Muscle force is determined also by muscle relative position: isolated effects

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Abstract

Effects on force of changes of the position of extensor digitorum longus muscle (EDL) relative to surrounding tissues were investigated in rat. Connective tissue at the muscle bellies of tibialis anterior (TA), extensor hallucis longus (EHL) and EDL was left intact, to allow myofascial force transmission. The position of EDL muscle was altered, without changing EDL muscle–tendon complex length, and force exerted at proximal and distal tendons of EDL as well as summed force exerted at the distal tendons of TA and EHL muscles (TA + EHL) were measured. Proximal and distal EDL forces as well as distal TA + EHL force changed significantly on repositioning EDL muscle.

These muscle position–force characteristics were assessed at two EDL lengths and two TA + EHL lengths. It was shown that changes of muscle force with length changes of a muscle is the result of the length changes per se, as well as of changes of relative position of parts of the muscle. It is concluded that in addition to length, muscle position relative to its surroundings co-determines isometric muscle force.

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1. Introduction

It is commonly known that skeletal muscle force is dependent on the degree of activation, muscle–tendon complex length, shortening velocity, fatigue, and contraction history. However, these muscle properties have been assessed predominantly using dissected muscles (e.g. Burke et al., 1976; Close, 1964; De Haan et al., 1989; Ettema et al., 1990; Meijer et al., 1998; Rack and Westbury, 1969), assuming implicitly that all muscle force is transmitted via its tendons to bone. In such a case, force at the proximal tendon should be equal to force at the distal tendon of that muscle. Therefore, in such experiments muscle force is measured exclusively at one tendon. Recent experiments simultaneously measur-

ing isometric force exerted at both proximal and distal tendons of extensor digitorum longus muscle (EDL), that was not dissected free from its surrounding tissues, proved that force is transmitted also out of muscle via other pathways than its tendons (Huijing and Baan, 2001a; Maas et al., 2001). Force may be transmitted via intermuscular connective tissue to adjacent muscles (intermuscular myofascial force transmission). Force may be transmitted also via extramuscular connective tissue to bone (extramuscular myofascial force transmission). Therefore, connective tissues embedding muscles play an important role for force transmission from muscle fibers. Severing this connective tissue network caused major changes in length–force characteristics of EDL muscle as well as in inter- and extramuscular myofascial force transmission (Huijing and Baan, 2001a; Huijing and Baan, 2001b). Furthermore, dissection of rat flexor carpi ulnaris muscle to simulate surgical procedures for tendon transpositions in human, caused substantial changes of its length–force characteristics (Smeulders et al., 2002).

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In vivo, joint movements involve simultaneous but opposite length changes of synergistic and antagonistic muscles. The magnitude of length changes as a function of joint angle depends on its moment arm, defined as the shortest distance between the line of action and the joint axes of rotation. Due to the fact that differences in moment arm between synergists exist, joint movements will also cause changes in relative position of different adjacent muscle bellies. Another major cause for such a change of muscle relative position is the fact that some muscles span only one joint (mono-articular muscles) and other muscles span more than one joint (bi or poly-articular muscles). Based on previous results regarding inter- and extramuscular myofascial force transmission, it seems likely that these relative motions of different muscle bellies will affect force transmission of the different muscles involved. However, in those studies effects of changing length were always combined with effects of changing relative position, but were ascribed in terms of effects of length.

The aim of the present study was to investigate effects of changes of relative position of muscle within the anterior crural compartment. This compartment envelops the poly-articular EDL, tibialis anterior (TA) and extensor hallucis longus (EHL) muscles. The position of EDL muscle relative to surrounding muscles and other connective tissues was altered without changing its muscle–tendon complex length, and isometric forces exerted at proximal and distal tendons of EDL muscle as well as at distal tendons of TA and EHL muscles were measured. EDL muscle position–force characteristics were assessed at several constant lengths of EDL muscle and the TA+EHL complex. We tested the null hypothesis that proximally and distally measured EDL forces are affected solely by length changes and not by changes of the position of EDL muscle.

2. Materials and 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.

2.1. Surgical procedures

Male Wistar rats ($n = 7$, body mass = 303.9 ± 24.7 g) were anaesthetized using intraperitoneally injected urethane (1.2 ml/100 g body mass 12.5% urethane solution, extra doses were given if necessary: maximally 1.5 ml). During surgery and data collection, the animals were placed on a heated water pad of approximately

37°C, to prevent hypothermia. Ambient temperature ($22 \pm 0.5^\circ\text{C}$) and air humidity ($80 \pm 2\%$) were kept constant by a computer controlled air-conditioning system (Holland Heating). Muscle and tendon tissue was further prevented from dehydration by regularly irrigating the tissue with isotonic saline.

The anterior crural compartment, which envelops TA, EDL and EHL muscles, was exposed by removing the skin and most of the biceps femoris muscle from the left hind limb. Connective tissue at the muscle bellies of TA, EHL and EDL was left intact. However, the transverse crural ligament and the crural cruciate ligament (retinaculæ near the ankle joint) were severed and a limited distal fasciotomy was performed to reach the distal tendons of EDL, TA and EHL. With knee and ankle joint at 90° (referred to as reference position) the four distal EDL tendons as well as the distal tendons of TA and EHL muscles were tied together, respectively. The latter complex will be referred to as the TA+EHL complex. Proximally, the femoral compartment had to be opened: (1) to detach the proximal tendon of EDL from the femur, and (2) to secure the femur (at a knee angle of 90°) with a metal clamp when the rat was in the experimental apparatus. The tendons of EDL muscle and the TA+EHL complex were cut and connected to force transducers (Hottinger Baldwin, maximal output error $< 0.1\%$, compliance of 0.0048 mm/N) with Kevlar thread (diameter 0.5 mm, 4% elongation at a break load of 800 N). The foot was attached to a plastic plate with tie wraps. To create a resistance free passage for this thread between tendon and force transducer, this plate was positioned in maximal plantar flexion of the ankle and approximately 40° pronation of the foot. For TA+EHL force measurements, the Kevlar thread was connected to the force transducer via a pulley. Both EDL ends were connected directly to the force transducers, which were positioned in the line of pull (Fig. 1). Experimental data indicating that differences in force between the two force transducers greater than 0.7% cannot be ascribed to this measurement system have been reported previously (Huijing and Baan, 2001a; Maas et al., 2001).

Within the femoral compartment, the sciatic nerve branches into 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 (Huijing and Baan, 2001b). Branches of the intact common peroneal nerve innervate EDL muscle as well as the muscles in the peroneal compartment. The tibial nerve, the sural branch as well as all other more proximal branches of the sciatic nerve were cut. The sciatic nerve, with only the common peroneal nerve branch left intact, was dissected, cut as proximally as possible and placed in a pair of silver electrodes.

Fig. 1. A schematic view of the experimental set-up and experimental protocol. (A) Experimental set-up, seen from above. FT 1 indicates the force transducer connected to the proximal tendon of EDL muscle, FT 2 indicates the force transducer connected to the tied distal tendons of EDL, and FT 3 indicates the force transducer connected to the tied distal tendons of TA and EHL muscles. A pulley guided the Kevlar thread from TA + EHL to FT 3. The origin of TA and EHL muscles was not manipulated. Dashed lines indicate tendons and solid lines indicate Kevlar thread that was used to connect the muscles to force transducers. Each relative position of EDL muscle (Δ EDL muscle position) was obtained by repositioning FT 1 as well as FT 2, in a random order, one mm in proximal direction. Δ EDL muscle position = 0 refers to the most distal position of EDL muscle. The distance between FT 1 and FT 2, i.e. $d(FT\ 1 - FT\ 2)$ and, thus also the muscle–tendon complex length of EDL muscle ($l_m + t\ EDL$) remained constant. The TA + EHL lengths at which these EDL muscle positions were measured are also indicated ((a) low = 9 mm below optimum length; (b) high = 2 mm over optimum length). The double arrow below FT 2 indicates that length changes of EDL muscle were obtained by changing the distal force transducer to different positions. (B) Experimental protocol. EDL muscle relative position–force characteristics were assessed for two lengths of EDL muscle ((1) low length = optimum length – 7 mm; (2) low length + 2 mm = optimum length – 5 mm), each tested at two lengths (illustrated in A) of the TA + EHL complex (not shown). The most distal and the most proximal EDL muscle relative positions are shown. Note that at low EDL length 6 positions of EDL muscle and at low length + 2 mm 8 EDL muscle positions could be imposed.

2.2. Experimental conditions

The sciatic nerve was stimulated supramaximally using electrodes connected to a constant current source (3 mA, pulse width 100 μ s). Branches of the intact common peroneal nerve innervate EDL, TA and EHL muscles and stimulation will therefore activate all three muscles simultaneously. It should be noted that this nerve also innervates the muscles in the peroneal compartment.

For each condition, two twitches were evoked followed by a tetanic contraction after 300 ms (pulse

train 400 ms, frequency 100 Hz). After each tetanic contraction the muscles were allowed to recover near active slack length for 2 min. Isometric force was measured just before and during the tetanic contraction of the muscles. Simultaneously, images of the anterior crural compartment muscles in passive and active state were recorded using a digital camera (DVC, JAI CV-M10, shutter speed 1/50 s). Stimulation of the nerve, A/D conversion (12-bit A/D converter, sampling frequency 1000 Hz, resolution of force 0.01 N), and photography were time-controlled by a computer. Movements of the different force transducers to bring

the muscles at the desired length and position, were performed not simultaneously but in a random order.

2.3. Optimum length of EDL muscle and the TA+EHL complex

Optimum length (l_0) and optimal force of EDL muscle were assessed by lengthening of the proximal tendon. This will be referred to as proximally determined optimum length. The tied four distal tendons of EDL muscle were kept at reference position -2 mm. The TA+EHL complex was kept at such a length that no force was exerted at its tied distal tendons.

Optimum length and optimal force of the TA+EHL complex were assessed by lengthening of the tied distal tendons (referred to as distally determined optimum length). The tied four distal tendons of EDL muscle were kept at reference position -2 mm and the proximal tendon was kept at optimum length -7 mm. This low EDL length corresponds to a force of approximately 20% of optimal active EDL force exerted proximally.

2.4. EDL muscle relative position–force characteristics

Isometric force exerted at proximal and distal tendons of EDL as well as at the tied distal tendons of the TA+EHL complex was measured at various positions of EDL muscle relative to its surroundings. While EDL muscle as well as the TA+EHL complex were kept at constant muscle–tendon complex length, the position of only EDL muscle was changed (Δ EDL muscle position), from a distal one to a proximal one, in steps of 1 mm. This is done by moving both proximal and distal tendons 1 mm in proximal direction (Fig. 1). The range of EDL muscle relative positions that could be imposed is dependent on the length of EDL muscle (Fig. 1B). The maximum EDL tendon positions were limited by the position at which the knot of the Kevlar thread on the tendon was just prevented from touching the compartmental fascia on activation.

EDL muscle relative position–force characteristics were assessed at several lengths of EDL muscle (7 and 5 mm below proximally determined optimum length) and the TA+EHL complex (9 mm below and 2 mm over distally determined optimum length). Length changes of EDL muscle were obtained by movement of the distal force transducer to different positions, while the position of the proximal force transducer was unchanged (Fig. 1B). Δ EDL muscle position = 0 mm refers to the most distal EDL muscle relative position of the experiment, which implies that the proximal tendon end is at its most distal position. Length changes of the TA+EHL complex were obtained by movement of the distal force transducer to different positions. EDL muscle relative position–

force characteristics were assessed in the following order (Fig. 1):

1. Low EDL length = $l_0 - 7$ mm
 - (a) low TA+EHL length = $l_0 - 9$ mm
 - (b) high TA+EHL length = $l_0 + 2$ mm
2. Low EDL length + 2 mm = $l_0 - 5$ mm
 - (a) low TA+EHL length = $l_0 - 9$ mm
 - (b) high TA+EHL length = $l_0 + 2$ mm

2.5. Treatment of data and statistics

Active muscle force (F_{ma}) was estimated by subtracting initial passive force (F_{mp}) from total force (F_m) during isometric contraction. For all data mean $\pm$ standard error of the mean (SE) were calculated.

To test for the effects of EDL muscle relative position on proximal and distal EDL forces as well as on distal TA+EHL force one-way ANOVA's for repeated measures (factor: EDL muscle relative position) were performed (Neter et al., 1996). To test for effects of lengthening EDL muscle and the TA+EHL complex two-way ANOVAs for repeated measures (factors: EDL muscle relative position and muscle–tendon complex length) were performed. P values < 0.05 were considered statistically significant.

3. Results

EDL muscle relative position–force characteristics were assessed for different length conditions of EDL muscle (i.e. of EDL muscle kept at low length or low length + 2 mm) and the TA+EHL complex (i.e. the TA+EHL complex kept at low or high length, i.e. low length + 11 mm).

3.1. Effects of moving EDL muscle in proximal direction at constant muscle–tendon complex length

Effects of relative position of EDL muscle on proximally and distally measured EDL forces as well as on distally measured TA+EHL force are shown in Fig. 2. Note that force is expressed as a function of EDL muscle relative position rather than muscle length, as EDL muscle–tendon complex length was kept constant (i.e. 5 mm below proximally determined optimum length = low length + 2 mm). The TA+EHL complex was also kept at constant length (i.e. 9 mm below distally determined optimum length = low length).

ANOVA indicated significant effects of EDL muscle relative position for proximal and distal EDL passive and active forces (Fig. 2A). Passive EDL force exerted at the proximal tendon was zero at the more distal EDL

Fig. 2. Isometric forces of EDL muscle and the TA + EHL complex, kept at constant length, with varying EDL muscle relative positions. (A) Proximally and distally measured active (F_{ma}) and passive (F_{mp}) forces of EDL muscle kept at constant length (low length + 2 mm) as a function of EDL muscle relative position (ΔEDL muscle position). (B) Distally measured forces of the TA + EHL complex, kept at constant low length, as a function of EDL muscle relative position. Note that TA + EHL force is expressed as the deviation (ΔF_{ma}) from the value (0.36 ± 0.19 N) measured at the most distal position of EDL muscle (ΔEDL muscle position = 0 mm). EDL muscle relative position is expressed as the deviation from the most distal position. Low EDL length corresponds to 7 mm below proximally determined optimum length. Low TA + EHL length corresponds to 9 mm below distally determined optimum length. Note that in A different y-axis with different scaling factors are shown for active (left axis) and passive forces (right axis). Note also that the x-axis does not cross the y-axis at zero. Values are shown as mean ± SE (*n* = 7).

muscle positions and increased exponentially with EDL muscle moving in proximal direction (i.e. from ΔEDL muscle position 0–7 mm). A similar pattern, but in inverse direction, was observed for distally exerted EDL passive force. The most likely pathway for these, muscle–tendon complex length independent, effects of EDL muscle relative position on EDL passive forces are the inter- and/or extramuscular connective tissues that are linked with the intramuscular connective tissue of EDL muscle.

Changing the relative position of EDL muscle from distal to more proximal locations, decreased distal EDL active force and increased proximal EDL active force significantly. Consequently, the difference between EDL proximal and distal active forces,

Fig. 3. Schematic drawings to illustrate configuration changes of inter- and extramuscular connective tissue. (A) General structure. EDL muscle, with proximal and distal tendons, is connected to surrounding tissues within the anterior crural compartment (represented as a rectangle), via inter- and extramuscular connective tissue (represented as straight connector lines). (B) Effects of moving EDL muscle from distal (left drawing) to proximal (right drawing): conditions resembling those of the experimental results shown in Fig. 2. The configuration of inter- and extramuscular connective tissue changed in such a way that net force is transmitted via inter- and extramuscular myofascial pathways to the proximal tendon ($F_{EDL_{prox}} > F_{EDL_{dist}}$) of EDL muscle compared to the distal tendons ($F_{EDL_{prox}} < F_{EDL_{dist}}$) at more distal EDL muscle relative positions. (C) Effects of lengthening EDL muscle distally: conditions resembling those of the experimental results shown in Fig. 4. It is illustrated that lengthening EDL muscle distally affects not solely EDL length but involves also a position change of distal parts of EDL muscle. Consequently, the increase of distal EDL active force was significantly higher than the increase of proximal EDL active force ($\Delta F_{EDL_{dist}} > \Delta F_{EDL_{prox}}$).

a direct measure of the magnitude of net inter- and extramuscular myofascial force transmission, changed from -0.87 ± 0.26 to 0.78 ± 0.14 N (i.e. $-32.7 \pm 9.5\%$ to $29.1 \pm 4.1\%$ of proximally determined optimal active force). These observations indicate that positioning EDL muscle more proximally changed the configuration of inter- and extramuscular connective tissue. At more distal relative positions, net force is transmitted via inter- and extramuscular myofascial pathways to the distal tendon of EDL muscle (i.e. $F_{EDL_{prox}} < F_{EDL_{dist}}$). In contrast, at more proximal EDL muscle relative positions such transmission is to the proximal tendon (i.e. $F_{EDL_{prox}} > F_{EDL_{dist}}$). Such a change of configuration, yielding results comparable to those of Fig. 2A, is illustrated schematically (Fig. 3B).

Active force of the TA+EHL complex, kept at constant low length, increased significantly if only EDL muscle was positioned more proximally (Fig. 2B). As the TA+EHL complex was kept at low length, passive force exerted by this complex remained negligible. Note that TA+EHL force is expressed as the deviation from the value (0.36 ± 0.19 N) measured at the most distal position of EDL muscle (i.e. Δ EDL muscle position = 0 mm). These results indicate mechanical interaction between EDL, TA and EHL muscles.

These results show that the relative position of whole EDL muscle–tendon complex with regard to TA and EHL muscles and other connective tissue structures within the anterior crural compartment is a major determinant of passive and active EDL force as well as of active TA+EHL force. These muscle length-independent effects indicate mechanical interactions between EDL muscle and its surroundings, via inter- and/or extramuscular connective tissue (i.e. inter- and extramuscular myofascial force transmission). Thus, the view that muscle–tendon complex length is the only determinant of passive and active isometric muscle force should be discarded for muscles operating within an intact compartment.

3.2. Length effects of EDL muscle on EDL forces are mediated partially by changes of relative position

A major determinant of isometric force exerted by a muscle is certainly the length of its muscle fibers. However, possible effects of muscle relative position should be considered as well. Effects of EDL muscle relative position on EDL proximal and distal active forces are shown in Fig. 4 for two EDL lengths (i.e. low length and low length + 2 mm). Length changes of EDL muscle were obtained by repositioning of the distal force transducer to different positions, while the position of the proximal force transducer was unchanged (illustrated schematically in Fig. 1B). Thus, a comparison between EDL lengths at each Δ EDL muscle position yields a comparison at an identical position of the proximal tendon and most proximal part of the muscle belly but at a different position of the distal tendons and distal parts of EDL muscle bellies. The TA+EHL complex was kept at constant low length (i.e. lo–9 mm).

EDL muscle relative position–active force characteristics, as assessed at proximal and distal tendons, are shown for two EDL lengths (Figs. 4A and B). Lengthening EDL muscle distally increased proximal (Fig. 4A) and distal (Fig. 4B) EDL active forces significantly at all EDL muscle relative positions. If this force increment was merely an effect of increased length, it would have been equal for EDL proximal and distal active force. However, at each EDL muscle relative position, the increase in distally measured EDL force is significantly higher than the increase in proximally

Fig. 4. Proximally and distally Δ EDL muscle position–active force curves at different lengths of EDL muscle (i.e. at low length and at low length + 2 mm). The TA+EHL complex was kept at constant low length (i.e. 9 mm below distally determined optimum length). (A) Proximal EDL active forces as a function of EDL muscle relative position (Δ EDL muscle position). (B) Distal EDL active forces as a function of EDL muscle relative position (Δ EDL muscle position). (C) Proximal and distal active forces of EDL muscle kept at low length and of EDL muscle kept at low length + 2 mm for the most distal EDL muscle relative position (Δ EDL muscle position = 0 mm). The effect of distally lengthening EDL muscle on proximal and distal forces is indicated (ΔF). EDL muscle relative position is expressed as the deviation from the most distal position. Low EDL length corresponds to 7 mm below proximally determined optimum length. Due to physical constraints, the range of EDL muscle relative positions was 5 mm at low length and 7 mm at low length + 2 mm. The F_{ma} represents active force. Values are shown as mean $\pm$ SE ($n = 7$).

measured EDL force. For the most distal EDL muscle relative position (i.e. Δ EDL muscle position = 0 mm), this discrepancy is illustrated in Fig. 4C. The higher increment of distal EDL force compared to proximal EDL force on lengthening EDL muscle distally is explained by additional force transmission to the distal tendon via inter- and/or extramuscular myofascial pathways. These results indicate that distal lengthening of EDL muscle also involves a change of relative position of distal parts of EDL muscle. The effect of such a change of relative position is mediated by changes of the configuration of the inter- and

extramuscular connected tissues (illustrated schematically in Fig. 3C).

It is concluded that if the length of EDL muscle is increased, the effects on proximal and distal EDL forces are mediated by changes of EDL muscle relative position as well as length per se. As the increment of proximal EDL force is predominantly caused by the change of EDL muscle length, at Δ EDL muscle position = 0 mm the relative contribution of relative position change of distal parts of EDL muscle in the increase of distal EDL force must be approximately 50%.

3.3. Length effects of the TA+EHL complex on EDL forces

Fig. 5 compares proximally and distally measured EDL muscle relative position–force curves at constant low and high length (i.e. low length + 11 mm) of the TA + EHL complex. The TA + EHL length increase was obtained by repositioning of the distal tendons. EDL muscle–tendon complex length was kept constant (i.e. low length + 2 mm).

ANOVA indicated significant effects of TA + EHL length on proximal and distal EDL passive and active forces. Distal TA + EHL lengthening increased proximally measured EDL passive force significantly at EDL muscle relative position 6 and 7 mm (Fig. 5A). Distal EDL passive force (Fig. 5B) increased also (at position 0 and 1 mm), but this increase is small if compared to the increase of proximal EDL passive force. If passive force is exerted at one tendon of EDL muscle exclusively, this indicates myofascial force transmission between EDL muscle and its surrounding structures. Therefore, it is concluded that mechanical interactions between the TA + EHL complex and EDL muscle affect the amount of passive force that is transmitted via inter- and/or extramuscular myofascial pathways.

Effects of lengthening the TA + EHL complex distally on proximal and distal EDL active forces varied with EDL muscle relative position. For the most distal EDL muscle relative position (i.e. Δ EDL muscle position = 0 mm), changing TA + EHL length caused active force, exerted at the proximal tendon of EDL muscle, to increase significantly (Fig. 5A). In contrast, at more proximal EDL muscle relative positions higher TA + EHL lengths decreased proximal EDL active force.

Note that the pattern of the change of distal EDL active force as a function of EDL muscle relative position was different on TA + EHL lengthening: it never reversed sign (Fig. 5B). Distal EDL active force decreased significantly at some muscle positions (i.e. Δ EDL muscle position = 0, 1, 6, and 7 mm), but was unchanged at other positions (i.e. Δ EDL muscle position = 2–5 mm).

Fig. 5. Effects of distally lengthening the TA + EHL complex on proximal and distal Δ EDL muscle position–active and passive force curves of EDL muscle kept at constant low length + 2 mm. (A) Proximal active and passive forces of EDL muscle kept at low length + 2 mm as a function of Δ EDL muscle position at low and high length of the TA + EHL complex. (B) Distal active and passive EDL forces of EDL muscle kept at low length + 2 mm as a function of Δ EDL muscle position at low and high length of the TA + EHL complex. EDL muscle relative position is expressed as the deviation from the most distal position. Low EDL length corresponds to 7 mm below proximally determined optimum length. Low TA + EHL length corresponds to 9 mm below distally determined optimum length. High TA + EHL length corresponds to 2 mm over distally determined optimum length. The Fma and Fmp represent active and passive force, respectively. Note that different y-axis with different scaling factors are shown for active (left axis) and passive forces (right axis). Values are shown as mean $\pm$ SE ($n = 7$).

The interaction between the length of the TA + EHL complex and proximal as well as distal forces of EDL muscle shows that isometric muscle force is dependent also on the length of adjacent muscles. This must be mediated by connective tissue linking EDL muscle and the TA + EHL complex. The differential effects on proximal and distal EDL forces indicate that the length increment of the TA + EHL complex has also changed the relative position of EDL muscle with respect to these muscles.

In summary, the position of EDL muscle relative to other muscles and to extramuscular structures is a major determinant of isometric muscle force. These effects are likely to be mediated by both inter- and extramuscular myofascial force transmission. Length changes of EDL

muscle and of the TA+EHL complex involve also position changes of parts of these muscles with regard to surrounding tissues. It is concluded that relative positions of (parts of) EDL, EHL and TA muscles play an important role for force transmission within an intact anterior crural compartment.

4. Discussion

Isometric length–force curves have been predominantly assessed for dissected *in situ* muscles (e.g. Close, 1964; Gareis et al., 1992; Rack and Westbury, 1969; Roszek et al., 1994). In such experiments, the muscle is dissected free of its surrounding tissues, leaving its origin as well as its nerve and blood supply intact. However, early work already indicated mechanical interactions via intermuscular connective tissue between soleus and gastrocnemius muscles, if these muscles were not dissected (Denny-Brown, 1929). In fact, dissection in that study was performed to remove those effects unwanted for the experiment. Several other studies also pointed towards a role of connective tissue that surrounds the muscle in force transmission from muscle fiber to the bony skeleton (Huijing et al., 1998; Pond, 1982). Implicit support for such muscle-connective tissue interactions can also be found in the literature (e.g. Garfin et al., 1981; Gerlach and Lierse, 1990; Riewald and Delp, 1997; Van der Wal, 1988).

Recent experiments yielded unequivocal evidence for force transmission between EDL muscle and other structures within its direct environment (Huijing, 1999a; Huijing and Baan, 2001a; Maas et al., 2001). For most lengths tested, it was found that force exerted at the proximal tendon was unequal to force exerted at the distal tendons of EDL muscle. Such a proximo-distal force difference is direct evidence for non-myotendinous force transmission between locations within EDL muscle and surrounding structures. Muscle fiber force may be transmitted via intermuscular connective tissue to surrounding muscles (i.e. intermuscular myofascial force transmission) and/or via extramuscular connective tissue to other surrounding tissues (i.e. extramuscular myofascial force transmission). The sum of forces transmitted at several locations via those myofascial pathways from or onto EDL muscle is measured as the difference between EDL proximal and distal forces. The proximo-distal force difference is, therefore, a direct measure of the magnitude of net inter- and extramuscular myofascial force transmission. It should be noted that on the basis of those experiments as well as on the basis of the present work, we cannot distinguish the individual contribution from each pathway.

Recent results indicated effects of muscle relative position on isometric muscle force (Huijing and Baan,

2003). However, effects of muscle length and relative position were not studied independently. In the present study, exclusive effects of EDL muscle position relative to surrounding tissues within the anterior crural compartment on force transmission of EDL muscle were investigated, as EDL muscle position was changed without imposing length changes on that muscle. Thus, effects of inter- and extramuscular connective tissue connections were assessed exclusively. The most striking result is that isometric force of EDL muscle as well as of the TA + EHL complex are affected significantly by the position of whole EDL muscle–tendon complex relative to neighboring muscles and extramuscular connective tissue structures within the anterior crural compartment. It is concluded that in addition to length, muscle position relative to its surroundings determines isometric force of a muscle.

Furthermore, it was found that isometric muscle force is dependent also on the length of adjacent muscles. This intermuscular interaction suggests intermuscular myofascial force transmission (Maas et al., 2001).

The present results also show that any change of active force with length changes of a muscle that is not dissected free from its surrounding tissues, is not solely determined by the global length changes *per se* but is affected also by changes of relative position of most parts of the muscle.

4.1. Effects of changing the relative position of (parts of) EDL muscle on passive and active components within the muscle

A difference between isometric force exerted at the proximal and at the distal tendons of a muscle, as found in the present study, indicates that an additional force must act on the muscle. As a result of force equilibrium, this net force is equal to the proximo-distal force difference. Inter- and extramuscular connective tissues appear to have sufficiently stiff connections to intramuscular connective tissue (Huijing and Baan, 2001b; Huijing et al., 2003; Maas et al., 2001). Muscle fibers are linked to this connective tissue network via transsarcolemmal linkages between cytoskeleton, extracellular matrix and endomysium (for review see Berthier and Blaineau, 1997; Patel and Lieber, 1997). It has been indicated that these myofascial connections are capable of bearing force (Goldberg et al., 1997; Huijing, 1999b; Huijing et al., 1998; Jaspers et al., 2002; Jaspers et al., 1999; Monti et al., 2001; Monti et al., 1999; Street, 1983; Street and Ramsey, 1965). Therefore, this additional force is expected to affect distributions of length of active (i.e. sarcomeres) and/or passive components (i.e. epimysium, perimysium and endomysium, transsarcolemmal linkages, non-contractile proteins within the sarcomeric cytoskeleton, such as titin) within the muscle. A higher proximal EDL force than distal EDL

force (Fig. 2A) is most easily explained if sarcomeres located proximally within muscle fibers attain higher lengths than sarcomeres located distally within the same muscle fibers. As the proximo-distal EDL force difference changes as a function of EDL muscle relative position, changes of the distribution of lengths of sarcomeres are to be expected.

In a most simple approach of such distributions, proximal and distal segments of EDL muscle fibers may be distinguished. Using this concept, a higher proximal compared to distal EDL passive force (Fig. 2A) is associated with a higher mean length of passive components within the proximal segment compared to these components within the distal segment of EDL muscle. Changes of proximally as well as distally measured passive force as a function of EDL muscle relative position indicates a redistribution of lengths of these passive structures within muscle fibers. The final distribution is dependent on the points of application of the inter- or extramuscular myofascial forces imposed on the muscle, their magnitude as well as direction (a more proximal or more distal orientation). Furthermore, these effects of EDL muscle relative position on passive forces indicate that inter- and/or extramuscular connective tissue act as series elastic components for EDL muscle.

If the length of a muscle is increased, passive force rises monotonically while active force may increase as well as decrease depending on the specific length range. This may explain the observation of the present study that proximal EDL active force is decreased at the more proximal EDL muscle relative positions on lengthening the TA+EHL complex distally (Fig. 5A). Sarcomeres within the proximal segment of muscle fibers could be pulled beyond their optimum length. This view is supported by the fact that, at the most proximal EDL muscle relative positions (Δ EDL muscle position = 6 and 7 mm), passive forces exerted proximally reach high levels. These forces are comparable to passive forces measured at over optimum length of EDL muscle (Huijing and Baan, 2001a,b; Maas et al., 2001).

Further research is necessary to elucidate effects of muscle relative position on length distributions of sarcomeres as well as of passive structures within the muscle. In the experimental conditions of the present study the muscle belly of EDL muscle is completely covered by TA muscle and its muscle fibers cannot be seen. To measure such length distributions within EDL muscle, the anterior crural compartment should be opened. Such fasciotomy will affect the results of the present study, because the pathways for inter- and extramuscular force transmission are affected or damaged. This problem may be solved by applying a mechanical model of the anterior crural compartment. A three-dimensional finite element model of skeletal muscle, which allows for intramuscular myofascial force

transmission, was described recently (Yucesoy et al., 2002). Effects of intermuscular myofascial force transmission on the distribution of lengths of sarcomeres, using a model of two linked muscles, have been reported (Yucesoy et al., 2001). Other noninvasive techniques to investigate skeletal muscle properties are ultrasonography (e.g. Fukunaga et al., 1997; Maganaris et al., 1998), and magnetic resonance imaging (MRI), such as magnetic resonance elastography (e.g. Dresner et al., 2001).

4.2. Intermuscular interactions on changing muscle length and muscle relative position

Based on previous experiments (Maas et al., 2001), it was expected and confirmed that distal lengthening TA+EHL decreased active force exerted at the distal tendons of EDL muscle. Force of adjacent muscles tends to be transmitted to the tendon of a muscle, which is at relatively high length. Lengthening one muscle changes the configuration (i.e. the length and angle) of its surrounding connective tissues in such a way that net force is transmitted via inter- and/or extramuscular myofascial pathways to the location at which the lengthening was imposed, as illustrated in Fig. 3C.

However, for some EDL muscle relative positions, distal EDL active force was unchanged on increasing TA+EHL length distally (Fig. 5B). These results indicate an interaction between length changes of the TA+EHL complex and relative position of EDL muscle. Note that both factors change the relative position of the different muscle bellies. Two explanations are suggested: (1) At those specific EDL muscle relative positions, the connective tissue that serves as a pathway for these intermuscular interactions is rather compliant. This is supported by the observation that at the same positions of EDL muscle (i.e. Δ EDL muscle position $\approx$ 3, 4 mm), changes of distal EDL force, as a function of EDL muscle relative position, were less pronounced than at other positions. (2) A decrease in distal EDL active force is cancelled by other factors, such as changes of the distribution of lengths of sarcomeres.

4.3. Relative position changes of muscles in vivo

In vivo, position changes of a muscle relative to adjacent synergists will be caused by (1) differences in moment arm between those muscles, and (2) the fact that some muscles span only one joint and adjacent muscles may span more than one joint. The position of a muscle relative to non-muscular (i.e. fixed) structures within a compartment (e.g. bone, fascia) will alter with any change of joint angle.

In rat, moment arms of the presently studied muscles at the ankle are expected to be different. For mice, it was

found that the average moment arm at the ankle of TA muscle is 17% higher than of EDL muscle (Lieber, 1997). This indicates that length changes of TA, as function of ankle angle, are 17% higher than of EDL muscle. Furthermore, the distal tendons of the muscles within the rat anterior crural compartment all cross the ankle joint. It should be noted that only the proximal tendon of rat EDL muscle crosses also the knee joint (knee extensor). Thus, movements of the knee joint involve length changes of EDL muscle without any changes of muscle–tendon complex length for TA and EHL muscles. Therefore, changes of relative position of (parts of) the muscles of the anterior crural compartment are expected to occur during in vivo rat movements.

Such changes of muscle relative position in rat anterior crural compartment have not been measured directly nor estimated using musculo-skeletal models. It has been reported that during treadmill stepping of rat the knee joint ranges between 54° and 125° , and the ankle joint ranges between 41° and 146° (Gruner et al., 1980). In addition, we have found that EDL muscle–tendon complex length increases by approximately 3 mm if the knee joint is moved from 45° to 135° and another 3 mm due to dorsal flexion of the ankle joint from 45° to 135° (unpublished observations). These observations indicate: (1) that the length of EDL muscle can change proximally by 3 mm without any length change of TA and EHL muscles, and (2) that the position of whole EDL muscle relative to non-muscular fixed structures within the anterior crural compartment can change by 3 mm. During in vivo rat movements, the ankle and knee joints move simultaneously (Gruner and Altman, 1980; Gruner et al., 1980). In such conditions, a change of muscle relative position exclusively without any length changes of adjacent muscles, as imposed experimentally on EDL muscle in the present study, will not occur. However, the purpose of the present study was to distinguish effects of changing muscle relative position from effects of changing muscle length.

In the present study, the relative position of EDL muscle was changed by 5 mm for low length and by 7 mm for low length + 2 mm (Fig. 4). Note that a change of EDL muscle relative position of 3 mm still causes substantial changes of proximal and distal EDL forces. Furthermore, a 2 mm increase of EDL muscle–tendon complex length, caused a significant higher increase of distal EDL force compared to proximal EDL force, indicating a change of relative position of parts of EDL muscle (Fig. 4C). This suggests that also for in vivo length and position ranges, effects of muscle relative position may play an important role.

In addition, substantial changes of relative position of human muscles have been measured in vivo, using cine phase-contrast magnetic resonance imaging (Asakawa et al., 2002). For a constant hip angle, length changes of

bi-articular rectus femoris (RF) and mono-articular vastus intermedius (VI) muscles were compared during active knee extension. In healthy subjects, it was found that position changes of a square region of interest of the muscle belly were on average 31% greater in RF than in VI. The higher length changes of RF compared to VI are explained by the fact that RF has a higher moment arm than VI (Buford et al., 1997; Visser et al., 1990). These results show that in vivo the relative position of adjacent muscle bellies is changed by joint movements in humans.

4.4. Implications and conclusions

The present results indicate that in vivo the assumption that isometric muscle force is constant, if muscle–tendon complex length is unchanged, is not tenable. Consequently, the assessment of length–force characteristics of mono- and bi-articular human muscles in vivo using this assumption (e.g. Herzog and ter Keurs, 1988b; Herzog and ter Keurs, 1988a; Huijing et al., 1986), may result in erroneous conclusions.

An important role of bi-articular muscles during multi-joint movements (e.g. running, jumping) is the capability to redistribute energy over the joints that are crossed, i.e. a transport of energy (e.g. Gregoire et al., 1984; Van Ingen Schenau et al., 1987). In rat for example, work performed by muscles in knee flexion, may be used for dorsal flexion of the ankle and/or toes via the poly-articular EDL muscle. Even if the length of the muscle would not change, the position of the muscle relative to surrounding tissues does change. The results of the present study suggest that in such a transport of energy not only the poly-articular muscle, as defined by location of origin and insertion, will play a role, but also adjacent muscles and other surrounding structures. Other implications of muscle relative position as a co-determinant of isometric muscle force have been described recently (Maas et al., 2003).

In conclusion, the position of a muscle relative to adjacent muscles and relative to other connective tissue structures is a major co-determinant of isometric muscle force. Length changes of muscle involve also position changes of most parts of the muscle relative to surrounding structures. Therefore, potential effects of surrounding tissues should always be considered if in vivo muscle properties are studied.

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