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Extramuscular myofascial force transmission also occurs between synergistic muscles and antagonistic muscles

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Abstract

The purpose of the present study was to test the hypothesis that myofascial force transmission may not be limited by compartmental boundaries of a muscle group to synergists. Muscles of the anterior tibial compartment in rat hindlimb as well as of the neighbouring peroneal compartment (antagonistic muscles) were excited maximally. Length–force data, based on proximal lengthening, of EDL, as well as distal lengthening of the tibial muscles (TA + EHL) and the peroneal muscle group (PER) were collected independently, while keeping the other two muscle groups at a constant muscle–tendon complex length. Simultaneously measured, distal and proximal EDL active forces were found to differ significantly throughout the experiment. The magnitude of this difference and its sign was affected after proximal lengthening of EDL itself, but also of the tibial muscle complex and of the peroneal muscle complex. Proximal lengthening of EDL predominantly affected its synergistic muscles within the anterior crural compartment (force decrease <4%). Lengthening of either TA or PER caused a decrease in distal EDL isometric force (by 5–6% of initial force). It is concluded also that mechanisms for mechanical intermuscular interaction extend beyond the limits of muscle compartments in the rat hindlimb. Even antagonistic muscles should not be considered fully independent units of muscular function.

Particular, strong mechanical interaction was found between antagonistic tibial anterior muscle and peroneal muscle complexes: Lengthening of the peroneal complex caused tibial complex force to decrease by approximately 25%, whereas for the reverse a 30% force decrease was found.

Keywords: Rat; Anterior tibial compartment; Peroneal compartment; Antagonistic; Muscle force; Myofascial force transmission; Connective tissue; Extracellular matrix; Mechanical interaction; Proximo-distal force difference

1. Introduction

To execute controlled bodily movements, moments and forces need to be exerted at various joints within the musculoskeletal system. In order to exert force onto the skeleton, active or passive force generated within sarcomeres of muscle fibres first has to be transmitted across the sarcolemma. It is generally accepted that the myotendinous junction is a main site for this force transmission (e.g. Tidball, 1991). However, apart from myotendinous force transmission, another pathway for force transmission has been shown to exist: force is transmitted from the muscle fibres onto the intramuscular connective tissue structures. This mechanism has been named (intramuscular) myofascial force transmission (Huijing, 1999a,b; Huijing et al., 1998). Similar mechanisms had previously been shown in: (1) isolated single muscle fibres (Ramsey and Street, 1940), (2) isolated small muscle fascicles (Street, 1983; Street and Ramsey, 1965) and were argued to be necessary for whole muscles containing non-spanning muscle fibres

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(Hijikata et al., 1993; Trotter, 1990; Trotter and Purslow, 1992).

For a number of years now, it has been shown also that myofascial force transmission may play a role in transmission of force from a muscle by paths other than myotendinous one (Huijing, 1999a,b; Huijing and Baan, 2001a,b; Maas et al., 2001, 2004, 2003a,b,c).

So far, predominantly intermuscular mechanical interactions between muscles within one compartment were studied, i.e. for synergistic muscles. The size of any difference of force exerted at proximal and distal tendons of rat EDL muscle is explained in terms of epimuscular myofascial force transmission from muscle i.e. transmission via other paths than the myotendinous ones (without further specification of the nature of the paths involved, but passing the epimysium). Changes of EDL active proximo-distal force differences were accompanied by changes (maximally 9%) in force exerted by synergistic muscle that were kept at constant muscle tendon complex length. The question arose if intermuscular interaction is also possible between muscles located in different compartments (Huijing, 2003). To asses the potential capability for this type of transmission a primary purpose of the present work is to test the following hypotheses: (1) myofascial force transmission is not active between antagonistic muscles. (2) If it would occur so, it would do so at similar magnitudes for EDL and for the tibial muscles of the crural and peroneal compartments.

2. Materials and methods

Surgical and experimental procedures were in 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.

2.1. Surgical procedure and experimental set-up

Six male Wistar rats (body mass 304.2 ± 7.0 g, mean $\pm$ SD) were anaesthetised with an intraperitoneal injection of diluted urethane (1.2 ml 12.5% urethane solution/100 g body mass). Supplementary injections of urethane (0.5 ml 12.5% urethane solution) were administered (maximally three times) to maintain deep anaesthesia. The animals were placed on a heated water pad (37 °C) during surgery and experimentation.

Surgical preparations involved removing the skin and the muscle belly of biceps femoris muscle from the left hindlimb. Local innervation and blood supply of the target muscles were kept intact.

The following tendons were dissected free from their surrounding tissues: (1) four distal tendons of extensor digitorum longus muscle (EDL), (2) the distal tendon of the tibialis anterior muscle and (3) the extensor hallucis longus muscle, and (4) the four distal tendons of the peroneal muscles (i.e. mm peroneus longus, brevis, quarti and quinti). This dissection left the compartmental borders at, and connective tissues around, the muscle bellies intact.

A reference position for each distal tendon was established with the knee and ankle joints at approximately 90°. This was done by marking each tendon at 1 mm distally from a fixed point on the distal edge of the crural fascia. To prevent tendons from sliding relative to each other when cut loose, the four distal EDL tendons (1) were tied together before tenotomy. This was also done for the four distal tendons of the peroneal muscles (2) and the distal tendons of TA and EHL (3). The tendons were tied together for practical reasons. The tendons were in such close proximity that independent measurement of force exerted at each tendon individually was not feasible. The complex of TA and EHL will further be referred to as the tibial muscle complex, as both muscles have origins on or very close to the tibia. The peroneal muscles together will be referred to as the peroneal muscle complex.

The retinaculae at the ankle (i.e. transverse crural ligament and the cruciate ligament) were removed while being observed using an operation microscope (Carl Zeiss, magnification 6–40×). Subsequently, the distal tendons of EDL, tibial and peroneal complexes were cut as distally as possible and tied to three kevlar threads (4% elongation at a break load of 800 N). Also, the proximal tendon of EDL was tied to a kevlar thread after cutting the tendon loose from the femur, with a piece of the lateral femur condyle still attached. The reference position of the proximal EDL tendon was defined as the position at which the piece of femur condyle was exactly over the point it originated from, with the knee at 90°. Applying silicone grease prevented dehydration of the exposed tendons.

Within the femoral compartment, the sciatic nerve was cut as proximally as possible and the sural, tibial, and articular branches were severed leaving only the common peroneal nerve intact.

The left foot was firmly attached to a plastic plate, using a kevlar thread. After positioning the rat in the experimental apparatus (Fig. 1), the femur was secured by means of a metal clamp. The plate to which the foot was attached was manipulated such that the ankle was in extreme plantar flexion (≈180°) and some supination (≈5°) to allow for the free passage of the kevlar threads, attached to the distal tendons. Each kevlar thread was connected to a force transducer (Hottinger Baldwin, maximal output error <0.1%, compliance 0.0048 mm N^{-1}) and the muscle tendon complexes were set at their reference positions. For practical reasons, the kevlar threads connected to the peroneal and tibial complexes had to be led over a low friction pulley to attain a 90° angle. The 3D co-ordinates of all force transducers were manipulated for alignment with the muscle lines of pull.

The distal end of the sciatic nerve, of which the tibial and articular branches were cut, was placed on a bipolar cuff electrode.

During the experiment, ambient room temperature was kept at 22 ± 0.5 °C and air humidity was kept at $80 \pm 2\%$

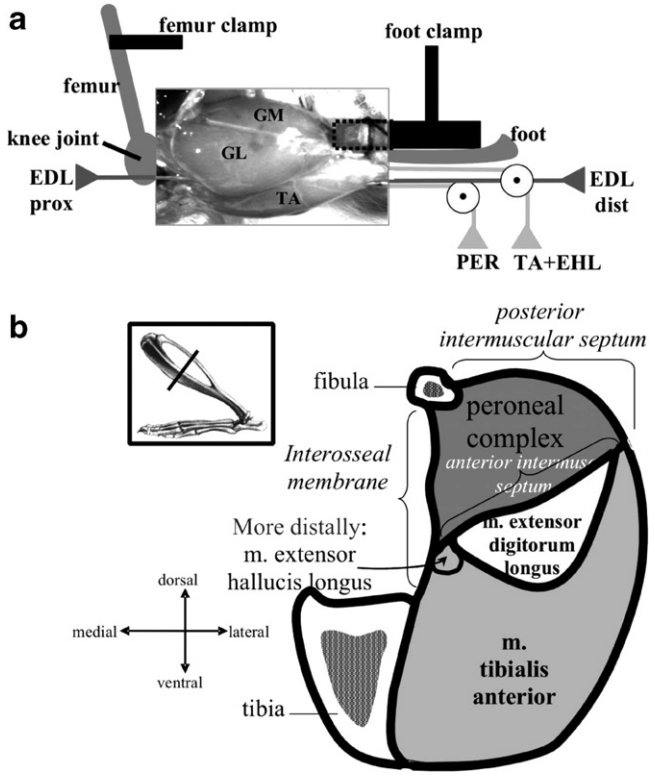

Fig. 1. Schematic representation of the morphology of the anterior crural and peroneal compartments and of the experimental configuration. (a) Deep flexors, m. triceps surae and m. biceps femoris, as well as m. plantaris are not depicted. The anterior tibial compartment, containing TA, EHL and EDL, is delimited by the anterior intermuscular septum (SIA), the crural fascia (covering the surface of TA), the interosseal membrane (MI, between tibia and fibula) and tibia. EHL is located near the intercept of SIA and MI. EDL was found to have no muscle fibre origin on its surrounding structures (all fibres originate from the proximal aponeurosis). The peroneal compartment contains the four peroneal muscles and is delimited by SIA, the intermuscular posterior septum (SIP), fibula, MI and tibia. PER originates from SIP, SIA and the fibula. However, despite close proximity, no muscle fibre of the PER muscle group was found to have their origin on MI. On the other hand, indirect connections between PER and MI by means of connective tissue sheets were present. (b) The foot was fixed to a plastic footplate with the ankle in extreme plantar flexion (180°) and approximately 5° supination. The femur was fixed by means of a metal clamp with the knee at a 90° angle. The tendons of EDL (proximal and distal), PER and TA + EHL were attached to four force transducers (indicated by triangles). For practical reasons, the kevlar threads connected to PER and TA + EHL had to be led over a pulley at a 90° angle. These pulleys were measured to have negligible resistance. The image, showing the muscles of the lower hindlimb, was obtained during one of the experiments. EDL and EHL are covered by the visible TA, whereas PER is covered by the denervated m. triceps surae (the lateral and medial gastrocnemius are visible, i.e. GM and GL, respectively) and m. plantaris.

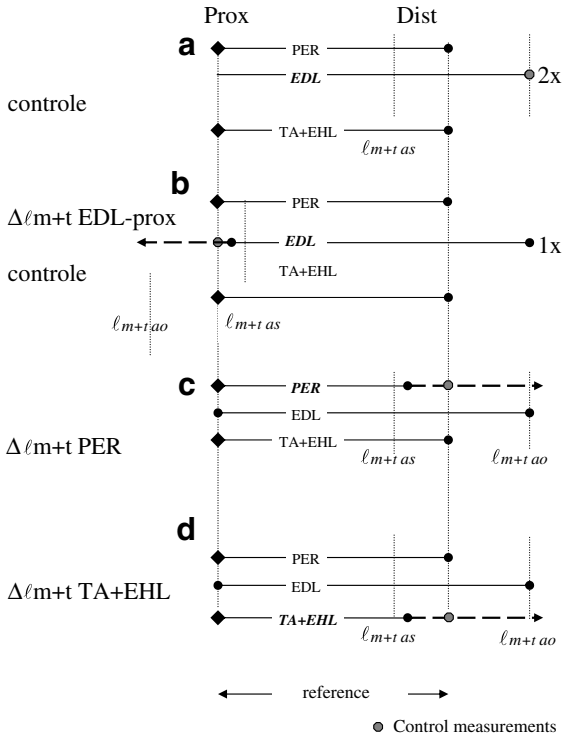

Fig. 2. Schematic representation of the muscle tendon complex lengths imposed during the experimental protocol. (a) Transducers of TA + EHL, as well as distal EDL and PER, were set at their reference positions and lengthening of EDL was imposed by moving its force transducer in proximal direction. (b) Transducers of TA + EHL, as well as distal and proximal EDL, were set at their reference positions and lengthening of PER was imposed by moving its force transducer in distal direction. (c) Transducers of PER, as well as distal and proximal EDL, were set at their reference positions and lengthening of TA + EHL was imposed by moving its force transducer in distal direction.

by a computer-controlled air conditioning system (Holland Heating). The surface area of the lower hindlimb was covered with a layer of paraffin oil to further prevent fluid loss.

2.2. Experimental procedure and data collection

All muscles within the peroneal and anterior crural compartment were excited by stimulating the distal end of the severed sciatic nerve supramaximally, using a pair of silver electrodes connected to a constant current source (3 mA, square pulse width 100 μs, pulse train 600 ms, 100 Hz). Preceding each tetanic contraction, a twitch was evoked. Some time (i.e. 400 ms) after this twitch, passive force of all muscle groups was measured. The tetanic contraction (duration 600 ms) followed 500 ms after the preceding twitch. During the tetanic plateau (i.e. 450 ms after starting the pulse train), isometric force was measured. Digital images showing the peroneal and anterior tibial compartment were acquired during the passive and active state using a VGA progressive Scan CCD camera with 16 mm lens and stored using an image handling system (version 6.0, Optimas Corp., Bothell, Washington, USA). Four hundred milliseconds after each contraction, another twitch was evoked. The interval between two subsequent tetanic contractions was 2 min, during which the muscle groups were allowed to recover at low length.

Force signals were acquired using an A/D converter (sampling frequency 1000 Hz, resolution of force 0.01 N) and recorded on a personal computer. The timing of stimulation, photography and the sampling of force signals was controlled by a special purpose microcomputer.

2.3. Experimental protocol

Preceding the experiment, the four force transducers with muscle groups in the peroneal and anterior crural compartment connected, were set at their standard experimental positions (i.e. the positions at which the transducers were set when kept at a constant position). In the initial conditions, these standard positions corresponded to: (a) peroneal muscle complex distal active force of approximately 5 N, (b) tibial muscle complex distal active force of approximately 3 N, (c-1) reference position of the proximal tendon of EDL (see above) and (c-2) optimal active EDL force exerted distally.

In addition to a set of control contractions at the standard positions to monitor the condition of the muscles during the course each experiment, three sets of length–force data were obtained (for a schematic of details of the protocol see Fig. 1). Each of three sets was obtained by distally increasing the length of a specific (passive) target muscle complex, by moving its distal force transducer, or in the case of EDL proximal force transducer, in steps of 1 mm, while the other force transducers were kept at their standard positions, subsequently all muscles were excited. This was done first for the EDL muscle, and peroneal muscle group (PER) and subsequently for the TA + EHL complex. Peroneal and tibial muscle complexes were lengthened starting near active slack length to approximately 2 mm over optimum length.

In one experiment, the order in which the length–force data were obtained was altered. Length–force data for TA + EHL were obtained prior to those for PER. This was done to observe whether changing the order of the obtained length–force curves would affect the principle of any mechanical interaction between the three muscle groups. This was found not to be the case.

2.4. Treatment of data

Data of passive muscle force as a function of muscle tendon complex length were least squares fitted using an exponential function:

$$y = e^{a_0 + a_1 x}, \quad (1)$$

where y represents passive muscle force, x represents muscle tendon complex length and a_0 and a_1 are coefficients determined in the fitting process. Active muscle force was calculated by subtracting passive force (Eq. 1) from total muscle force for the appropriate muscle lengths. The active forces as a function of muscle tendon complex length were fitted using a polynomial:

$$y = a_0 + a_1 x + a_2 x^2 + \cdots + a_n x^n, \quad (2)$$

where y represents active muscle force, x represents muscle tendon complex length and a_0 through a_n are coefficients determined in the fitting process. The functions obtained were used to average the data of the six experiments and calculate standard deviations. Optimum muscle tendon complex length was defined as the length at which the polynomial for active muscle force reached a maximum. All muscle lengths were expressed as deviations from the individual optimum muscle tendon complex length.

2.5. Morphological observations

Morphological observations of the anterior and peroneal compartments were made in two additional animals. As such description is not readily available in the literature a detailed description of some relevant aspects of the rat anatomy is provided below. The dissection procedure involved removing the skin, the biceps femoris muscle, the triceps surae muscle and the plantaris muscle from the left hind limbs. The blood supply to the peroneal and anterior tibial compartments was kept intact.

The anterior tibial compartment is delimited by the anterior intermuscular septum, the crural fascia (covering the surface of tibialis anterior muscle), the interosseal membrane (between tibia and fibula) and tibia itself.

The anterior intermuscular septum, the posterior intermuscular septum, fibula, the interosseal membrane and the tibia (Fig. 3) delimit the peroneal compartment.

So, the two compartments do share the anterior intermuscular septum as a boundary. In fact, several muscles within these compartments share this structure also as location of muscle fibre origins: (1) Extensor hallucis longus muscle originates from the most medial part of anterior face of the anterior septum, near the interosseal membrane (Fig. 4b). (2) Parts of the posterior face of the anterior intermuscular septum serve as a proximal aponeurosis for peroneus longus and brevis muscles. (3) A small part of TA (approximately 5% of TA cross-sectional area) directly originates from the proximal, superficial (i.e. most lateral) part of the anterior muscular septum (Fig. 4a).

In addition, muscle fibres from the peroneal muscle complex (i.e. for peroneus longus, quarti and quinti muscles) originate also from the posterior septum as well as from the fibula. Muscle fibres of EDL only originate from the EDL proximal aponeurosis (i.e. they have no origin on any septum). The proximal aponeurosis common to all four EDL heads, proximally forms the proximal tendon with an origin at the lateral femur condyle.

It should be noted that important differences exist between an aponeurosis of a muscle and intermuscular septum. The latter does not transform into a tendon with a limited and well-defined insertion on bone, but continues as sheet shaped elements of the compartments. Because of the structural continuity of anterior and posterior septa and the general fascia, they are linked mechanically. In addition, the muscles within the compartments are intimately connected to each other through intermuscular connective tissue structures. Extramuscular connective tissues (such as the collagen reinforced neurovascular tracts containing the superficial and deep peroneal nerves and blood vessels, as well as more distal extensions of this tract), connect the intramuscular connective tissue stroma to the compartment boundaries. Little is known about the mechanical properties

of these different types of connections, but it is not uncommon for them to be classified as 'loose connective tissue'.

At the ankle, the four distal tendons of the peroneal muscle complex pass at the dorsal side of the lateral (i.e. fibular) malleolus and continue distally to insert at different locations within the foot. Both the distal tendon of tibialis anterior muscle and the distal extensor hallucis longus tendon ventrally pass the medial (i.e. tibial) malleolus, to continue to their insertions within the foot.

EDL muscle fibres insert onto four distal aponeuroses forming four distal tendons ventrally pass the medial (i.e. tibial) malleolus, to continue to their insertions on the most distal digits.

Note that rat, in contrast to humans; EDL crosses the knee in addition to the ankle joint, as well as the more distal joints within the foot. However, its moment arm at the knee joint is rather small relative to the moment arm at the ankle joint.

2.6. Statistics

The fitting procedure for the length–force data started with a first order polynomial, and the order was increased to a maximum value of six. One-way ANOVA was used to select the highest order polynomial that still added a significant improvement to the description of muscle length–force characteristics.

To test for the effects of lengthening a muscle group on the force of muscle groups that were kept at a constant length, one-way ANOVA for repeated measures was performed (factor: length of muscle–tendon complex).

If significant main effects or interaction effects were found, posthoc tests were performed using the Bonferroni procedure to locate the significant differences. Differences were considered significant at $p < 0.05$.

3. Results

3.1. Test contractions

At identical reference lengths and positions shows that active force exerted by tibial muscles and by peroneal muscles (Fig. 1) shows only minor variation during the full course of the experiment. Therefore, any major changes of force encountered during experimental manipulation of lengths of muscles or muscle groups cannot be ascribed to history effects related to the sequence of the experiment.

3.2. Effects of length of different muscles on synergistic and antagonistic muscle force

Absolute values of initial isometric active forces exerted by these three muscle groups are shown in Table 1.

3.2.1. Distal lengthening of the peroneal muscle group

Fig. 2a shows isometric length-distal force characteristics of the peroneal muscle complex obtained after distal lengthening. Note the relatively low lengths at which substantial passive force is still exerted ($\Delta\ell m + t > -2$ mm).

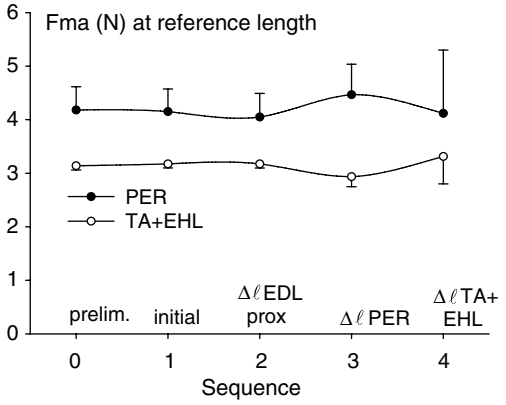

Fig. 3. The approximate constancy of force exerted by PER and TA + EHL during the course of the experiment. Control contractions under standard conditions of lengths and relative positions (see Fig. 2) were performed regularly throughout the experiment. The sequence of measurements are numbered on the *x*-axis. The labels over the sequence number indicate the experimental phase during which the measurements were made. The last three measurements (i.e. sequence # 2–4) were made during collection of length force data for which the lengthened muscle ($\Delta\ell n$) is indicated.

3.2.1.1. Effects on antagonistic EDL. Despite a slightly curved feature of the proximal active EDL force curve (Fig. 2a), no significant effect of length of the peroneal group on proximal active EDL force could be shown (ANOVA). In contrast, distal EDL active force decreased significantly (Fig. 2c; $0 < \Delta F_{ma} < -6\%$ of initial force). Therefore, distal lengthening of the peroneal group significantly affected the EDL proximo-distal active force difference: negative values of this difference (i.e. $F_{ma\text{-}dist} > F_{ma\text{-}prox}$) were almost tripled at high peroneal lengths (Fig. 2b). This is indicative of a progressively increasing distally oriented myofascial load on EDL as peroneal muscle group is lengthened. This net distal myofascial load causes force exerted more proximally within EDL muscle fibres to partially be transmitted sideways to neighbouring structures within the compartment. This part of the EDL force is thus no longer exerted at the EDL distal tendon.

It is concluded that epimuscular myofascial transmission loading of EDL, kept at constant length, is much increased by lengthening of the antagonistic peroneal group within the adjacent compartment. The rate of increase of this distal loading with peroneal lengthening decreases with increasing length until no further increases are seen (at $\Delta\ell m + t > 0.5$ mm).

3.2.1.2. Effects on antagonistic tibial muscle group. High and significant decreases in active force ($0 < \Delta F < -25\%$) were found for the tibial muscle complex on progressive lengthening of the peroneal complex (Fig. 4c).

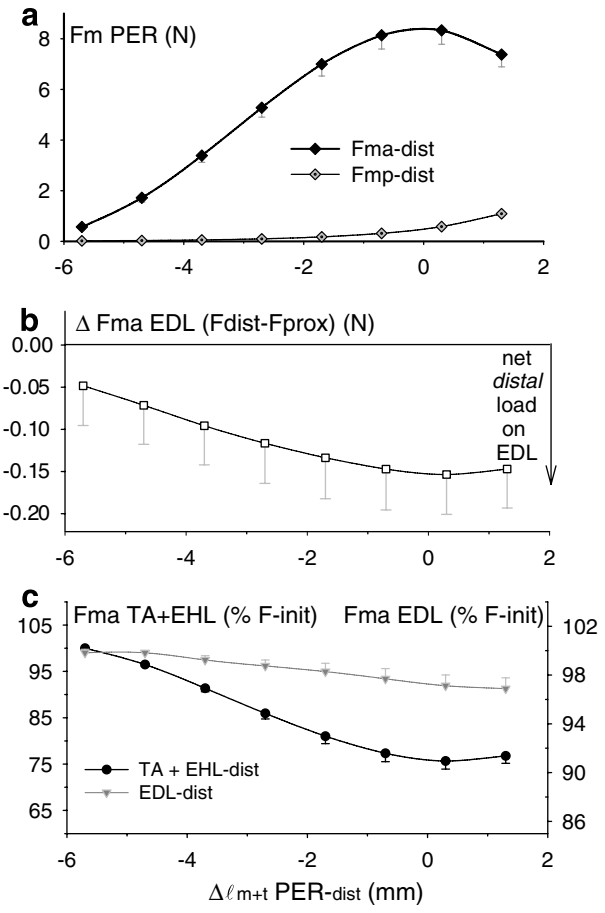

Fig. 4. Effects of distal lengthening of the peroneus muscle group on force exerted by other muscles studied. (a) Length-distal force characteristics of the peroneus muscle group (PER) active (F_{ma}) and passive (F_{mp}) force are shown. (b) The proximo-distal difference in EDL active force (ΔF_{ma}) as a function of increasing PER length. Note that EDL muscle–tendon complex length was kept unchanged. A negative proximo-distal force difference (calculated as F_{dist}–F_{prox}) is indicative for a net distal myofascial load on EDL (arrow). This load is integrated in EDL force until transmitted from the muscle by additional myofascial paths or the myotendinous path. (c) Effects of PER length on normalized distal active force (F_{ma}) exerted by EDL (EDL dist, use right y-axis) and by TA + EHL (use left y-axis). Note that EDL and TA + EHL were kept at constant muscle–tendon complex length during this part of the experiment. EDL and TA + EHL forces were normalized for their initial values, i.e. at low PER length (see Table 1). Length changes of PER were imposed at its distal tendons and are expressed as deviation from PER-dist optimum length ($\Delta\ell m + t$).

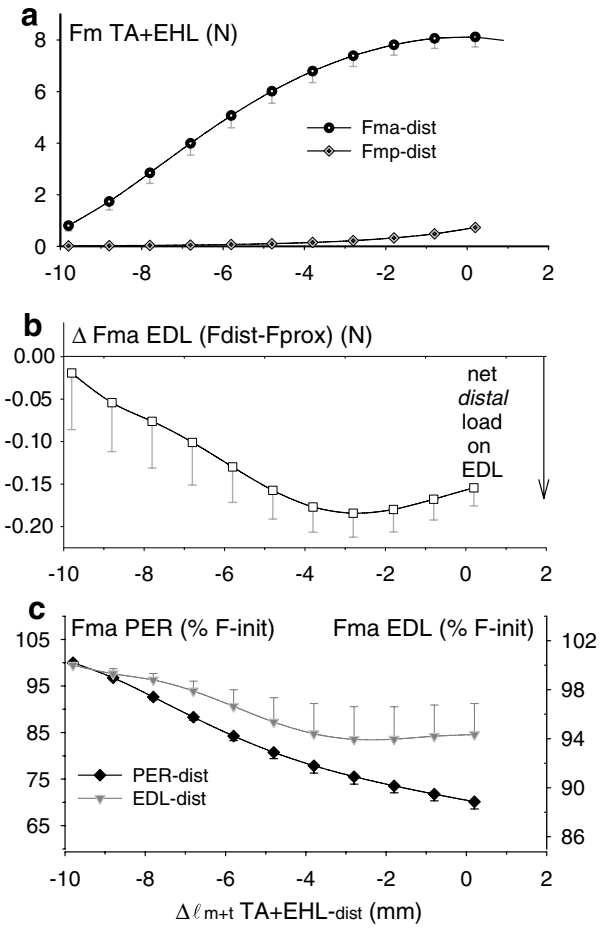

Fig. 5. Effects of distal lengthening of the TA + EHL muscle complex on force exerted by other muscles studied. (a) Length-distal force characteristics of the tibial muscle complex (TA + EHL). Distal active ($F_{ma\text{-}dist}$) and passive ($F_{mp\text{-}dist}$) forces are shown. (b) The proximo-distal difference in EDL active force (ΔF_{ma}) as a function of increasing TA + EHL length. Note that EDL muscle–tendon complex length was kept unchanged. A negative proximo-distal force difference (calculated as F_{dist}–F_{prox}) is indicative for a net distal myofascial load on EDL (arrow). This load is integrated in EDL force until transmitted from the muscle by additional myofascial paths or the myotendinous path. (c) Effects of TA + EHL length on normalized distal active force exerted by EDL (EDL –dist, use right y-axis) and by PER (PER-dist, use left y-axis). Note that EDL and PER were kept at constant muscle–tendon complex length during this part of the experiment. EDL and distal forces and PER forces were normalized for their initial values, i.e. at low TA + EHL length (see Table 1). Length changes of TA + EHL were imposed at the distal tendons of the complex and are expressed as deviation from TA + EHL-dist optimum length ($\Delta\ell m + t$).

3.2.2. Distal lengthening of tibial muscles

Fig. 4a shows isometric length–force characteristics obtained after distal lengthening of the tibial muscle complex (TA + EHL). Note that the length range of active force generation for this muscle group is bigger than for PER (≈10 mm vs. 6 mm). This may be related to the smaller moment arm of TA + EHL. Also note the very low

Table 1
Mean initial active forces of EDL, PER and TA + EHL in the two experimental conditions

Muscle to be lengthened	Mean ± SD initial active force (N)			
	EDLdist	EDLprox	PER-dist	TA + EHL-dist
EDL-prox	1.92 ± 0.24	1.04 ± 0.24	4.45 ± 0.45	3.01 ± 0.20
PER-dist	2.67 ± 0.22	2.71 ± 0.27	0.07 ± 0.14	3.24 ± 0.42
TA + EHL-dist	2.68 ± 0.23	2.65 ± 0.30	4.12 ± 0.77	0.15 ± 0.17

lengths at which substantial passive force is still exerted ($\Delta\ell m + t > -6$ mm).

3.2.2.1. Effects on synergistic EDL. No significant effect of distal lengthening of this group on proximal active EDL force (Fig. 2b) could be found (ANOVA). In contrast, distal EDL active force (Fig. 4c) decreased significantly ($\Delta F < -5\%$ of maximal force).

At very low TA + EHL lengths (Fig. 4b), the difference between distally and proximally exerted EDL active forces approximates zero, a condition indicative for very low net myofascial force transmission to or from EDL. Distal lengthening of TA + EHL significantly affected the EDL proximo-distal active force difference: increasing negative values of this difference (i.e. $F_{\text{ma-dist}} < F_{\text{ma-prox}}$) reaching a maximal difference of approximately −0.17 N (Fig. 2b). This is indicative of an increasing distally oriented myofascial load on EDL as the tibial muscle complex is lengthened. After its maximum value is attained (at $\Delta lm + t \approx -3$ mm), the difference does not increase further (Fig. 4b).

It is concluded that epimuscular myofascial transmission of force from EDL, kept at constant muscle tendon complex length, in distal direction is much increased by progressively lengthening of its synergistic muscles. Also in this condition, progressively increasing fractions of EDL force is transmitted sideways onto neighbouring structures and no longer exerted at the EDL distal tendon.

3.2.2.2. Effects on antagonistic peroneal muscle group. Significant effects of considerable size (e.g. maximal $\Delta F \approx -30\%$ of initial force) were found on the antagonistic peroneal muscle group within the adjacent compartment (Fig. 4c), even though that muscle group was kept at constant muscle–tendon complex length. Note that the effect on these antagonistic muscles is much bigger than the effect on neighbouring synergistic EDL.

3.2.3. Proximal lengthening of EDL

Fig. 5 shows EDL active length force characteristics. EDL was not lengthened proximally much, because the distal position of EDL already corresponded to high EDL length. This is also apparent high passive forces.

3.2.3.1. Effects on EDL proximo-distal force difference. At low EDL lengths, the EDL proximo-distal force difference is positive indicating a net proximally directed myofascial load on EDL. At higher EDL length after declining the sign of this difference (and thus the direction of the net load on EDL) reverses(i.e. $\Delta\ell m + t$EDL-prox $= -1.5$ mm), so that at higher lengths the net myofascial load on EDL is applied in distal direction (Figs. 6 and 7).

3.2.3.2. Effects on forces exerted by antagonistic and synergistic muscles. Lengthening of EDL has no appreciable or significant effect on peroneal force (Fig. 6c). In contrast (Fig. 6c), initially proximally lengthening of EDL increases significantly TA + EHL force (by ≈6%), but at higher lengths it decreases it again (by ≈2%), the maximum of TA + EHL force occurring at $\Delta\ell m + t$EDL-prox $= -0.5$ mm. Also this result indicates a change in direction of myofascial events.

For the experimental conditions imposed, an overall conclusion is drawn that distal lengthening of a muscle

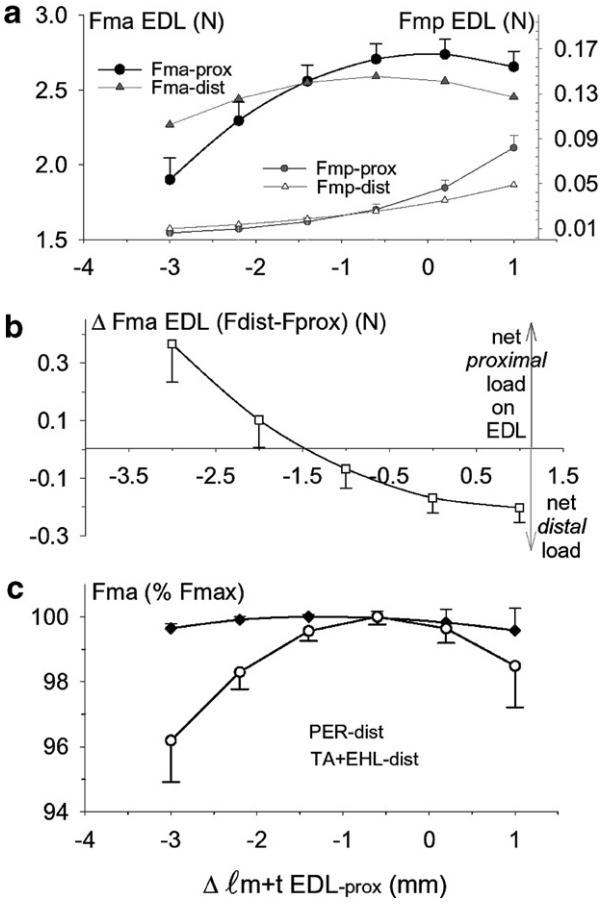

Fig. 6. Effects of proximal lengthening of EDL muscle on force exerted by other muscles studied. (a) Length-distal force characteristics of EDL distal active force ($F_{\text{ma-dist}}$, use left y-axis) as well as proximal active ($F_{\text{ma-prox}}$, also use left y-axis) and passive forces ($F_{\text{mp-dist}}$ and $F_{\text{mp-prox}}$, use right y-axis) are shown. (b) The proximo-distal difference in EDL active force (ΔF_{ma}) as a function of increasing EDL length. Note that in this case EDL muscle–tendon complex length was changed. A negative proximo-distal force difference (calculated as F_{dist}–F_{prox}) is indicative for a net distal myofascial load on EDL (grey arrow), inversely a positive difference is indicative of a net proximally directed myofascial load on EDL. These loads re integrated in EDL force until transmitted from the muscle by additional myofascial paths or the myotendinous path. Note that the direction of the net myofascial load changes approximately half way the imposed EDL length range. (c) Effects of EDL length on normalized distal active force (F_{ma}) exerted by the peroneal muscle group (PER-dist) and by the tibial muscle complex (TA + EHL). Note that PER and TA + EHL were kept at constant muscle–tendon complex length during this part of the experiment. PER and TA + EHL forces were normalized for their initial values, i.e. at low EDL length (see Table 1). Length changes of EDL were imposed at the proximal tendon of the complex and are expressed as deviation from EDL-prox optimum length ($\Delta\ell m + t$).

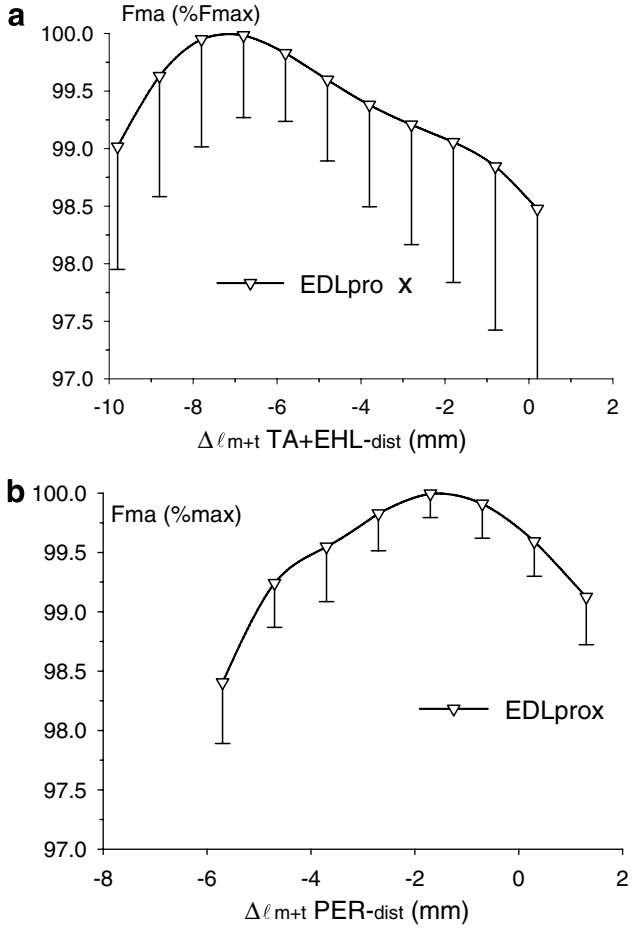

Fig. 7. Effects of length of the peroneal muscle group and the tibial muscle complex on active force exerted at the proximal EDL tendon. (a) Effects of increasing PER length on normalized proximal active force (F_{ma}) exerted by EDL muscle group (EDL-prox). (b) Effects of increasing TA + EHL length on normalized proximal active force (F_{ma}) exerted by EDL muscle (EDL-prox). Note that EDL was kept at constant muscle–tendon complex length during both parts of the experiment. EDL forces were normalized for their maximal values attained within the PER and TA + EHL length range (see Table 1). Length changes of PER and of TA + EHL were imposed at the distal tendons of the complex and are expressed as deviation from their respective optimum length ($\Delta\ell m + t$).

group, and the accompanying increases in active force causes nearby muscles or muscle groups to decrease active force exerted at their distal tendons, even if these groups are antagonist muscles.

It is concluded even antagonistic muscles if working within their natural connective tissue context should not be viewed as being fully independent in their action.

4. Discussion

Our present results on myofascial interaction between adjacent synergistic muscle and the occurrence of EDL proximo-distal force differences is in accordance with previous work from our group.

A major new result of this study is the substantial mechanical interaction also between neighbouring antagonistic muscle groups. Most of this interaction is ascribed to extramuscular myofascial force transmission between neighbouring antagonistic muscles. This has very important functional implications, as even antagonistic muscles cannot be viewed any longer as fully independent force generators.

It also means that forces generated within sarcomeres of antagonistic muscles within a neighbouring compartment may be partially exerted at tendons of an agonist muscle.

For a more extended discussion of this conclusion see also elsewhere in this journal issue (Huijing, 2007; Meijer et al., 2007; Rijkelijkhuizen et al., 2007; Yucesoy and Huijing, 2007).

4.1. Proximo-distal force differences and the direction of the net myofascial load

As the EDL proximo-distal force difference is calculated as F_{dist}–F_{prox}, a positive result indicates that $F_{prox} < F_{dist}$. Since the sum of proximally and distally directed forces should equal to zero, this can occur exclusively if an additional distal load is borne by the muscle in addition to the one measured by the proximal force transducer. Inversely, a negative proximo-distal force difference indicates a distally directed myofascial load.

The characteristics of the curves describing the EDL proximo-distal active force differences indicate that, depending on length and relative positions, net proximally directed, as well as net distally directed myofascial loads are applied on EDL during the present experiment. However, net distally directed loads occurred more frequently for the experimental conditions imposed. Only during manipulation of EDL length proximally, at low lengths net proximally directed loads were encountered which decreased as EDL was lengthened proximally.

From our present results it is clear that lengthening of a muscle or a muscle group at its distal tendon, even an antagonistic one, will place a distally directed myofascial load on other muscles in the region (neighbouring antagonists as well as synergists). Therefore, a fraction of the muscle force is not exerted at the distal tendons of those muscles, but at the distal tendon of the lengthened muscle and possibly at distal non-muscular targets.

The only candidate pathways for such myofascial force transmission between neighbouring antagonistic muscles are the connective tissues that form connections between the two compartments, i.e. the anterior and posterior intermuscular septum being continuous via the general fascia, the interosseal membrane and as well as the so-called neurovascular tract (reinforcing the bundles of nerves and blood vessels passing between the compartments through the fenestrated septum) and the general fascia itself. Our present results do not provide unequivocal indications of the exact substrates and targets of these pathways. However, for further discussion of this topic see also Meyer et al. (2007), Huijing (2007), Yucesoy and Huijing (2007).

In the present work, the occurrence of proximo-distal force differences can only be proved work for EDL sine only for that muscle we are able to measure both proximal and distal forces independently from those of other muscles. However, one should realize that such force differences will also occur in the other muscles studied. Finite element modeling supports such concepts (Yucesoy et al., 2005; Yucesoy et al., in press, 2006; Yucesoy and Huijing, 2007), but also the changing distal forces in muscles of which the lengths are not manipulated are indications for myofascial loads causing such features.

4.2. Proximal EDL force and indications for myofascial pathways

The fact that lengthening of TA + EHL or PER hardly affected at all the force exerted at the proximal tendon of EDL (Fig. 3: $+1.0\% > \Delta F_{max} < -1.2\%$, and $+1.5\% > \Delta F_{max} < -1.0\%$, respectively, both no significant changes) may be quite relevant for a discussion on myofascial pathways. If exclusively a distal myofascial load would be exerted onto the muscle fibres of EDL, the load would be borne by the combination of all sarcomeres and the associated collagen reinforced extracellular matrix located proximal to the point of application on each muscle fibre. In such exclusive conditions this load would be integrated into the force exerted at the proximal tendon. Therefore, if such conditions were to be present, lengthening of the synergistic or antagonistic muscle would lead to strongly enhanced proximal EDL forces. In our present experimental results (Fig. 3), this is obviously not the case. Therefore, we conclude that the additional load on EDL caused by TA + EHL or PER lengthening is not fully integrated in the force exerted at the proximal EDL tendon, but that most of that force is transmitted again from EDL via proximally located myofascial connections to other muscular and/or non-muscular structures. The net proximally directed myofascial load seen for these conditions (see Figs. 1b and 2b) are compatible with this interpretation. For further discussion of this topic see also Huijing et al. (2007) and Meijer et al. (2007).

In sum, it is concluded that neither synergistic muscles within a muscle compartment nor neighbouring muscle groups cannot be seen as independent force generators.

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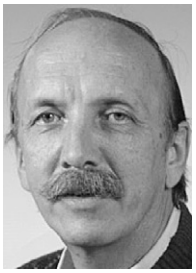

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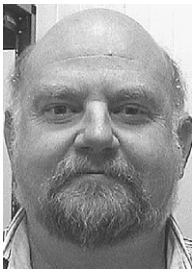

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