Myofascial force transmission between a single muscle head and adjacent tissues: length effects of head III of rat EDL

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Submitted 3 March 2003; accepted in final form 25 June 2003

Maas, Huub, Richard T. Jaspers, Guus C. Baan, and Peter A. Huijing. Myofascial force transmission between a single muscle head and adjacent tissues: length effects of head III of rat EDL. J Appl Physiol 95: 2004–2013, 2003. First published July 3, 2003; 10.1152/japplphysiol.00220.2003.— Force transmission from muscle fibers via the connective tissue network (i.e., myofascial force transmission) is an important determinant of muscle function. This study investigates the role of myofascial pathways for force transmission from multitendoned extensor digitorum longus (EDL) muscle within an intact anterior crural compartment. Effects of length changes exclusively of head III of rat EDL muscle (EDL III) on myofascial force transmission were assessed. EDL III was lengthened at the distal tendon. For different lengths of EDL III, isometric forces were measured at the distal tendon of EDL III, as well as at the proximal tendon of whole EDL and at the distal tendons of tibialis anterior and extensor hallucis longus (TA+EHL) muscles. Lengthening of EDL III caused high changes in force exerted at the distal tendon of EDL III (from 0 to 1.03 ± 0.07 N). In contrast, only minor changes were found in force exerted at the proximal EDL tendon (from 2.37 ± 0.09 to 2.53 ± 0.10 N). Increasing the length of EDL III decreased TA+EHL force significantly (by 7%, i.e., from 5.62 ± 0.27 to 5.22 ± 0.32 N). These results show that force is transmitted between EDL III and adjacent tissues via myofascial pathways. Optimal force exerted at the distal tendon of EDL III (1.03 ± 0.07 N) was more than twice the force expected on the basis of the physiological cross-sectional area of EDL III muscle fibers (0.42 N). Therefore, a substantial fraction of this force must originate from sources other than EDL III. It is concluded that myofascial pathways play an important role in force transmission from multitendoned muscles.

connective tissue; extensor digitorum longus muscle; tibialis anterior muscle; extensor hallucis longus muscle; length-force characteristics

SEVERAL HUMAN TASKS, SUCH as typing on a keyboard and playing a musical instrument, require movements of fingers relative to each other. In general, multitendoned muscles of the forearm contribute to finger movements. In both humans (18) and monkeys (36), it has been shown that it is hardly possible to move a single digit without movements of adjacent digits. Furthermore, voluntary exertion of force by one finger is, in most cases, accompanied by force exertion by the nontarget fingers (19, 23, 41).

It has been hypothesized that mechanical interactions at the level of the muscle belly could be one of the factors limiting the independent control of the position and force of the fingers (26). Previous studies on fully dissected rat extensor digitorum longus (EDL) muscle, a multitendoned muscle with distal insertions on digits II–V within the foot (1), yielded clear evidence of transmission of force between muscle heads via connective tissues at their interfaces (12, 15). Within a muscle, there are several pathways via which force generated by a sarcomere is transmitted to the tendon (for reviews see Refs. 8, 9, 31): 1) via sarcomeres arranged in series within a muscle fiber and the myotendinous junction (i.e., myotendinous force transmission); and 2) via complexes of structural proteins connecting parallel sarcomeres onto the subsarcolemmal cytoskeleton and endomysium (2, 34). From the endomysium, force is transmitted to neighboring fibers or directly onto the aponeurosis (i.e., intramuscular myofascial force transmission).

In vivo, skeletal muscles are surrounded by synergists and embedded within the connective tissues of a compartment, which comprises 1) intermuscular connective tissue (i.e., connective tissue at the interface between muscle bellies), as well as 2) extramuscular connective tissues (e.g., connective tissue that supports the nerves and blood vessels and fascia representing the compartmental borders). Recent experiments on rat EDL muscle (10, 26) have shown that inter- and extramuscular connective tissues may be the pathways for transmission of a substantial fraction (up to 37%) of force to or from the muscle. Such transmission is referred to as inter- and extramuscular myofascial force transmission. In those experiments, whole EDL muscle was studied, and the four heads of EDL muscle were manipulated as one unit. However, movements of digits relative to each other require the individual heads of a multitendoned muscle to be active at different lengths and thus to move with respect to each other.

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In the present study, effects of changing the length of only one head of rat EDL muscle (head III, referred to as EDL III) on myofascial force transmission are studied. For different lengths of EDL III, isometric forces were measured at the distal tendon of EDL III, as well as at the proximal tendon of whole EDL and at the distal tendons of tibialis anterior (TA) and extensor hallucis longus muscles (EHL; TA+EHL).

We tested the following hypotheses: 1) force is transmitted via myofascial pathways to the distal tendon of EDL III; 2) changes in force exerted at the proximal tendon of whole EDL muscle as EDL III is lengthened are not equal to changes of force exerted at the distal tendon of EDL III; and 3) force exerted by synergistic muscles (i.e., TA and EHL) is affected by length changes of EDL III.

**METHODS**

Surgical and experimental procedures were in strict agreement with the guidelines and regulations concerning animal welfare and experimentation set forth by Dutch law and approved by the Committee on Ethics of Animal Experimentation at the Vrije Universiteit.

**Surgical Procedures**

Male Wistar rats (n = 6, body mass = 305.2 ± 6.8 g) were anesthetized by using intraperitoneally injected urethane (1.2 ml/100 g body mass, 12.5% urethane solution, wt/vol, extra doses were given if necessary: maximum 1.5 ml). To prevent hypothermia during surgery and data collection, the animals were placed on a heated water pad of ~37°C. Ambient temperature (22 ± 0.5°C) and air humidity (50 ± 2%) were kept constant by a computer-controlled air-conditioning system (Holland Heating, Waalwijk, The Netherlands). Dehydration of muscle and tendon tissue was prevented by regular irrigation with isotonic saline.

Removing the skin and most of the biceps femoris muscle from the left hindlimb exposed the anterior crural compartment, which envelops the TA, EDL, and EHL muscles. Connective tissues of the compartment at the muscle bellies of TA, EHL, and EDL, as well as the retinaculae at the ankle (i.e., transverse crural ligament and the crural cruciate ligament) were left intact.

In the foot, the distal tendon of EDL III was dissected free from surrounding tissues. Limited crural fasciotomy was performed only distally to reach the distal tendons of TA and EHL muscles. The distal tendons of TA and EHL muscles are, for a substantial part of their length, quite close to one another. As it is difficult to measure force exerted at each tendon individually without friction between them, the distal tendons of TA and EHL were tied together by using polyester thread, with the ankle joint at 90°. This complex of muscles will be referred to as the TA+EHL complex. The distal tendon of EDL III and the distal tendons of the TA+EHL complex were cut, and Kevlar threads (diameter = 0.5 mm, tensile modulus = 58 GPa, 3.7% extension to breaking; Goodfellow, Cambridge, UK) were tied to them. The foot was attached to a plastic plate with tie wraps. The femoral compartment was opened 1) to cut a small piece of the lateral epicondyle of the femur (i.e., the origin of EDL muscle) for attaching it to Kevlar thread, 2) to secure a metal clamp to the femur for later fixation at a knee angle of 100° in the experimental apparatus, and 3) to dissect the sciatic nerve.

Within the femoral compartment, the sciatic nerve branches to the tibial nerve, the sural branch, and the common peroneal nerve. The common peroneal nerve enters the anterior crural compartment from the peroneal compartment through a fenestration within the anterior intermuscular septum (11). Branches of the common peroneal nerve innervate EDL, TA, and EHL muscles, as well as the muscles in the peroneal compartment. The tibial nerve, the sural nerve, and all other proximal branches of the sciatic nerve were cut. The sciatic nerve, with only the common peroneal nerve branch left intact, was dissected and cut as proximally as possible.

**Mounting the Animal in the Experimental Apparatus**

The rat was placed on a platform. The metal clamp was used to secure the femur at a knee angle of 100°. The plastic foot plate was positioned in such a way that the ankle angle was 90° (Fig. 1). With the use of the Kevlar threads, the proximal tendon of EDL muscle as well as the distal tendons of the TA+EHL complex were connected to force transducers (maximal output error <0.1%, compliance of 0.0048 mm/N; Hottinger Baldwin, Darmstadt, Germany) mounted on single-axis micropositioners. The distal tendon of EDL III was also connected to a force transducer (compliance 0.014 mm/N) (39). The other distal tendons of EDL muscle were left attached to their insertions on the digits (i.e., II, IV, and V) within the foot. For TA+EHL force measurements, the Kevlar thread was connected to the force transducer via a low-friction pulley that, because of limited space, was placed parallel to the other force transducers. For EDL III, the retinaculae at the ankle cause the line of pull to be in parallel with the foot. To connect the Kevlar thread to the force transducer on the ergometer, an additional pulley was needed. The proximal tendon of EDL muscle was connected directly to the force transducer, which was positioned in the line of pull.

The sciatic nerve, with only the common peroneal nerve branch left intact, was placed in a pair of silver electrodes. The nerve was prevented from dehydration, by covering it with paper tissue saturated with isotonic saline covered by a thin piece of latex. In all experimental conditions, the sciatic nerve was stimulated supramaximally by using electrodes connected to a constant current source (3 mA, pulse width 100 μs).

**Isometric Length-Distal Force Characteristics of EDL III**

The length of the TA+EHL complex (corresponding to an ankle joint at 90°) was kept constant. This was also the case for the position of the proximal tendon of EDL muscle (corresponding to a knee joint at 100°). In addition, the distal tendons of EDL heads II, IV, and V were left attached to their insertions. Therefore, their lengths were also kept constant.

Length-distal force characteristics of EDL III were assessed. Isometric force was measured at various lengths of EDL III. EDL III was lengthened at its distal tendon (Fig. 1) with 1-mm increments starting at active slack length (i.e., the lowest length at which active force approaches zero) until ~2 mm over optimum length. Subsequently, measurements of length-force characteristics of EDL III were repeated two times to assess the reproducibility.

Before excitation of the muscles, EDL III was brought to the target length. Two twitches were evoked, followed by a tetanic contraction of the muscles after 500 ms (pulse train 400 ms, frequency 100 Hz). Muscle force was measured just before the tetanic contraction (i.e., passive force) and during the tetanic plateau (i.e., 275 ms after evoking tetanic stimulation, total force). Simultaneously, images of the anterior crural compartment with muscles in the passive and active state were recorded with an 800 line camera (i.e., 2.5 cycles/mm).

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state were recorded by using a digital camera (DVC, JAI CV-M10, shutter speed 1/50 s). Timing of stimulation of the nerve, analog-to-digital conversion (12-bit analog-to-digital converter, sampling frequency 1,000 Hz, resolution of force 0.01 N), and photography were controlled by a special-purpose microcomputer. After each contraction, EDL III was allowed to recover near active slack length for 2 min.

Treatment of Isometric Length-Force Data

The individual data for length of the muscle-tendon complex \( l_{m+t} \) and passive muscle force \( F_{mp} \) were fitted with an exponential curve (Eq. 1), using a least squares criterion

\[
y = e^{a_1 + a_2 x}
\]

where \( y \) represents \( F_{mp} \), \( x \) represents \( l_{m+t} \), and \( a_1 \) and \( a_2 \) are coefficients determined in the fitting process. For each \( l_{m+t} \) studied, active muscle force \( F_{ma} \) was assessed by subtracting fitted \( F_{mp} \) from total muscle force. These length-.active force data were fitted by a polynomial (Eq. 2)

\[
y = b_0 + b_1 x + b_2 x^2 + b_3 x^3 + b_4 x^4 + \ldots + b_n x^n
\]

where \( y \) and \( x \) represent \( F_{ma} \) and \( l_{m+t} \), respectively, and \( b_0 \) through \( b_n \) are coefficients determined in the fitting process. The order of the polynomial most adequately describing the relationship was selected (see Statistics). Fitted curves were used to calculate mean data and SE, as well as to determine optimal force and optimum \( l_{m+t} \). The \( l_{m+t} \) was expressed as the deviation from active slack length \( \Delta l_{m+t} \).

Although forces exerted at the distal tendons of EDL III and the TA+EHL complex are in opposite direction to forces exerted at the proximal tendon of EDL, all forces will be presented as positive values.

Morphology of EDL Muscle

After the experimental measurements, the masses of the individual EDL heads were measured and expressed as a percentage of total muscle mass. As the number of sarcomeres in series within fibers of different heads has been shown to be rather similar (12), values of normalized mass may be considered as adequate estimates of normalized physiological cross-sectional area and thus of relative contribution of individual heads to total EDL \( F_{ma} \). Means and SE were calculated.

Two additional animals (body mass = 304 and 324 g, respectively) were used to study the morphological characteristics of EDL muscle. EDL muscle was excised from the left hindlimb. Intramuscular fasciotomy was performed to separate the heads of EDL muscle. Images were made of the heads and their corresponding distal aponeuroses and tendons. Before cross-sectioning, a layer of graphite powder was applied at the interface between the different muscle heads. The distal tendons were tied together, and the muscle, kept at a constant length, was fixed in a buffered formaldehyde solution (0.4% formaldehyde, vol/vol). The muscle was dehydrated in a series of buffered ethanol dilutes (70–95% ethanol, vol/vol) and embedded (70-2218-500 Historesin embedding kit, Jung, Heidelberg, Germany). Subsequently, serial

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Fig. 1. Bottom: schematic representation of the experimental setup. FT1, force transducer connected to the proximal (prox) tendon of extensor-digititorum longus (EDL) muscle; FT2, force transducer mounted on a multipurpose muscle-nerve-ergometer connected to the distal tendon of EDL head III (EDL III); FT3, force transducer connected to the tied distal tendons of tibialis anterior (TA) and extensor hallucis longus (EHL) muscles. Kevlar thread was used to connect the muscles to force transducers. A low-friction pulley guided the Kevlar thread from TA+EHL to FT3 that, for reasons of space, was placed perpendicular to the other force transducers. The proximal tendon of EDL muscle was connected directly to the force transducer, which was positioned in the line of pull. The distal tendon of EDL III was connected to the force transducer via a low-friction pulley. Various muscle-tendon complex lengths \( l_{m+t} \) of EDL III were obtained by repositioning FT2, as indicated by the double arrow. Top: lateral view of the experimental setup, zoomed in on the lower leg of the rat left hindlimb. Bar = 10 mm. Because the EDL and EHL muscles are enclosed by TA muscle, only the latter muscle is visible. \( \Delta l_{m+t} \), Deviation from \( l_{m+t} \).
transverse sections (10 μm) of the midbelly region were cut by using a microtome (type K, HK3 knife, Reichert-Jung, Heidelberg, Germany). The sections were stained for 2 min in a 0.02% (wt/vol) toluidine blue (art. 1273, Merck, Amsterdam, The Netherlands) solution and finally sealed with a coverslip by using Entellan (catalog no. 1.07961, Merck).

**Statistics**

For fitting the length-active force data, a stepwise polynomial regression procedure was used. In this procedure, the curve fit is determined by increasing the order of the polynomial, as long as this yields a significant improvement to the description of the length-active force data, as determined by one-way ANOVA.

To test for effects of EDL III length on force exerted at the proximal tendon of whole EDL muscle, at the distal tendon of EDL III force as well as at the distal tendons of TA+EHL, one-way ANOVAs for repeated measures were performed (factor: \(l_{m+t}\), EDL III). Two-way ANOVA for repeated measures (factors: \(l_{m+t}\) EDL III and repetition of length-force assessment) was performed to test for differences between subsequent measured length-force curves. If significant effects were found, Bonferroni post hoc tests were performed to locate significant differences. \(P\) values < 0.05 were considered significant.

**RESULTS**

**Morphological Characteristics of EDL Muscle**

Figure 2A shows the four EDL heads, which are separated partially after dissection. Muscle fibers of these heads insert distally to different aponeuroses and tendons and proximally to a common aponeurosis and tendon. The cross-section of EDL muscle (Fig. 2B) shows that, within EDL muscle, head III shares intramuscular connective tissue predominantly with head II and head IV. However, laterally within EDL muscle, the injected graphite layer indicates that head III is also connected to head V. It is shown also that EDL III shares intermuscular connective tissue with TA muscle. Note that the surface of the intermuscular TA-EDL III interface is considerably smaller than the intramuscular interface of EDL III. In addition, EDL muscle is connected to nonmuscular structures of the anterior crural compartment (e.g., bone, fascia, anterior intermuscular septum) via extramuscular connective tissues (e.g., connective tissue that supports the neurovascular tract of the compartment).

The images of EDL muscle show that the cross-sectional area of heads II, III, and IV is smaller than that of head V. Physiological cross-sectional area of EDL III, normalized for the physiological cross-sectional area of whole EDL, was estimated to be only 16 ± 2.2%, whereas heads II, IV, and V represent 20 ± 1.4, 19 ± 1.8, and 45 ± 0.6%, respectively.

**Acute Effects of Changes of EDL III Length**

**EDL proximal force.** See Fig. 3A. ANOVA revealed significant effects of EDL III length on active and passive force exerted at the proximal tendon of whole EDL. For low lengths of EDL III, a small passive force (minimum \(F_{mp} = 0.02 \pm 0.00\) N, right axis in Fig. 3A) was exerted at the proximal tendon. Proximal passive EDL force increased exponentially as a function of EDL III length (maximum \(F_{mp} = 0.10 \pm 0.03\) N). Proximal active EDL force increased also as a function of EDL III length: from 2.37 ± 0.09 N (at \(\Delta l_{m+t} = 0\) mm) to a maximum of 2.53 ± 0.10 N (at \(\Delta l_{m+t} = 5.9\) mm). A further increase of EDL III length caused a decrease in proximal EDL force (to 2.36 ± 0.15 N). These results show that substantial changes of length of EDL III (\(\Delta l_{m+t} = 9\) mm) cause only minor effects on isometric force exerted at the proximal tendon of EDL muscle.

**Distal EDL III force.** See Fig. 3B. ANOVA revealed significant effects of EDL III length on passive and active forces exerted at the distal tendon of EDL III. Passive force was zero at low EDL III lengths and increased exponentially after lengthening EDL III (maximum \(F_{mp} = 0.17 \pm 0.04\) N). EDL III optimum length deviated 8.3 mm from active slack length (\(\Delta l_{m+t} = 0\) mm), and optimal force was 1.03 ± 0.07 N.

A comparison between changes of proximal EDL force and of distal EDL III force, both expressed as a function of EDL III length, reveals several remarkable features (Fig. 4). 1) Between \(\Delta l_{m+t} = 0\) mm and 5.9 mm (i.e., the length of EDL III that corresponds to maximal force of proximal EDL), proximally measured active EDL force increased by only 0.15 ± 0.03 N (Fig. 4A), whereas, for the same EDL III length range, force exerted at the distal tendon of EDL III increased by 0.77 ± 0.06 N (i.e., 5 times higher than the increase of proximal EDL force). 2) The increase of EDL III passive force (\(\Delta F_{mp} = 0.17 \pm 0.04\) N) was also significantly higher than the increase of proximally measured EDL passive force (\(\Delta F_{mp} = 0.08 \pm 0.03\) N) (Fig. 4B). 3) Maximal proximal EDL active force was found at lower length of EDL III (\(\Delta l_{m+t} = 5.9\) mm) than optimal force of EDL III (\(\Delta l_{m+t} = 8.3\) mm). As a consequence, maximal EDL force is decreasing, whereas distal EDL III force is still increasing on lengthening EDL III (from \(\Delta l_{m+t} = 5.9\) to 8.3 mm).

Thus length changes of EDL III cause different effects on proximal EDL and distal EDL III forces. If force transmission between EDL III and adjacent tissues were absent, changes of force exerted at the proximal tendon of EDL would equal the changes of force exerted at the distal tendon of EDL III. Therefore, these results show that force is transmitted via intra-, inter-, and/or extramuscular myofascial pathways from or to EDL III.

**TA+EHL complex force.** See Fig. 5. ANOVA revealed significant effects of EDL III length on active force exerted at the distal tendons of TA+EHL. Because the TA+EHL complex was kept at a constant moderate length, passive force exerted by the TA+EHL complex remained negligible. Increasing the length of EDL III decreased TA+EHL force significantly (i.e., from 5.62 ± 0.27 to 5.22 ± 0.32 N) (Fig. 5A). These results indicate mechanical interactions between EDL III and the TA+EHL complex.
Fig. 2. Morphology of multitendoned EDL muscle of the rat. A: muscle fibers of 4 muscle heads insert distally onto different aponeuroses and tendons and proximally onto a common aponeurosis and tendon. The heads are named after their insertions on digits II–V of the toes. The distal aponeuroses are a continuation of the distal tendons and located at the opposite site of the muscle bellies. A remainder of the nerve branch innervating EDL muscle is indicated (arrow). Within an intact EDL muscle, these muscle heads are connected to each other by intramuscular connective tissue. Therefore, intramuscular fasciectomy was performed to make the different heads distinguishable in the figure. The approximate level of cross-section (B) is indicated. The division of the ruler shown represents 1 mm. B: distal view of a cross-section of EDL muscle after the muscle heads were separated by using a layer of graphite powder. The section (thickness = 10 μm) was stained with a toluidine blue solution. It should be noted that, within an intact EDL muscle, the layer of connective tissue between muscle heads is rather thin. The thickness of the graphite layer between muscle heads, as shown in the cross-section, is caused by the applied method. It shows that head III shares intramuscular connective tissue with heads II, IV, and V. EDL III interfaces intermuscularly with TA. Furthermore, EDL muscle is connected to nonmuscular structures of the anterior crural compartment via extramuscular connective tissues (e.g., connective tissue that supports the nerves and blood vessels of the compartment). The approximate location of the neurovascular tract and the anterior intermuscular septum is indicated. Bar = 500 μm. C: schematic outline of the muscles within the anterior crural compartment, as well as the location of the neurovascular tract and the anterior intermuscular septum. Anatomic orientation for B and C is indicated (cross of arrows).
Repeated Isometric Length-Force Measurements of EDL III

EDL proximal force. See Fig. 6A. For active and passive forces, ANOVA indicated no significant differences between repeated measurements on proximal EDL force curves. Therefore, it is concluded that proximal EDL force expressed as a function of EDL III length is reproducible.

Distal EDL III force. See Fig. 6B. In contrast to proximally measured EDL force, length-force characteristics of EDL III were altered significantly in subsequent length-force measurements. Passive force of EDL III measured at high lengths (Δl_{m+1} EDL III = 7–9 mm) was decreased significantly subsequent to measurements for the first length-force curve. Particularly at higher lengths (Δl_{m+1} EDL III = 5–9 mm), active forces differed significantly. In contrast, for the lower lengths (Δl_{m+1} EDL III = 0–4 mm), no significant differences in active force were shown. Furthermore, EDL III optimum length was shifted to a higher length (at least by 0.7 mm), whereas active slack length was not changed. A subsequently measured length-force curve (i.e., LF3) was not significantly different from the previous one (i.e., LF2).

These results indicate that previous isometric contractions, particularly at high lengths of EDL III, modify the length-distal force characteristics of EDL III. As muscle fibers of head III insert also to the proximal aponeurosis of EDL muscle, it is remarkable that these effects were not measured at the proximal tendon of EDL muscle. This is another indication of effects of myofascial force transmission between EDL III and adjacent tissues.

TA+EHL complex force. See Fig. 6C. ANOVA revealed significant effects of EDL III length-force measurements.

Fig. 3. Length-distal force characteristics of EDL III and the simultaneously measured proximal EDL force. A: active (F_{ma}) and passive (F_{mp}) forces exerted at the proximal EDL tendon plotted as a function of Δl_{m+1} of EDL III. B: length-distal force characteristics of EDL III. Note that different y-axes with different scaling factors are shown for F_{ma} (left axis) and F_{mp} (right axis). Values are means ± SE (n = 6), dist, Distal.

Fig. 4. Comparison of changes in proximal EDL force and EDL III distal force. Changes are shown of F_{ma} (A) and F_{mp} (B), both plotted as a function of Δl_{m+1} of EDL III. Forces are expressed as the deviation from the initial value (i.e., measured at active slack length of EDL III, i.e., Δl_{m+1} EDL III = 0 mm): for proximal EDL F_{mp} = 0.02 ± 0.00 N, F_{ma} = 2.37 ± 0.09 N; for EDL III, F_{mp} and F_{ma} are zero. Values are means ± SE (n = 6).
measurements on active force of the TA+EHL complex. The slope of the EDL III length-TA+EHL force curve decreased subsequent to measurements for the first length-force curve of EDL III. As a consequence, the decrement of TA+EHL force after lengthening EDL III by 9 mm was less pronounced, but significant, during the measurements for the second and third length-force curves of EDL III (i.e., 0.17 ± 0.03 and 0.15 ± 0.03 N, respectively), if compared with the force decrement during the first measurement (i.e., 0.40 ± 0.08 N). These results indicate that the degree of intramuscular interaction between EDL III and TA+EHL was decreased. As such interaction is attributed to myofascial force transmission, this is explained by a decreased stiffness of the structures representing the myofascial pathways between the muscle belly of EDL III and the muscle bellies of TA and EHL muscles.

DISCUSSION

The most important results of the present study are that 1) changes in isometric force exerted at the proximal tendon of whole EDL muscle as a function of EDL III length are not equal to changes in force exerted at the distal tendon of EDL III, 2) isometric force exerted at the distal tendons of TA+EHL decreased significantly after lengthening of EDL III, and 3) isometric activity, particularly at high lengths of EDL III, changed EDL III length-force characteristics as well as TA+EHL force, whereas no such changes of proximal EDL force were found.

These results are explained in terms of myofascial force transmission between EDL III and adjacent tissues. Excitation of a muscle leads to shortening of sarcomeres until active force exerted by cross bridges...
between the actin and myosin filaments, together with passive force exerted by intrasarcomeric passive elements (e.g., titin), is equal to the sum of opposing forces (i.e., the reaction force). The reaction force may originate from 1) sarcomeres in series, which are linked to each other by the Z-lines, or from 2) the endomysium, which is linked to the subsarcolemmal cytoskeleton and the sarcomeres via complexes of structural proteins (i.e., the myofascial pathway). Proteins that may be involved have been reviewed recently (2, 34).

Within a muscle, force exerted at a particular location of the endomysium can, in principle, be transmitted onto the tendon 1) via neighboring fibers and their myotendinous junction or 2) via the endomysial-perimysial network.

If a muscle is isolated from surrounding tissues, muscle force can only be transmitted via the muscular origin and insertion onto bone. In vivo, however, muscles are embedded within connective tissues of a compartment and surrounded by synergists. It has been shown that muscle force exerted at the endomysial-perimysial network is also transmitted via intermuscular connective tissue onto the intramuscular connective tissue network of adjacent muscles (9, 26, 27). In addition, force is transmitted between muscle and extramuscular connective tissues (10, 13, 29). Effects of inter- and extramuscular myofascial force transmission on muscle properties have been reviewed recently (28).

In the present study, a surprisingly high optimal force of EDL III was found (i.e., 1.03 ± 0.07 N). In a previous study, optimal force for whole EDL muscle of rats with similar body mass was 2.60 ± 0.14 N (26). If a comparable optimal EDL force is assumed for the present study, at optimum length of EDL III, 40% of active force of whole EDL muscle is exerted at the distal tendon of EDL III. This is in sharp contrast to the value for relative physiological cross-sectional area of EDL III, which was only 16 ± 2.2% of whole EDL muscle. Therefore, a substantial fraction of active force...

Fig. 6. Effects of repeated length-force measurements of EDL III on proximal EDL force, distal EDL III force, and distal TA+EHL force. A: EDL proximal F\(_{ma}\) and F\(_{mp}\) plotted as a function of EDL III \(\Delta l_{m-t}\) of repeated measurements (LF1, LF2, and LF3). B: F\(_{ma}\) and F\(_{mp}\) exerted at the distal tendon of EDL III plotted as a function of EDL III \(\Delta l_{m-t}\). C: distally measured F\(_{ma}\) of the TA+EHL complex plotted as a function of EDL III \(\Delta l_{m-t}\). Note that TA+EHL force is expressed as the deviation from the initial value (i.e., F\(_{ma}\) LF1 = 5.62 ± 0.26 N, F\(_{ma}\) LF2 = 5.29 ± 0.32 N, F\(_{ma}\) LF3 = 5.21 ± 0.34 N, measured at \(\Delta l_{m-t}\) EDL III = 0 mm). Note that, in A and B, different y-axes with different scaling factors are shown for F\(_{ma}\) (left axis) and F\(_{mp}\) (right axis). Values are means ± SE (n = 6).
Exerted at the distal tendon of EDL III originated from sources other than from muscle fibers of head III. As the endomysial-perimysial strata of EDL III is a part of the continuous connective tissue network of the anterior crural compartment (11, 13, 26), such sources may be 1) fibers within surrounding muscles (i.e., TA and EHL) and/or 2) fibers within the other heads of EDL. Therefore, it is concluded that force is transmitted to the distal tendon of a single muscle head of multitendoned muscle via inter-and extramuscular myofascial pathways, as well as via intramuscular myofascial pathways.

Moreover, we showed that an increase of length of a single head of multitendoned EDL muscle simultaneously decreased force exerted at the distal tendons of synergistic muscles (i.e., TA and EHL) (Fig. 5). This means that partitioning of force over the different pathways of force transmission is altered by length changes of EDL III. As EDL III is lengthened, force previously exerted at the distal tendons of TA+EHL is exerted at the distal tendon of EDL III. As the other EDL heads are also connected to EDL III, it is expected that, in the present experiment, forces exerted at distal tendons of the other heads of EDL (not measured) were affected also.

In vivo, movement of a single finger requires a change of length of the corresponding head of multitendoned muscle. If the antagonist forces remain equal, changes of force exerted at the distal tendons of muscle heads other than the target one will result in joint movements of the corresponding fingers. This indicates that myofascial force transmission is one of the mechanisms, which explains that, during single-finger tasks, changes of force or movements are measured also in the nontest fingers. The limited independent control of the position and force of the fingers has been attributed to central neural factors, as well as to mechanical factors at the muscle-tendon level (e.g., Refs. 18, 22, 41). Until now, mechanical factors that have been postulated are as follows: 1) transmission of force from fibers, inserting on the same tendon, via the intramuscular connective tissue network to adjacent heads (i.e., intramuscular myofascial force transmission) and 2) force transmission via tendinous connections between the distal tendons of multitendoned extensors and flexors of the fingers. The present results indicate that 3) intermuscular and 4) extramuscular myofascial force transmission should also be considered as important factors. It has been reported that surgically removing those intertendinous connections improves finger independence (16, 20, 21, 25, 30, 32, 37). However, for most cases, full independent digit movement was not obtained, even if the central neural factors were excluded (16, 32, 37). This indicates that both intertendinous and myofascial force transmission contribute to involuntary movements of the fingers.

It should be noted that, in the present experiment, tendon forces were measured while all four EDL muscle bellies as well as TA and EHL muscles were excited simultaneously and maximally. For most movements in vivo, such activation pattern is not found. It may be argued that the stiffness of intra-, inter-, and/or extramuscular connective tissues in the present study was higher than during in vivo patterns of muscle activation. Nevertheless, effects of myofascial force transmission were also found for passive muscles (Fig. 4B). Furthermore, during normal rat behavior, motor units of EDL muscle are occasionally activated at ~100 Hz (i.e., the stimulation frequency imposed on EDL muscle in the present study) (5, 6). Also, coactivation of synergists during normal limb movements (e.g., Ref. 33) and coactivation of nontarget muscle heads of multitendoned muscle during voluntary flexion of one finger (18) have been reported in humans. Therefore, it is expected that, also in vivo, myofascial force transmission is an important feature for multitendoned muscles.

Repeated Isometric Length-Force Measurements

We found that isometric contractions, particularly at high lengths of EDL III, shifted optimum length of EDL III to higher lengths (Fig. 6B) and, consequently, increased the length range between active slack length and optimum length. There are three possible explanations for such an increase of length range. The first is an increase of the compliance of elastic components in series with the sarcomeres (7, 17, 24, 40). The present finding of decreased passive forces of EDL III (Fig. 6B), subsequent to previous isometric contractions at high lengths, is in agreement with an increase of series elastic compliance for EDL III.

The second is an increase of the distribution of lengths of sarcomeres arranged in series within muscle fibers (4, 14, 35), or third is an increase of the distribution of fiber mean sarcomere length (i.e., higher differences of mean sarcomere length between fibers within a muscle) (3, 38). It has been shown that interfering with the connective tissues surrounding EDL muscle (i.e., blunt dissection of the EDL-TA interface and full lateral fasciotomy of the anterior crural compartment) changes the length-force curves of EDL muscle in a fashion compatible with an increased distribution of fiber mean sarcomere length (11, 13). These results suggest that inter- and extramuscular connective tissues affect the distribution of fiber mean sarcomere length.

It was found that the slope of the EDL III length-TA+EHL force curve decreased after the measurements for the first length-force curve of EDL III (Fig. 6C), indicating a decrease of the degree of intermuscular interaction between EDL III and TA+EHL. This is explained by a decreased stiffness of the connective tissues between these muscle bellies. Such a decreased stiffness may have changed the distribution of fiber mean sarcomere length and, consequently, the length-force characteristics of EDL III.

Conclusions

The present study shows that a substantial amount of force can be transmitted between a single head of a multitendoned muscle and surrounding muscle heads, adjacent synergists, and/or extramuscular structures.
Such myofascial force transmission should be considered as a mechanism that contributes to the inability of humans to move a single finger without movements of adjacent fingers.

The authors acknowledge Dr. Bente R. Jensen for raising questions from the field of occupational health, regarding force transmission from different muscles and muscle heads of multitendoned muscle during movements of fingers relative to each other. This stimulated us to design the protocol of the present study.

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