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FORCE TRANSMISSION BETWEEN RAT ANKLE PLANTAR FLEXION MUSCLES: IMPLICATIONS FOR ASSESSMENT OF *IN VIVO* LENGTH-FORCE CHARACTERISTICS

Michel Bernabei, Jaap van Dieen and Huub Maas
MOVE Research Institute, Faculty of Human Movement, VU University Amsterdam, The Netherlands
email: m.bernabei@vu.nl

SUMMARY
The aim of this *in situ* study was to quantify the transmission of force via epimuscular myofascial linkages between lateral gastrocnemius and plantaris complex (LG-PL) and soleus (SO) muscle in the rat. Isometric forces exerted at proximal and distal LG-PL, as well as distal SO tendons were measured for several muscle lengths and relative positions, which correspond to the physiological range of motion (ROM) of ankle and knee joint angles. A significant effect of LG-PL proximal lengthening on passive and active forces exerted at the distal SO tendon was found. These results indicate force transmission between synergistic muscles for in vivo muscle lengths and relative positions. We conclude that LG-PL and SO muscles cannot be considered as independent actuators. It is shown that ignoring this property of the muscular system when length-force characteristics of human muscles are assessed, introduces substantial errors.

INTRODUCTION
In situ studies have shown that connective tissues linking adjacent muscles can bear substantial force. Such epimuscular myofascial force transmission (EMFT) challenges the assumptions applied in most biomechanical models and *in vivo* studies defining muscles as independent force actuators [1]. However, due to the supraphysiological muscle lengths and relative positions previously imposed, the relevance and the effects of EMFT within *in vivo* length ranges remain controversial and unclear.

Our aim was to study the transmission of force between two-joint (LG-PL) and one-joint (SO) muscles for selected combinations of ankle and knee joint positions in the rat. Consequences for the reconstruction of *in vivo* MTU-length-force characteristic are assessed.

METHODS
In deeply anesthetized Wistar rats (n=9, 300±20 g), the posterior crural compartment was exposed by removing the skin and most of the biceps femoris. Distal and proximal tendons of LG-PL complex and the distal SO tendon were severed from the femoral and the calcaneal bones and each connected to force transducers. The tibial nerve - innervating LG, PL and SO muscles - was stimulated supramaximally using a bipolar cuff electrode connected to a constant current source (100Hz, 0.4 ± 0.1mA, 500ms).

Isometric forces exerted at all three locations were measured simultaneously for different lengths and relative positions of LG-PL and SO muscles. Length changes of LG-PL (6 mm range) without MTU length changes of its synergists were obtained by repositioning the proximal LG-PL tendon exclusively, simulating changes in knee joint angle (from 45º to 130º, included angles). Such proximal LG-PL length changes were imposed for three different positions of the distal tendons of LG-PL and SO muscles, corresponding to three different ankle angles (60º, 90º, 130º). MTU length-joint angle relationships were estimated using a musculoskeletal model of the rat hindlimb [2]. Active forces were calculated by subtracting passive force from total force at equal MTU length and relative position. Passive length-force data were fitted with an exponential function proposed by Hoang et al. [3]. These functions were used to estimate slack lengths for distally and proximally measured LG-PL length-force data.

The selected muscle configurations involve measuring distal force of SO at the same MTU length, but with a different position of SO relative to LG and PL muscles. Changes in SO force are indicative of mechanical interactions between synergistic muscles via epimuscular myofascial pathways. In addition, proximal and distal LG-PL forces at equal MTU lengths but for multiple positions of LG-PL relative to SO were measured. Proximo-distal LG-PL force differences at equal MTU length are direct proof of EMFT.

RESULTS AND DISCUSSION
Repeated measures ANOVA indicated a significant main effect of LG-PL proximal position on SO active and passive forces ($p<0.05$). Distal active SO forces for different MTU lengths of LG-PL are shown in Figure 1. For both active and passive (not shown) data, SO force showed a significant increase for each of the three conditions imposed at the distal tendons. SO active force increased up to 0.15N, while the passive force increase was up to 0.007N (12% and 36% of the active and passive force at the 0mm ΔP_{MTC} LG-PL proximal position, respectively).

Active forces exerted at the LG-PL proximal tendon are shown in Figure 2. The three curves represent the force exerted by LG-PL for a range of simulated knee angles (i.e., different position of its proximal tendon) at ankle angles of 60º, 90º and 130º. Repeated measures ANOVA indicated a significant main effect of muscle relative position on proximally and distally measured active as well as passive

LG-PL forces ($p<0.05$, only proximal active forces are shown). For various MTU lengths, a significant difference in LG-PL force was found. This difference varied between 0.16 N and 0.64 N among the equal MTU lengths, but different muscle relative positions. Differences in passive force due to changes in LG-PL relative position were up to 0.036±0.002N.

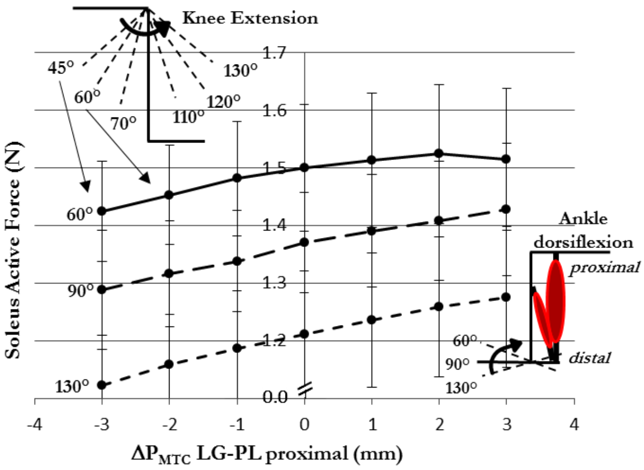

Figure 1: Active force exerted at the distal tendon of SO (mean ± SD) plotted as a function of the position of the proximal tendon of LG-PL for three different simulated ankle positions. LG-PL proximal position is expressed as the deviation from the position corresponding to a 90º knee angle.

In addition to effects of muscle relative position on LG-PL forces at each tendon separately, significant ($p<0.05$) but small differences between proximally and distally measured forces at equal MTU lengths were found (up to 2.2% of optimal force). Such proximo-distal force differences are direct measures of the magnitude of net EMFT. Differences between proximal and distal passive forces resulted in various estimates of LG-PL slack length. The mean difference in the slack lengths estimated based on proximal or distal LG-PL passive forces was quite high, i.e. 6.7 ± 4.2 mm (19% of the mean estimated slack length, 36 ± 4.3 mm).

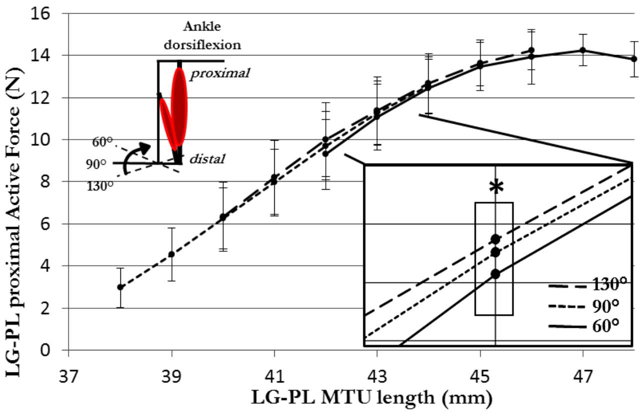

Figure 2: Active force exerted at the proximal tendon of LG-PL (mean ± SD) plotted as a function of its MTU length for three different simulated ankle positions.

The increase in SO active force with lengthening LG-PL proximally can be explained by the transmission of force between LG-PL and SO. Such changes in SO forces while the MTU was kept at a constant length violate the assumption by which the isometric muscle force is constant for a given MTU length. The same mechanism can be held responsible for the different forces measured at the proximal and distal tendons of LG-PL. Methods used for length-force curve reconstruction in humans exploit linear summation of forces/moments from muscles spanning a common joint, assuming a unique isometric force corresponding to a certain MTU length [3,4]. We showed that if the relative position of LG-PL with respect to SO muscle changes, forces exerted at the insertion and origin of LG-PL are affected significantly as a result of mechanical interactions. The three different segments shown in figure 2 represent three equally possible realizations for the LG-PL active length-force curve, depending on different joint configurations.

CONCLUSIONS

Unlike most previous experiments on EMFT, the imposed length ranges in the present study span the physiological ROM for the considered joints. Our result showed that EMFT does affect tendon force within such a range, indicating that EMFT can play a role *in vivo*. We conclude that MTU length cannot be assumed as the only determinant of isometric muscle force. One of the implications of the present results is that, due to EMFT, a unique length-force relation does not exist for the targeted muscles. Hence, commonly used methods for length-force curve reconstruction in humans assuming mechanically-independent muscles may lead to erroneous solutions.

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