed to measure directly the mechanical interactions between muscles in conditions that simulate those present during normal movements [28]. The latter was assured by testing the muscles in a nearly intact limb of the cat. The tendons were not cut, but left attached to their insertion sites. Length changes were obtained by movements of the joints and, thus, only physiological relative movements could be imposed. The mechanical interactions between the one-joint SO and its two-joint synergistic muscles were studied. The muscle bellies of LG and plantaris

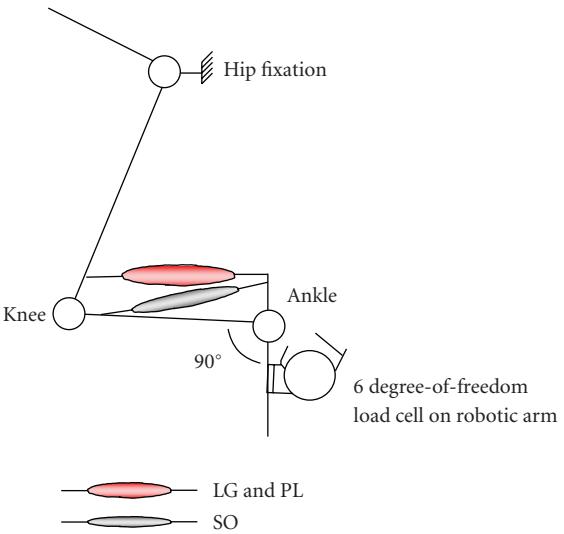


FIGURE 3: A schematic presentation of the cat hindlimb in the experimental setup used to investigate inter-synergist interactions [28].

(PL) muscles share an interface with SO [29]. Ankle moment exerted upon the isolated excitation of SO was measured at various knee angles while the ankle was kept at a constant position ($\sim 90^\circ$), using a 6-degree-of-freedom load cell coupled to a 6-degree-of-freedom robotic manipulator (Figure 3). Note that knee movements will only alter the length and relative position of the two-joint muscles, but not of SO. This involves the greatest relative displacements between these muscles *in vivo*. We hypothesized that force transmission from SO muscle fibers will be affected by length changes of its synergists through configuration changes of connective tissues between these muscles.

Changing the knee angle from 70° to 140° lengthened LG and PL profoundly (4.5–7.2 mm), as calculated using the geometric model presented by Goslow et al. [30]. In contrast to our expectations, active ankle moment generated by SO and the rate of muscle relaxation were not significantly affected by changes in knee angle. These results demonstrate that the presence of relative muscle movements does not necessarily mean force transmission between muscles. To further test the apparent independency of SO, an additional set of experiments was performed. With minimal disruption of the connective tissues at the muscle belly level, the distal tendon of SO was dissected free from the other tendons in the Achilles tendon complex, cut, and connected to a force transducer. As this eliminated force transmission to its insertion on the calcaneus, any ankle joint moment following SO excitation was attributed to force transmission via epimuscular myofascial pathways to the Achilles tendon. If the tendon of SO was placed at its original position, corresponding to the above reported ankle joint angle, the moment exerted at the ankle was close to zero while force exerted at the distal tendon of SO was near its optimal value. A substantial ankle moment was found only if SO was excited at positions distant from physiological. These results confirm

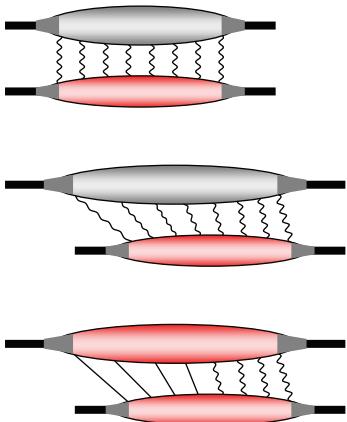


FIGURE 4: Drawings to illustrate length changes of connective tissue linkages between passive (grey) and active (red) synergistic muscles. Changing the length of one muscle results in reorientation as well as unfolding of those linkages. Unfolding is also seen with coactivation. Such straightening of macroscopic crimp in collagen fibrils is correlated to the toe region of the stress-strain curve [35]. Modified from Maas and Sandercock [28].

that for *in vivo* muscle lengths and relative positions force generated in SO muscle fibers is transmitted to its distal tendon.

The above-described nearly linear force summation between MG and LG/SO as well as between rectus femoris and vastus lateralis is in agreement with this finding. Others have found that human SO fascicle length was not affected by changes in knee angle, as measured in both passive and maximally active conditions of the ankle plantar flexors [31]. In contrast, recent imaging studies in humans suggest that mechanical connections between gastrocnemius and SO muscles are effective also within the *in vivo* length range. Isolated excitation of MG at a fixed angle of the ankle and knee joints elicited a decrease in fascicle length, not only in the excited muscle, but also in SO [32, 33]. However, MG activation did not cause displacements in flexor hallucis longus muscle [33], suggesting that not all muscles are equally connected. In addition, effects of knee movements on SO muscle have been reported [33, 34]. Note that the mechanical effects (e.g., ankle moment) of such displacements in SO were not measured.

How can the different results between the rat and cat studies be explained? We have hypothesized that the intermuscular linkages between SO and adjacent muscles within the intact cat may be slack or operate on the toe region of their lumped stress-strain curve (Figure 4, see also [28]). The steep portion of this curve and, hence, epimuscular force transmission will then be attained only with supraphysiological displacements. The stiffness of the intermuscular linkages may also be a local property, being more compliant in the proximal region of the cat ankle extensors. Note that Maas and Sandercock [28] lengthened the two-joint muscles by knee movements; thus, there was more movement proximally. Preliminary data suggest indeed that cat SO muscle is more rigidly connected to LG

distally than proximally (Sandercock and Maas, unpublished observations). Also in line with this hypothesis are the results of an earlier study in the rat in which lengthening a muscle distally resulted in substantial force changes exerted at the distal tendon of a neighboring muscle, while effects of proximal lengthening were not significant [17].

A major difference between the experiments on epimuscular myofascial force transmission in the rat (see above) and the cat [28] is the number of muscles that is activated simultaneously. In the rat studies all synergists and some antagonists were activated versus a single muscle in the cat. Coactivation leads to several changes within the muscle compartment that may affect the mechanical interaction between adjacent muscles. Muscle fibers contract and, hence, the muscle belly shortens and expands radially. The former will result in a small change of the muscle relative position, whereas the expansion will increase the lateral tension of the connective tissue network. In a recent study, we tested the hypothesis that the net effect of coactivation is an increase in the stiffness of the epimuscular pathways (Figure 4), which will facilitate force transmission between muscles. Effects of antagonist coactivation on mechanical interactions between synergistic muscles in the rat forelimb were assessed [36]. In contrast to the hypothesis, changes in force of the restrained muscle with length changes of its synergist were unaffected by antagonist coactivation. Testing intermuscular interaction with other combinations of active muscles (e.g., excluding the activity of some synergistic muscles) may be necessary to elucidate the effects of muscle coactivation on the magnitude of epimuscular myofascial force transmission.

Finally, it is also conceivable that the mechanical characteristics of the connective tissue system are different between muscle groups within an animal and across species. The muscle-connective tissue architecture and composition of each synergistic group is different. Therefore, generalizing the current results to the whole musculoskeletal system should be done with caution. Although mechanical interactions between synergistic muscles have been shown in many animals (e.g., mouse, rat, cat, locust, frog), differences in connective tissue mechanical properties or differences in animal size may affect the importance of such force transmission. In contrast to mammals, it has been reported that amphibians have a relatively poorly developed connective tissue network [37] and that insects contain very little connective tissue [38, 39]. Another aspect that should be taken into account is the scaling of muscle surface area (to the 2nd power) versus muscle volume (to the 3rd power). This means that, for example, mice have a relatively larger epimysial surface to volume ratio than humans. To date, whether these variations between species lead also to different mechanical interactions remains unclear.

The contradictory findings between the rat and cat studies are not fully understood and, thus, the responsible mechanisms requires further investigation. Specifically, future studies should continue to test if the magnitude of intermuscular force transmission is dependent on the number of muscles that is simultaneously activated. Is the extent of force transmission between muscles the same throughout the body? This is another question that needs to

be addressed. In conclusion, the importance of epimuscular myofascial pathways for muscle function during normal movements remains unclear.

2.4. Connective Tissue Function in Pathological Muscle-Tendon Conditions. Besides a potential role for normal muscle function, epimuscular myofascial pathways may be important in pathological conditions of the musculoskeletal system. Street observed [41], “*After the distal tendon of a frog’s semitendinosus muscle is cut, pathological changes appear first in the distal part. We found that when part of a muscle was normal the muscle as a whole generally developed the normal amount of tension and we guessed that some cell component other than the myofilament arrays served as a tension bypass through or around the damaged areas (Ramsey and Street, unpublished).*” In the same paper, Street suggested [41], “*In injured whole muscle it is probable that the connective tissue sheath near damaged fibers can pick up and transfer active tension generated in normal areas and, at the same time, stabilize abnormal areas against length changes. This might promote healing.*” This suggests the hypothesis that the connective tissue network may act also as a safety net for traumatic events in muscle or tendon. In other words, due to the presence of myofascial pathways, the acute effects of muscle or tendon trauma are limited and muscle function is preserved.

Injury within a muscle or tendon is a common occurrence, especially during sport activities (e.g., [42, 43]). Thus, it is essential that basic function is maintained while the injury is healed. In the same study by Maas and Sandercock [28] that showed little epimuscular force transmission in intact SO, they also showed that during complete tendon transection the SO can produce substantial force. The insertion of the SO on the calcaneus was completely severed, yet the SO produced an extensor moment at the ankle that was about 45% of normal. There was greater shortening, 17 mm compared to 1 mm, than before tendon transection. Yet function was partially maintained possibly allowing use during recovery.

The results of several previous studies support the idea that connective tissues within and surrounding muscles can limit injury and support repair. It has been reported that one of the four distal tendons of rat EDL (a multitendoned muscle, see [44]) can be cut or considerably shortened with minimal effects on force measured at the proximal tendon [45, 46]. This can only be explained by transmission of force from the tenotomized muscle fibers to the intact distal tendons via the endomysial-perimysial network. Similar phenomena have been reported following transection of the whole distal or proximal tendon. During some of the above-described rat experiments, the connection between tendon and force transducer was suddenly severed. Following such a release of the proximal EDL tendon, a substantial force was still found at the distal tendon [47]. The muscle fibers of EDL are thus prevented from shortening all the way, most likely by inter- and/or extramuscular connective tissues. In a different experiment, the connection of the TA + EHL tendon was released

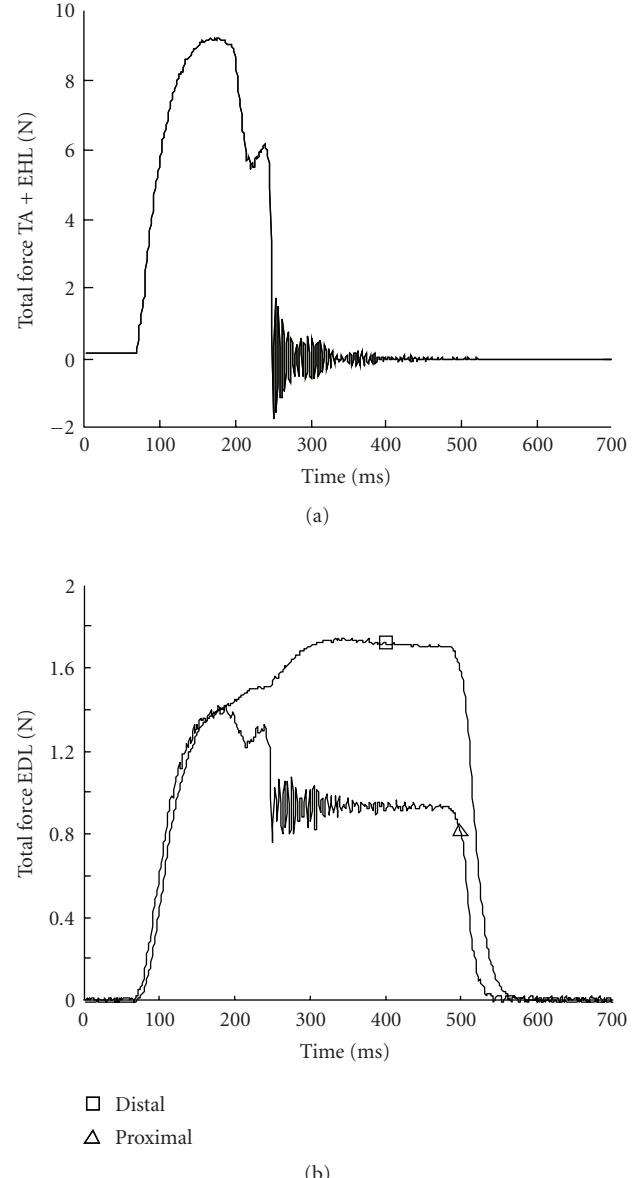


FIGURE 5: Waveforms of simultaneously measured force exerted at the distal tendon of TA + EHL (a) and forces exerted at the tendons of EDL muscle (b). During isometric contraction, the connection between TA + EHL and the force transducer was severed ($t \sim 200$ ms). TA + EHL force dropped to zero and at the same time proximal EDL force decreased and distal EDL force increased. These results have been presented in abstract form [40].

suddenly. Proximal TA + EHL force was not measured, but the changes in proximal and distal EDL forces clearly indicate mechanical interactions between these synergistic muscles (Figure 5).

In addition to the acute backup from connective tissues following muscle and tendon trauma, long-term adaptations also suggest that myofascial pathways serve temporarily as a safety net. It has been reported that the integrin-vinculin mediated connections between the subsarcolemmal

cytoskeleton and extracellular matrix are temporarily reinforced in ruptured muscle fibers [48, 49]. As a consequence, force generated within the sarcomeres of these damaged fibers will be transmitted via the endomysium. This will reduce the load on the injured site allowing repair with less chance of rerupture. In the case that not the muscle fibers but the tendon is fully or partially torn, connective tissue linkages with adjacent structures may in a similar fashion prevent further trauma and facilitate the recovery process. Such adhesions have been reported in chronically tenotomized muscle in the rat, cat, and rabbit [50–52], which ultimately results in reattachment of the tendon. Nonsurgical treatment (e.g., immobilization at low length) is also frequently applied following tendon ruptures in humans (e.g., [53]). Preserving and restoring function after injury clearly is important in wild animals and will be selected for. In contrast to humans, where the damage can be treated in a hospital, most animals must maintain some degree of function while the muscle-tendon injury heals.

Epimuscular myofascial transmission may also be important during reconstructive surgery. Several surgical interventions include manipulation of tendon, muscle, and/or the surrounding connective tissues (e.g., fasciotomy in compartment syndrome, tendon transfer in cerebral palsy). In tendon transfer surgery limb function is improved in a patient by cutting and reattaching a tendon to a new insertion point (e.g., [54]). Preliminary results suggest that scar tissue formation following an agonist-to-antagonist tendon transfer in the rat significantly affects transmission of forces from the transferred muscle [55]. Therefore, knowledge of the acute and long-term effects of disrupting connective tissues has important implications for surgical practice.

3. Conclusions

In the last decade, the potential of force transmission between skeletal muscles via inter- and extramuscular connective tissues has been demonstrated. Investigators have definitively shown that epimuscular pathways can transmit substantial force. More recent efforts have resulted in new insights regarding effects of epimuscular myofascial force transmission in more physiologically relevant muscle conditions (e.g., *in vivo* relative muscle movements). While not conclusive, these insights suggest that the role of this pathway may be small in normal undamaged muscles. Future studies should investigate force transmission during muscle activation patterns that resemble those of normal movements. In particular, effects of decreasing the number of muscles that are active simultaneously on the mechanical connectivity between muscles need to be investigated. Furthermore, the material properties of the connective tissue links need to be characterized. A full understanding requires knowing how the deformation of the border of a muscle affects the strain throughout the muscle. While the significance of epimuscular myofascial force transmission for muscle function *in vivo* remains unclear, potential functions for pathological muscle-tendon conditions (e.g., tendon rupture) have emerged.

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