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ORIGINAL ARTICLE

Negligible epimuscular myofascial force transmission between the human rectus femoris and vastus lateralis muscles in passive conditions

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Abstract

Purpose There have been contradictory reports of the effects of epimuscular myofascial force transmission in humans. This study investigated the transmission of myofascial force to the human vastus lateralis muscle by determining whether vastus lateralis slack angle changed with hip angle. Since the distance between the origin and insertion of the vastus lateralis muscle does not change when hip angle changes, any change in vastus lateralis slack angle with hip position can be attributed to epimuscular myofascial force transmission.

Methods Nineteen young adults were tested in hip flexed (80°) and neutral (0°) positions. Ultrasound images of the vastus lateralis muscle were obtained as the knee was passively flexed at 5°/s. The knee angle at which vastus lateralis muscle fascicles began to lengthen was used to identify muscle slack angle.

Results Overall, there was a negligible effect of hip position on vastus lateralis slack angle (0.6° [−0.7 to 1.9]; mean [95% confidence interval]). However, a small and variable effect was noted in 3/19 participants.

Conclusion This result indicates that, over the range of joint angles tested here, there is little or no epimuscular myofascial force transmission between the vastus lateralis muscle and neighbouring bi-articular structures under passive conditions. More broadly, this result provides additional evidence that epimuscular myofascial force transmission tends to be small and variable under passive conditions in healthy human muscle.

Keywords Epimuscular myofascial force transmission · Muscle tendon unit · Muscle fascicle · M. rectus femoris · M. vastus lateralis

Introduction

When a relaxed muscle is stretched, it resists lengthening by exerting passive tension. If that muscle is adjacent to a muscle that does not undergo stretch, a portion of the passive force may be transmitted to the neighbouring, unstretched muscle (Huijing and Baan 2003; Maas and Sandercock 2008; Bernabei et al. 2015; Tijs et al. 2016). This transmission of force is possible because muscles are connected to one another and to surrounding non-muscular structures through connective tissue attachments to the epimysium, the fibrous sheath that surrounds skeletal muscle (Huijing 2009; Maas and Sandercock 2010; Wilke et al. 2018).

Some evidence suggests that, in healthy human muscles, little force is transmitted through epimuscular myofascial pathways under passive conditions (Carvalhais et al. 2013; Yoshitake et al. 2018; Diong et al. 2019; Maas 2019). When present, epimuscular myofascial force transmission is often

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(Bojsen-Moller et al. 2010; Huijing et al. 2011; Ates et al. 2018), but not always (Tian et al. 2012), observed in muscles that share a tendon (e.g. gastrocnemii and soleus muscles). The functional importance of epimuscular myofascial force transmission remains unclear (Maas 2019). However, Smilde et al. (2016) have noted that epimuscular myofascial force transmission can alter proprioceptive signals from adjacent, unstretched muscles. Specifically, passively stretching a muscle can increase the discharge rate of stretch-sensitive muscle spindles in a neighbouring, unstretched muscle. This intriguing observation has potential implications for motor control, and represents a potential functional role for even small amounts of epimuscular myofascial force transmission (Smilde et al. 2016). The study of this phenomenon requires a sensitive, non-invasive method for detecting the presence of epimuscular myofascial force transmission in humans.

Recently, we devised a simple ultrasound-based approach to investigate the history-dependence of passive mechanical properties in single human muscles (Stubbs et al. 2018). This approach takes advantage of the observation that, at short lengths, some human muscles fall slack (Hoang et al. 2007; Herbert et al. 2011, i.e., they do not exert any passive tension). When a large amplitude stretch is applied, muscle fascicles do not initially change length. Only when slack is taken up do they start to lengthen. This point, when muscle fascicles start to lengthen in response to an imposed stretch, is the muscle-tendon slack length (Herbert et al. 2011, 2015). However, it is easier to measure joint angle than muscle-tendon length, and joint angle is a good proxy for the length of a relaxed muscle-tendon unit. Thus, for convenience, in our previous study and here, we refer to the knee joint angle at which the slack is taken up as the muscle slack angle.

Using this approach, we quantified the effect of a preceding stretch or contraction on vastus lateralis muscle slack angle (Stubbs et al. 2018). More recently, we investigated the effect of contraction intensity, stretch amplitude and time on the history-dependence of muscle slack angle (Héroux et al. 2020). Across both studies, measures of muscle slack angle were reproducible and sensitive to small experimental manipulations, suggesting this approach could be used to study epimuscular myofascial force transmission in humans.

Epimuscular myofascial force transmission in humans is typically studied in a mono-articular muscle adjacent to a bi-articular muscle (Bojsen-Moller et al. 2010; Tian et al. 2012; Carvalhais et al. 2013; Yoshitake et al. 2018; Diong et al. 2019). By moving the joint crossed only by the bi-articular muscle, a muscle-specific stretch can be imposed. Freitas et al. (2019) investigated the effect of changing hip angle from neutral to 80° flexion on epimuscular myofascial force transmission between the vastus muscles and bi-articular structures that cross the hip and knee joints (presumably the rectus femoris muscle and the ilio-tibial band). Shear-wave elastography was used to show that passive stiffness of the vastus lateralis and medialis muscles did not change with hip angle. Thus, it was concluded that epimuscular myofascial force transmission does not occur between these structures under passive conditions. However, due to the small size of the effect investigated and possible inaccuracies in shear-wave elastography measures (Ruby et al. 2019; Sarabon et al. 2019; Wang et al. 2020; Kozinc and Sarabon 2020), it could be that the study by Freitas et al. (2019) failed to detect epimuscular myofascial force transmission that was present. Recently, Yanase et al. (2021) argued that Freitas et al. (2019) did not sufficiently stretch the rectus femoris muscle. Thus, they conducted a similar experiment where the pelvis was fixed and the hip was positioned in more extreme ranges and observed differences in the passive stiffness of the vastus lateralis and medialis muscles. This was interpreted as evidence of epimuscular myofascial force transmission. However, the muscles were not fully at rest and the amount of muscle activity present—a few percent of maximal muscle activity—generates sufficient torque to impact measures of passive range of motion (Diong et al. 2019) and, importantly, muscle stiffness (Le Sant et al. 2019). This amount of muscle activity is likely sufficient to also impact measures of muscle stiffness. Thus, differences in the amount of muscle activity present when the hip was in different extreme ranges could, in theory, account for the differences observed by Yanase et al. (2021).

The aim of the current study was to investigate, in passive muscle, epimuscular myofascial force transmission to the vastus lateralis muscle using slack length rather than muscle stiffness as the outcome of interest as slack length may be a more sensitive indicator of epimuscular myofascial force transmission than muscle stiffness. For the mono-articular vastus lateralis muscle, a change in muscle slack angle with hip angle would be indicative of epimuscular myofascial forces transmission between the vastus lateralis muscle and bi-articular structures that cross the hip and knee joints.

Methods

Ethical approval

This experiment was approved by the University of New South Wales Human Research Ethics Committee (approval number: HC15006) and was performed in accordance with the Declaration of Helsinki (2013), except for registration in a database. Participants provided informed consent in writing.

Participants

Twenty healthy individuals with no history of lower limb, hip, or back injury in the last 12 months were recruited.

One participant was unable to relax the leg muscles during the experimental procedures and so was excluded. Thus, data are reported for 19 participants (11 females, mean age 26 years (SD 5.8), mean height, 1.74 m (SD 0.06), mean weight 71 kg (SD 10)).

Experimental set-up

Participants were seated with the shank of the right leg strapped to a dynamometer (Cybex Norm with Humac, CSMi, Stoughton MA, USA) that flexed and extended the knee at 5°/s. The apparatus axis was aligned with the mediolateral rotational axis of the knee (Fig. 1A). For each participant, knee range of motion was kept constant across the hip neutral and hip flexed experimental conditions. The axis of the dynamometer was repositioned until changes in the inclination of the shank and the dynamometer input arm—both measured with a digital inclinometer—were the same (±2°). To minimise changes in joint alignment when participants performed conditioning maximal knee extension contractions (for details see Section Experimental protocol), the dynamometer cushion under the thigh was replaced with a steel plate with a rounded edge. With this plate in place, the maximal change in knee angle during contractions was ~ 1°. The dynamometer generated a knee angle signal that was sampled at 50 Hz (16-bit DAQ, 1401, CED, Cambridge, UK).

Electromyography (EMG) signals were recorded from the right vastus lateralis (distal portion), rectus femoris and medial gastrocnemius muscles with pairs of Ag-AgCl electrodes (Cleartrace; ConMed Corporation, Utica, NY, USA; diameter 10 mm, spacing 30 mm). The ground electrode was placed over the patella. EMG signals were amplified (x3000), band-pass filtered (20–500 Hz; isolated pre-amplifier, 1902, CED, Cambridge, UK), and sampled at 2 kHz.

Ultrasound images of vastus lateralis muscle fascicles were obtained using two 46 mm linear array ultrasound transducers (MyLab25 with LA522E transducers, operating at 12 MHz; Esaote, Firenze, Italy) held together in a custom built mould (Herbert et al. 2011, 2015). The use of two ultrasound transducers increased the field of view (Fig. 1A). The transducers were placed over the mid-belly of the vastus lateralis muscle and the orientation of the transducers was adjusted to generate the clearest possible image of the muscle fascicles (Kwah et al. 2013). The position and orientation of the transducer was maintained manually when the knee was passively flexed (Fig. 1C). The outline of the transducers on the skin was marked with tape to facilitate consistent placement throughout the experiment. Images from the two transducers were captured synchronously with a dual channel

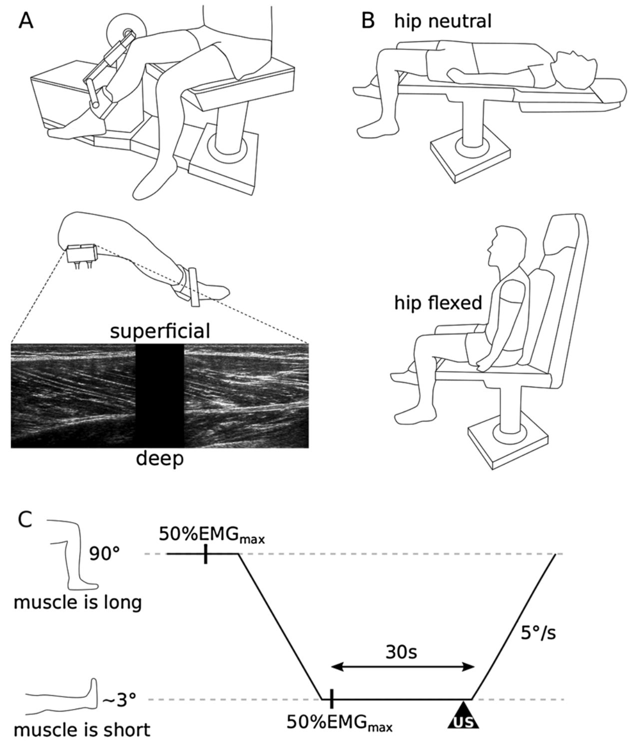

Fig. 1 Experimental set-up. **A** Participants were seated with their right shank strapped to a dynamometer. Ultrasound images were recorded from the right vastus lateralis muscle using two probes held together in a rigid mould. **B** There were two experimental conditions: hip neutral (0°) and hip flexed (80°). **C** The horizontal axis represents time and the vertical axis represents knee angle (a surrogate for muscle-tendon length). All trials started with participants performing a 2–3 s 50% of maximum voluntary isometric knee extension contraction ($50\%EMG_{max}$) at long muscle length (knee flexed 90°). The knee was then passively extended to as far as the participant comfortably tolerated (~ 3°) at a rate of 5°/s. Participants then performed another 2–3 s $50\%EMG_{max}$ contraction. The knee stayed in 0° of flexion until muscle slack angle was measured with ultrasound (the start of which is indicated by a black triangle)

video capture card at 15 Hz with Spike2 software and the S2video plug-in (CED, Cambridge, UK). The ultrasound image sequences obtained from the two transducers were stitched together to provide a composite image sequence with a 110 mm field of view. The composite images had an 18 mm gap between the two transducers (Fig. 1A).

Apart from performing the conditioning isometric knee extension contractions that were part of the experimental protocol, participants were instructed to stay completely relaxed. EMG signals and ultrasound images were constantly monitored and any trials with overt muscle activity (e.g., trials in which there was a clear burst of activity on EMG recordings or twitch-like fascicle shortening visible on ultrasound) were stopped and repeated.

Experimental protocol

Maximum vastus lateralis muscle EMG amplitude was determined at the start of the experiment. Participants performed three maximum voluntary knee extension contractions at the start of the study with the knee in 90° of flexion. A 60 s rest period was provided between contractions. The EMG signal from the vastus lateralis muscle was digitally rectified and smoothed (0.05 s time constant) and the maximum EMG amplitude across all three contractions was determined.

Two experimental conditions were investigated, *hip flexed* (Fig. 1A) and *hip neutral* (Fig. 1B). The procedures for these two conditions were identical, except that for the *hip flexed* condition participants sat supported with their hips flexed ~ 80° and for the *hip neutral* condition they lay with their hips flexed ~ 0°. Thus, the length of the vastus lateralis muscle was the same across both conditions, whereas the length of the bi-articular structures that cross the hip and knee joints (e.g. rectus femoris muscle, ilio-tibial band) were at longer lengths in the *hip neutral* condition. While more extreme hip flexion or extension would have provided greater opportunity for epimuscular myofascial force transmission to occur (Ates et al. 2018), our previous two studies taught us that, with the hip flexed ≥ 90°, few participants can generate large knee extension condition contractions and subsequently fully relax their muscles. Similarly, pilot experiments indicated participants had difficulty relaxing their thigh muscles when their hip was extended and their knee was passively flexed. Thus, the current hip angles were chosen to ensure measurements were obtained under passive conditions. Five trials were completed per condition. The order of testing was block randomized across participants.

All trials were identical (Fig. 1C). At the start of each trial, the knee was passively positioned in 90° of flexion (i.e., with the vastus lateralis muscle moderately stretched; Fig. 1C). Participants then performed a 2–3 s isometric knee extension contraction to 50% of maximal EMG amplitude. This contraction intensity reduces muscle slack angle as much as a maximal contraction (Héroux et al. 2020), but is less likely to induce muscle fatigue. Thus, it ensured all trials started with the same contraction history. The knee was then passively extended to ~ 3°, approximating the shortest in vivo muscle length. Participants then performed a 2–3 s conditioning isometric knee extension contraction to 50% of maximal EMG amplitude. This contraction ensured vastus lateralis muscle fascicles were maximally shortened at this knee angle. Participants received visual feedback of the smoothed and rectified EMG of the vastus lateralis muscle and the target EMG level during these contractions. With the leg muscles fully relaxed, the knee remained in this position until muscle slack angle was tested 30 s later.

To measure muscle slack angle, the knee was passively flexed (i.e., the vastus lateralis muscle was passively lengthened) at 5°/s from the maximally extended position (i.e., from the shortest in vivo muscle length). Ultrasound images were obtained as the knee was flexed. The ultrasound images were used to determine muscle slack angle.

Data analysis

Muscle fascicles were tracked on the composite ultrasound image sequence using a semi-automated procedure (Herbert et al. 2011). A clearly visible muscle fascicle from each image sequence was tracked. Tracking involved identifying the location of the proximal and distal ends of the muscle fascicle—where it inserted into the internal border of the superficial and deep aponeuroses—in each frame of the image sequence. Muscle fascicle length was defined as the distance between the proximal and distal ends of the muscle fascicle; note that, therefore, 'muscle fascicle length' as defined here differs from the length of the path along the fascicle, which may have been curved. Fascicle length was plotted as a function of knee angle. A semi-automated algorithm determined the muscle slack angle by finding the knee angle at which there was the greatest change in fascicle length with respect to knee angle (Stubbs et al. 2018; Héroux et al. 2020). The knee angle signal was downsampled to 15 Hz for this analysis. Given the knee was flexed at 5°/s, measures of muscle slack angle thus had a theoretical resolution of 0.333°. The algorithm was supervised by two investigators who were blind to experimental condition. Both investigators reviewed each trial. If either assessor thought the slack length selected by the algorithm differed by more than 5° from the slack length selected by eye, the trial was flagged for manual slack length identification. This occurred in six out of 190 trials across four participants.

The EMG data were filtered (4th order, 20–450 Hz band-pass, zero-lag Butterworth), mean removed, rectified and again filtered (4th order, 25 Hz low-pass, zero-lag Butterworth); The peak in EMG activity across the three maximal contractions was determined and used to normalise EMG data from each trial. For each participant, plots of knee angle, change in fascicle length and EMG were generated for each trial and visually inspected to ensure the muscles were relaxed as ultrasound was recorded. Across participants and trials, there was no evidence of bursts of EMG activity or abrupt changes in muscle fascicle length that would have impacted our measure of muscle slack angle. In approximately 10% of trials, small amounts of EMG activity were visible in either the vastus lateralis or rectus femoris muscles as the knee neared mid-range (40°–50° of knee flexion). Importantly, the onset of EMG activity was always well after the muscle slack angle. There was no EMG activity in the medial gastrocnemius muscle in any of the trials. To quantify background EMG of the vastus lateralis and rectus femoris muscles during each trial, mean EMG amplitude was computed for the time window consisting of 5 s before the start of the passive knee flexion to 2 s after the muscle slack angle. Rectus femoris muscle EMG data could not be processed for one participant as it was contaminated by 50 Hz line noise.

Statistical analysis

An estimation approach based on confidence intervals was used to quantify the systematic effect of hip angle on the history-dependence of muscle slack angle (Calin-Jageman and Cumming 2019). To ensure that the assumption of independence of observations was met, the mean muscle slack angle for each participant for each of the two conditions was used as the unit of observation. 95% confidence intervals were computed for the mean of each condition, an the difference between those means, using the relevant t-distribution.

To quantify the variability of individual muscle slack angle values, their standard deviation (SD) was computed for the *hip flexed* and *hip neutral* conditions.

Because five measures were obtained in the *hip flexed* and *hip neutral* conditions, it was possible to test the null hypothesis that, for a given participant, there was no effect of hip angle on muscle slack angle. A total of 19 unpaired *t*-tests were performed, with the resulting p-values compared to a Bonferroni-corrected statistical threshold ($\alpha = 0.05/19 = 0.00264$).

The Python programming language (Python Software Foundation, version 3.7) was used for statistical analyses.

Results

Two of the 190 trials had to be excluded: one because it was not possible to track the ultrasound video, the other because a brief contraction was visible on the ultrasound video.

Average background vastus lateralis muscle EMG activity ($n = 19$) was 0.5% maximal muscle activity (SD 0.21) in the *hip flexed* condition and 0.6% (SD 0.21) in the *hip neutral* conditions, whereas, for the rectus femoris muscle ($n = 18$), it was 0.5% (SD 0.23) in the *hip flexed* condition and 0.6% (SD 0.21) in the *hip neutral* conditions.

All trials from a single subject are presented in Fig. 2. As can be seen, there was little to no difference in muscle slack angles across both experimental conditions.

The variability of muscle slack angle values within a participant was, on average, 1.7° (SD 1.2) for the *hip flexed* condition and 1.8° (SD 1.2) for the *hip neutral* condition.

Across participants, muscle slack angle was 9.4° [8.1–10.7] (mean [95% confidence interval]) for the *hip flexed* condition and 10.0° [8.6–11.4] for the *hip neutral* condition (Fig. 3). The mean difference between conditions was 0.6° [−0.7 to 1.9]. In terms of individual participants, hip angle had an effect on muscle slack angle in 3 of 19 participants (Table 1).

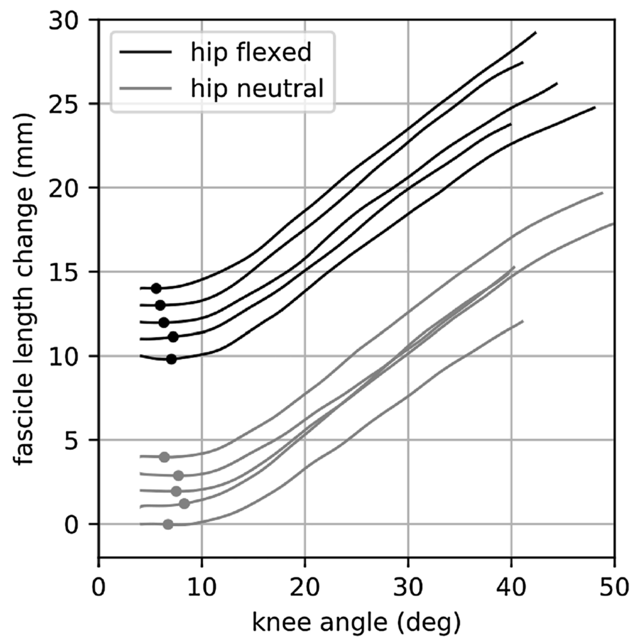

Fig. 2 Raw data from a single subject showing how muscle slack angle was determined. The vertical axis is change in muscle fascicle length, measured from composite ultrasound image sequences. For clarity, initial fascicle lengths have been offset vertically. Muscle slack angle is represented by the knee angle at which fascicle length first starts to increase, indicated by a circle on each trace. Note that the variation in slack angle is minimal

Discussion

The novel approach used in the present study yielded a precise estimate of effects of epimuscular myofascial force transmission between the mono-articular vastus lateralis muscle and neighboring bi-articular structures. In keeping with several previous studies that used different experimental paradigms, the group-level data were indicative of little or no epimuscular myofascial force transmission under passive physiological conditions in humans.

While there was no evidence of a systematic effect (i.e., of an effect averaged across participants) of hip joint angle on muscle slack angle, there was weak evidence of a small, variable and inconsistent effect in 3 of 19 participants. The observed effects were small because the absolute effects were 2°, 3° and 5°, they were variable because hip extension decreased muscle slack angle in two participants and increased muscle slack angle in one participant, and they were inconsistent because they were only detected in 16% of participants. These observations provide only weak evidence of an effect in those individuals because the design

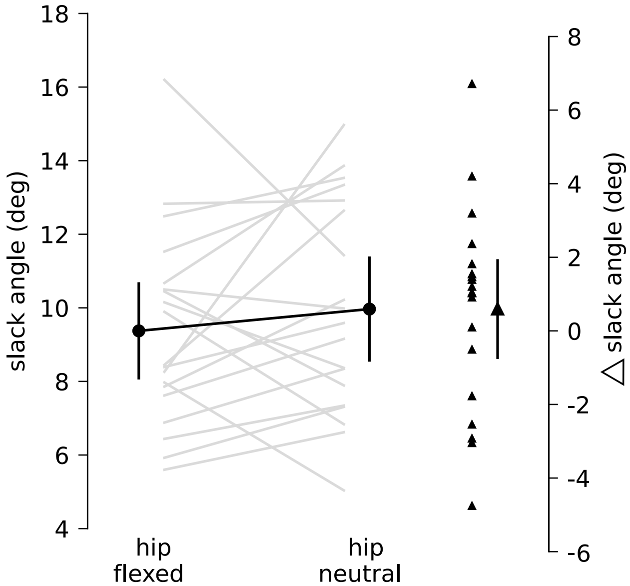

Fig. 3 Effect of hip angle on vastus lateralis muscle slack angle. Mean muscle slack angles for each participant (n = 19, gray lines) for the *hip flexed* (~ 80° hip flexion) and *hip neutral* (~ 0° hip flexion) conditions. The means of participants' means for each condition are also shown (black circles with 95% confidence intervals). Right axis shows difference in muscle slack angles between the *hip flexed* and *hip neutral* conditions. Individual participant differences (small black triangles) are shown, as is the mean difference across participants (black triangle with 95% confidence intervals)

Table 1 Statistical results for participant-level effects of hip angle on muscle slack angle

t-value	*p*-value	Mean difference (°)
5.55	0.0005	4.8
4.58	0.0018	2.9
– 4.40	0.0023	– 1.5

controlled for order effects at the study level (so the estimate of average effect across participants should be unbiased) but did not control for order effects at the level of the individual (so participant-specific estimates of effect could be biased by order effects).

Why might hip position have no systematic effect on the slack length of the vastus lateralis muscle? The vastus lateralis muscle has a proximal tendon that inserts at the base of the greater trochanter and a distal tendon that inserts into the superolateral border of the patella. In addition, the vastus lateralis muscle is known to have as many as three additional discrete attachment sites: the lateral intermuscular septum, the iliotibial band, and the tendon of the rectus femoris muscle (Becker et al. 2010). However, the attachments to the iliotibial band and the tendon of the rectus femoris muscle tendon are small and may not be able to transmit substantial force (Becker et al. 2010). Freitas et al. (2019) hypothesised that, in passive conditions, epimuscular myofascial force transmission may occur in the vastus lateralis muscle only when neighbouring bi-articular structures undergo a large stretch. This is certainly a possibility, and would be consistent with the findings of Ates et al. (2018). They noted that, compared to when the knee was flexed 90°, the shear modulus of the bi-articular lateral gastrocnemius muscle and the proximal aspect of the mono-articular soleus muscle increased when the knee was fully extended and the ankle was near-fully dorsiflexed (10°–20°). Presumably, the stretch imposed on the lateral gastrocnemius muscle generated passive force that was transmitted to the soleus muscle via epimuscular myofascial pathway. However, these muscles share a distal tendon, so they are connected anatomically by other than epimuscular myofascial pathways. Also, a similar effect was not observed in other neighbouring muscles. Thus, there remains some uncertainty regarding the cause of the shear wave modulus changes in the soleus muscle. More recently, Yanase et al. (2021) investigated how extremes of hip range of motion, which impose a greater stretch on the rectus femoris muscle, impact stiffness in the mono-articular vastus medialis and lateralis muscles. While they noted changes in muscle stiffness with changes in hip angle, the muscles were not fully relaxed during the experimental procedures, which may have impacted their measures of muscle stiffness. Regardless, it is uncommon in everyday activity for the hips to be nearly fully extended while the knees are nearly fully flexed. So even if there is systematic epimuscular myofascial force transmission at more extreme joint positions than were tested in the present study, its functional significance is questionable.

Anatomical variation is another factor that may have influenced our results. There may be gross differences between participants, such as the tendon slips from the flexor pollicis longus to the flexor digitorum profundus that are present in at least one hand of ~25% of the population (Linburg and Comstock 1979). There may also be smaller differences between participants, for example, in the thickness and orientation of connective tissue attachments. Finally, there may also be regional variation within muscle and the impact of epimuscular myofascial force transmission on its muscle fibres (Maas and Sandercock 2010). If present, such differences could account for some of the subject-to-subject variability present in our results, as well as the small and variable effect noted in 3 of 19 participants.

In humans, the functional importance of epimuscular myofascial force transmission remains unknown (Bojsen-Moller et al. 2010; Huijing et al. 2011; Ates et al. 2018; Maas 2019). The present results provide additional evidence that the passive force transmitted between the vastus lateralis muscle and neighbouring bi-articular structures is likely small and, in the joint ranges tested here, unlikely to be mechanically important. Our results are consistent with those of Freitas et al. (2019) who conducted a similar experiment using shear-wave elastography. They are also consistent with the results of several studies that found evidence of little or no epimuscular myofascial force transmission under passive conditions in humans (Tian et al. 2012; Carvalhais et al. 2013; Diong et al. 2019, e.g.), but are inconsistent with others where epimuscular myofascial force transmission was also investigated under passive conditions (Bojsen-Moller et al. 2010; Huijing et al. 2011; Ates et al. 2018; Yoshitake et al. 2018, e.g.). However, these comparisons are based on gross, full-muscle epimuscular myofascial force transmission; with our data we cannot exclude the possibility that epimuscular myofascial force transmission caused local sarcomere length changes in vastus lateralis muscle (Tijs et al. 2015; Smilde et al. 2016).

What might explain these divergent findings? First, the methods used to quantify passive epimuscular myofascial force transmission differ between studies. Second, some of the studies reporting the presence of epimuscular myofascial force transmission involved small number of participants (Bojsen-Moller et al. 2010; Huijing et al. 2011; Yaman et al. 2013, e.g. n = 5–7), which, when investigating what are likely small physiological effects, increases the risk of false-positive results and can inflate effect sizes (Ioannidis 2005; Button et al. 2013; Halsey et al. 2015) Third, the muscles investigated tend to differ between studies. For example, we found little to no evidence of epimuscular myofascial force transmission to the vastus lateralis, whereas others have reported 'substantial mechanical interaction' and 'non-negligible intermuscular mechanical interaction' between the mono-articular soleus muscle and the bi-articular gastrocnemius muscles (Bojsen-Moller et al. 2010; Huijing et al. 2011; Ates et al. 2018).

An important next step would be to use the same experimental measure to quantify passive epimuscular myofascial force transmission in two different muscles in the same individuals, focusing on sites where diverging results have been reported. Similarly, it would be important to compare the results obtained from two or more currently used experimental measures (e.g. MRI, shear-wave elastography, ultrasound-based measurements of muscle slack angle) at the same anatomical site in the same individuals. To obtain precise estimates of effects, these studies should involve a substantial number of participants.

Many studies, including this one, have investigated epimuscular myofascial force transmission under passive conditions. However, a few studies have investigated force transmission under active conditions in humans. For example, intra-operative measures obtained in children with cerebral palsy indicate that maximally activating one muscle slightly increases tension in neighbouring muscles (Ates et al. 2014; Kaya et al. 2018). This intriguing observation raises questions about whether the observed epimuscular myofascial force transmission is due to the muscular adaptations or contractures that are often present in children with cerebral palsy (Graham et al. 2021), and whether the results obtained with maximal electrical stimulation of an isolated muscle reflect physiological conditions. For example, it is not usual to have a maximally activated muscle next to a fully relaxed muscle, and epimuscular myofascial force transmission measured under such conditions may not reflect what occurs under physiological conditions. Epimuscular myofascial force transmission in active conditions is an interesting avenue for future research. The challenge will be to do so in a manner than yields physiologically relevant results.

For now, we conclude that epimuscular myofascial force transmission is negligible, and possibly non-existent, in the human vastus lateralis muscle under passive conditions.

Author contributions MEH, HM, REH conceived and designed the study, and MEH and RMW conducted the experiments. MEH and RWM analyzed the data. MEH AND RWM drafted the manuscript. All authors read, edited and approved the manuscript.

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Availability of data and materials The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code Availability The code used during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest/competing interests The authors have no relevant financial or non-financial interests to disclose.

Ethical approval This study was performed in line with the principles of the Declaration of Helsinki, except for registration in a database. Approval was granted by the Human Research Ethics Committee of the University of New South Wales (approval number: HC15006).

Consent to participate Informed consent was obtained from all individual participants included in the study.

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