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Passive and dynamic muscle architecture during transverse loading for gastrocnemius medialis in man

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ABSTRACT

External forces from our environment impose transverse loads on our muscles. Studies in rats have shown that transverse loads result in a decrease in the longitudinal muscle force. Changes in muscle architecture during contraction may contribute to the observed force decrease. The aim of this study was to quantify changes in pennation angle, fascicle dimensions, and muscle thickness during contraction under external transverse load.

Electrical stimuli were elicited to evoke maximal force twitches in the right calf muscles of humans. Trials were conducted with transverse loads of 2, 4.5, and 10 kg. An ultrasound probe was placed on the medial gastrocnemius in line with the transverse load to quantify muscle characteristics during muscle twitches.

Maximum twitch force decreased with increased transverse muscle loading. The 2, 4.5, and 10 kg of transverse load showed a 9, 13, and 16% decrease in longitudinal force, respectively. Within the field of view of the ultrasound images, and thus directly beneath the external load, loading of the muscle resulted in a decrease in the muscle thickness and pennation angle, with higher loads causing greater decreases. During twitches the muscle transiently increased in thickness and pennation angle, as did fascicle thickness. Higher transverse loads showed a reduced increase in muscle thickness. Smaller increases in pennation angle and fascicle thickness strain also occurred with higher transverse loads.

This study shows that increased transverse loading caused a decrease in ankle moment, muscle thickness, and pennation angle, as well as transverse deformation of the fascicles.

1. Introduction

During muscle contractions, muscle architecture undergoes transient changes (Narici et al., 1996; Maganaris et al., 1998), and such changes have been shown to be influenced by external compression generated by compression bandages (Wakeling et al., 2013). Unidirectional transverse loading of rat muscle causes a decrease in muscle force during contraction (Siebert et al., 2014a, 2016), however, the mechanisms involved are not fully understood. This study aimed to characterise the changes in architecture that occur with transverse loading, and its relation to reductions in muscle force.

Magnetic resonance imaging (MRI) is able to provide detailed images of muscle shape, position, and volume in vivo, however due to the long acquisition times this method is most suitable for passive and prolonged low-level contractions (Kawakami et al., 1995; Finni et al., 2003; Lansdown et al., 2007; Infantolino et al., 2012; Schenk et al., 2013; Bolsterlee et al., 2015). The imaging of muscle architecture is possible in passive and contracting muscle using ultrasound, with negligible acquisition times (Herbert and Gandevia, 1995; Narici et al., 1996; Maganaris et al., 1998; Rana and Wakeling, 2011, 2013; Wakeling and Randhawa, 2014), and changes in muscle thickness, pennation angle, fascicle length, and fascicle thickness have been measured.

Many studies into the behaviour of muscle contraction have been done in isolated muscle or muscle fibres (Hill, 1938; Gordon et al., 1966). However, external compression from either adjacent muscles and tissues, or loads external to the body can change the contractile behaviour of muscle (Reinhardt et al., 2016; Wick et al., 2018; Fontana et al., 2018). For instance the medial and lateral gastrocnemius and soleus muscles of the triceps surae contract synergistically to perform ankle plantarflexion. Although these muscles are activated separately, they are in apposition and so bulging of one of these muscles may lead to

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compression in the others: muscles undergo very limited volume changes during contraction (Abbott and Baskin, 1962; Baskin and Paolini, 1967) and are thus nearly isovolumetric and as a result will bulge when they contract. The bulging of one muscle into another will result in transverse loads on these muscles (Reinhardt et al., 2016). Furthermore, tight packing of muscles in muscle packages leads to transverse forces in between muscles influencing muscle shape and architecture (Wick et al., 2018). This is not the only way in which muscles can undergo transverse loading. With many of our muscles having a superficial placement in our body, our surroundings are also able to cause transverse loads on our muscles, for instance in our gluteal muscles when we sit.

When transverse loads are applied to a muscle, they can change the muscle architecture and forces developed by the muscle belly. In isolated rat muscle (Siebert et al., 2014a), the force production in the longitudinal direction decreased as transverse load was increased. In humans, compression bandages applied to the leg reduced the muscle thickness and pennation angle, and resulted in longer fascicles during contraction (Wakeling et al., 2013). In leopard frogs, rigid tubes that prevented transverse expansion of the muscle resulted in reduced external work done during contraction (Azizi et al., 2017).

It is important to understand how transverse and longitudinal forces can be linked to each other because it has been shown that changes in the former result in changes in the latter. An important feature of muscle to consider is that muscle is made up of around 80% water (Van Loocke et al., 2008). The combination of a near isovolumetric muscle filled with fluid allows for pressure changes in the muscle. These changes can have a big influence on the forces throughout the muscle and influence the shape of the muscle. To study the significance of intramuscular fluid, fluid volumes were manipulated in bullfrog muscle and a sleeve fitted bladder (Sleboda and Roberts, 2017). Increases in fluid volume showed an increase in passive force in both muscle and bladder. This showed that internal fluid and muscle structure interact to influence muscle shape changes. As fibres contract, their longitudinal forces act to shorten them. The pressure changes within the fibre translate shortening to transverse expansion. Transverse expansion will result in rotation of the fascicles to a higher pennation angle. Thus, observing the fibre deformations provides an opportunity to examine the mechanisms that link transverse and longitudinal forces and deformations.

Previous studies have shown that transverse loads reduce muscle force in isolated single muscle experiments. The aim of this study was to determine the changes in human muscle architecture resulting from transverse load and how they relate to force reduction. We hypothesize that transverse loading will cause a significant flattening of the muscle and this results in changes in pennation angle, fascicle length, and thickness. Furthermore, greater changes will be seen with greater transverse loads.

2. Materials and methods

Twenty-nine healthy young adults participated in this study (age 25 ± 5 yrs, body height 181.0 ± 7.4 cm, body mass 76.5 ± 9.4 kg). All participants gave informed consent before taking part in the study. The study was conducted in accordance to the latest declaration of Helsinki. Ethical approval for the study was received from Simon Fraser University, Canada, and the ethical committee of the university hospital of Tuebingen, Germany.

Before testing, participants were asked to warm up by running on a treadmill for 5 min, perform 3 sets of 10 repetitions of calf raises and 10 calf jumps. Participants lay prone on a platform with their right foot flat on the force plate with toes pointing straight down (Fig. 1). Two self-adhesive electrodes were placed on the lower leg: the anode was fixed in the popliteal fossa and the cathode about 2 cm proximal to the patella.

Electrical stimuli were elicited in the posterior tibialis nerve, to evoke maximal force twitches in the triceps surae muscles of the right leg using a current stimulator (DS7AH Digitimer, Herfordshire, UK). To find maximum twitch force (MTF), the current was slowly ramped up, starting at 5 mA, until twitch force plateaued. Stimuli were administered as double-twitches (i.e., 2 consecutive stimuli with an interstimuli interval of 10 ms).

An unloaded set of pretest and posttest twitches were delivered. A force plate (Type 9260 AA3, Kistler Instrumente AG, Winterthur, Switzerland) was used to measure MTF (Fig. 1a). If the posttest forces were within 5% of the pretest forces we assumed no changes to the experimental design occurred and that fatigue was minimal during testing, and the collected data were taken to be valid. No ultrasound data were collected during the unloaded trials because the ultrasound probe and the attached equipment already placed 0.92 kg of load on the muscle and so the measured forces would not have reflected unconstrained twitch forces.

Three trials with five twitches per trial were conducted for each participant, with transverse loads of 2, 4.5, and 10 kg presented in a random order. Transverse loading was achieved by placing a rod in line with gravity inside a frame to maintain its vertical alignment. A plate was positioned at the upper end of the rod (Fig. 1b) and was loaded with weights to get the desired transverse load. The lower end of the rod was affixed to a block (34 × 100 mm) (Fig. 1c) that was used to transfer the transverse load from the rod to the muscle.

A linear ultrasound probe (Echoblaster 128, Telemed, Lithuania) was placed on the right medial gastrocnemius (MG) in line with the transverse load by placing the probe inside the block on the lower end of the rod. The probe and transverse load were positioned medial to the midline of the lower leg. The subject was slightly rotated using supports so that the vertical probe compressed rather than displaced the MG, imaged the muscle belly close to its optimal location (Bolsterlee et al., 2016) and was aligned with the fascicles parallel to the scanning plane. This gave continuous, quantitative data on muscle architecture throughout muscle twitches. Ultrasound videos (604 × 515 pixels; 80 Hz) were collected from the ultrasound system, providing a 65 mm field of view with a 50 mm scanning depth. The superficial and deep aponeuroses of the MG were manually traced. A second order polynomial was fitted to the traces and eroded by 10 pixels. This allowed a region of interest for the muscle belly to be isolated. A straight midline between the aponeuroses was taken as the line of action of the muscle. The muscle thickness was the mean distance between the aponeuroses in the direction perpendicular to the midline of the muscle.

A multi-scale vessel enhancement filter (Frangi et al., 1998) enhanced fascicles with high vesselness, and supressed blob-like elements (Rana et al., 2009), and a Hough transform identified line segments from the fascicles. The angle of the midline of the muscle and the mean angle of the fascicle lines were used to calculate the mean pennation angle. A 2D-Discrete Fourier transform was applied to the filtered region of interest to find the transverse wavelength across the muscle fascicles (Wakeling and Randhawa, 2014). Stripes in the ultrasound images are considered to lie in the same direction as the muscle fascicles. As the fascicles dilate, the spacing of these stripes gets wider; thus their transverse wavelength is proportional to the fascicle width. Fascicle lengths were approximated by

$$l_f = \frac{T_m}{\sin\alpha} \tag{1}$$

where l_f is fascicle length, T_m is muscle thickness, and α is pennation angle.

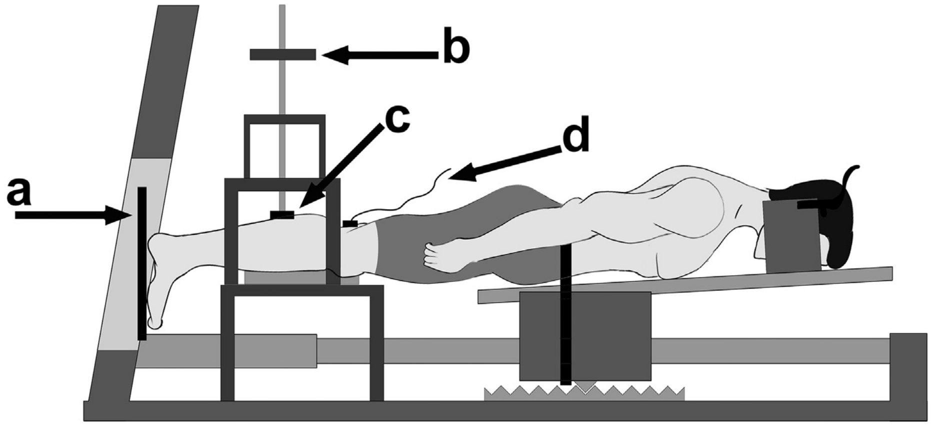

Fig. 1. Schematic of the experimental design. Showing the position of the force plate (a) and the point at which load was added (b). The point of contact between the gastrocnemius and the transversal load is at the same position that the ultrasound probe was positioned (c). The calf muscles of the participants were stimulated in the popliteal fossa with a current stimulator (d).

Pennation angle, muscle belly thickness, muscle fascicle thickness, and fascicle length were quantified for the initial testing state (100 ms before each muscle twitch), and for the value that showed the largest deviation from the initial state during each twitch. All data are presented as mean ± standard deviations (Table 1). The data were tested using a one-way ANOVA for repeated measures, with a post-hoc Bonferroni test, to see if significant differences existed between the different loading trials. Tests were considered significant when $p < 0.05$. All statistical analyses were performed using IBM SPSS Statistics for macOS (Version 25 IBM Corp., Armonk, NY).

3. Results

Electrical stimulation caused the MG to twitch, peaking after about 60 ms, and this caused a transient increase in force on the force plate (Fig. 3G). The ultrasound images showed that during each twitch the muscle fascicles underwent transient shortening, coupled with a transient increase in thickness and pennation angle; the muscle belly also increased in thickness during each twitch.

Mean MTF for the unloaded pretests and posttests showed no significant differences between each other (Fig. 2). MTF decreased with increased transverse loading. The 2, 4.5, and 10 kg trials showed twitch forces of 147.4 ± 7.5, 141.8 ± 7.4, and 136.1 ± 7.2 N, respectively. Compared to unloaded values this equates to decreases of 9, 13, and 16%, respectively. The twitch forces for the loaded trials were significantly different from the pretest and the posttest values, and all loaded trials were found to be significantly different from each other (Fig. 2).

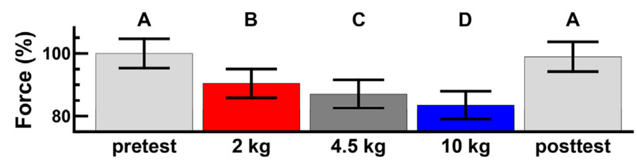

Fig. 2. Mean maximum twitch forces (MTF; mean ± SE), for each trial, given as percentage of pretest twitch force. Statistics showed no significant differences between pretest and posttest force. The forces for each loaded trial were significantly different from one and other as well as from the pre- and posttest. Means with different letters are significantly different ($p < 0.001$).

When the transverse loads were applied to the muscle the initial muscle thickness and pennation angle both decreased with this decrease being greater at higher loads. As the muscle contracted with the applied loads there were reduced increases in pennation angle (Fig. 3A), muscle thickness (Fig. 3C), and fascicle thickness (Fig. 3E) during each twitch with increasing load. There was no significant effect of the transverse load on the initial fascicle length

Table 1
The values (mean ± SE) for each trial of the measured muscle architecture. The values are given for muscle at rest (passive), at peak active contraction (active), and the change that have occurred. Significant differences between trials are given († – sign. differences between 2 kg and 4.5 kg, ‡ – sign. differences between 4.5 kg and 10 kg, + – sign. differences between 2 kg and 10 kg). The transverse wavelength corresponds to fascicle thickness.

	2 kg	4.5 kg	10 kg	Significance
Pennation angle (°)	n = 155	n = 149	n = 152	
Passive	11.9 ± 3.3	11.0 ± 3.2	10.3 ± 2.9	†, +
Active	18.3 ± 3.1	16.7 ± 3.6	14.2 ± 3.3	†, +, ‡
Change	6.3 ± 2.4	5.8 ± 2.1	3.9 ± 2.2	†, +, ‡
Muscle thickness (mm)	n = 159	n = 156	n = 153	
Passive	13.4 ± 3.4	12.7 ± 3.6	12.2 ± 3.6	†, +
Active	18.9 ± 5.7	18.0 ± 5.5	15.8 ± 4.6	†, +, ‡
Change	5.5 ± 3.2	5.2 ± 2.9	3.7 ± 1.8	+, ‡
Transverse wavelength (mm)	n = 157	n = 156	n = 153	
Passive	1.2 ± 0.07	1.2 ± 0.07	1.2 ± 0.07	
Active	1.5 ± 0.4	1.3 ± 0.1	1.3 ± 0.2	†, +
Change	0.3 ± 0.4	0.1 ± 0.1	0.1 ± 0.1	†, +
Fascicle length (mm)	n = 156	n = 149	n = 152	
Passive	65.4 ± 12.1	68.1 ± 13.6	71.9 ± 36.7	
Active	52.2 ± 5.5	56.3 ± 4.9	58.1 ± 7.0	†, +, ‡
Change	−13.2 ± 12.1	−11.8 ± 12.7	−13.8 ± 32.0	

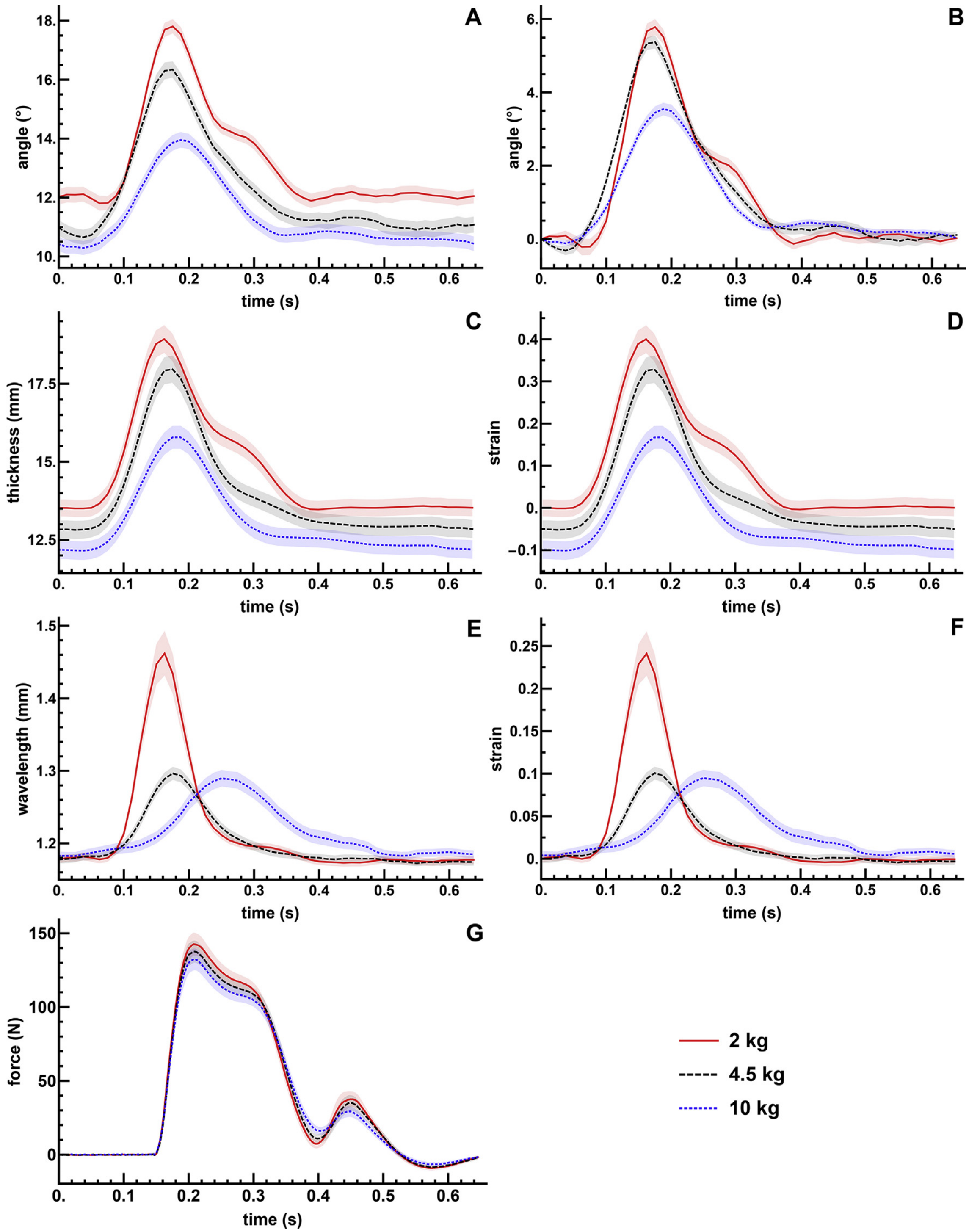

Fig. 3. Changes in muscle architecture induced by transverse muscle loading. Absolute values for pennation angle (A), muscle thickness (C), and transverse wavelength (E) as well as corresponding changes in pennation angle (B) and strains for muscle thickness (D) and transverse wavelength (F). Twitch force is presented in (G). Note that, the transverse strain of wavelengths corresponds to the transverse strain of the fascicles. The graphs show the mean of all participants with standard errors for the 2 (red), 4.5 (black), and 10 kg (blue) trials. Muscle thickness and transverse wavelength changes were scaled to the 2 kg trials. Higher transverse loads show lower absolute values both for passive values and during contraction. The changes in transverse wavelength were interpreted as fascicle thickness strains. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Fig. 4) or thickness (Fig. 3E, F). Trials with the highest transverse load (10 kg) showed the smallest increases in muscle thickness (Fig. 3D) and pennation angle (Fig. 3B) during each twitch. The extent and significance of these effects is shown in Table 1. A representation of the individual measured values are shown in Fig. 5 for the three main measurements (muscle thickness (Fig. 5A), pennation angle (Fig. 5B), and wavelength (Fig. 5C)).

4. Discussion

Transverse loading has an observable effect on muscle deformation and contraction dynamics. Reduced increases in muscle thickness (Fig. 3C, D) showed that the transverse loading restricted the muscle from bulging under the applied load during contraction. Likewise, the transverse load limited the increases in the pennation

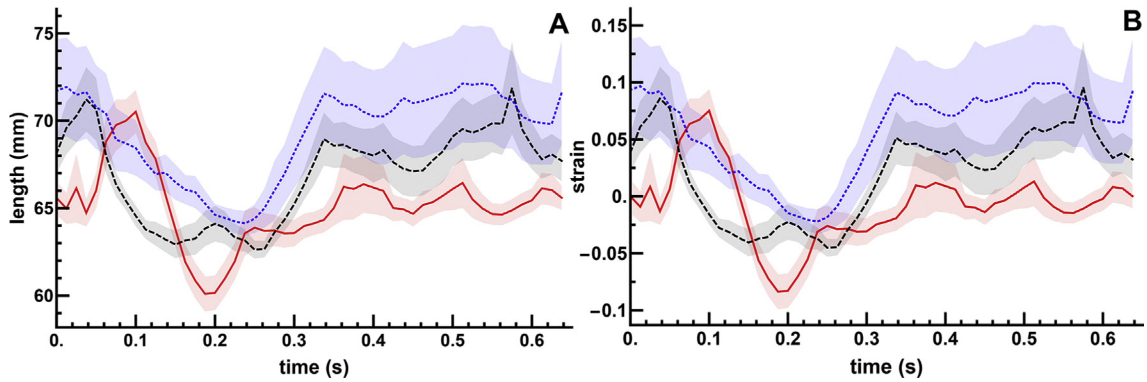

Fig. 4. Fascicle lengths (A) and fascicle length changes (B) during contraction for the 2 (red), 4.5 (black), and 10 kg (blue) trials (mean ± SE). The changes were scaled to the 2 kg trials. Fascicle length was calculated as a function of pennation angle and muscle thickness. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

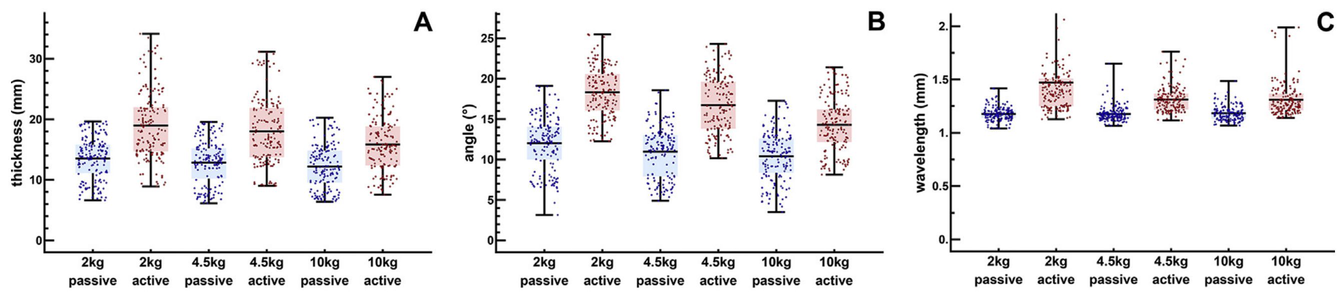

Fig. 5. Measured values for muscle thickness (A), pennation angle (B), and wavelength (C) for individual measurements. The values are given for muscle at rest (blue), and at peak active contraction (red). The box plots show the mean with 25 and 75% quantiles with the whiskers showing the minimum and maximum values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

angle (Fig. 3A, B). These findings were mirrored at the fascicle level where the smallest transverse expansion concurred with the greatest transverse load (Fig. 3E, F).

Plantarflexion force was measured for twitches at MTF. As a result of transverse loading MTF decreased, and increases in transverse load resulted in a greater decrease (Fig. 3G). These findings are consistent with studies done on rat gastrocnemius muscle (Siebert et al., 2014a) where maximum isometric contractions showed a decrease in force between 4.8% and 12.8% for lowest to highest transverse load, respectively. Comparatively, our study found decreases in MTF between 9% and 16% for lowest to highest transverse load, respectively. Both studies match up well, albeit that our study found higher decreases in force. Although different contraction types were used (supramaximal stimulation vs. double-twitch stimulation), the durations of contraction were similar (300 ms in rat; 250 ms in man). Furthermore, the transverse pressures applied were of similar magnitude (1.3–5.3 N cm^{-2} in rat; 0.6–2.9 N cm^{-2} in man).

Due to volumetric constraints muscle fascicles expand in girth when they shorten in length, however transverse deformations in a contracting muscle can be anisotropic (Rahemi et al., 2014; Randhawa and Wakeling, 2018), in part due to asymmetries in the stress through the muscle that would be affected by the transverse loads applied in this study. Furthermore, the local deformations in the muscle belly within the field of view of the ultrasound image should not be expected to be representative to all regions of the muscle or to all directions. To create space for the fascicles to expand they need to rotate to a higher pennation angle (Herbert and Gandevia, 1995). Rotation to a higher pennation angle can result in an increase in muscle thickness, depending on the amount of fascicle shortening. This explanation is consistent with the increases in muscle thickness that were measured in this study. The transverse load has a large component in line with fascicle thickness, and even more so as higher loads decrease pennation angles. Therefore, it is probable that transverse load restricts the expansion in fascicle thickness, with higher loads imposing greater restrictions. The restriction in muscle thickness expansion will lead to smaller changes in pennation angle, as is shown in this study. In turn, muscle thickness will also be restricted in how much it can change, which is also shown in this study.

When transverse load was applied to the passive muscle the pennation angle decreased to between 10.5 and 12.1 degrees (Fig. 3A). These pennation angles are less than those reported for the unloaded MG (17.3–22.3 degrees) (Narici et al., 1996; Maganaris et al., 1998), and so the reduced pennation angle in the initial inactive state here is consistent with reductions in pennation angle due to transverse load. Pennation angles can increase by 18–20 degrees during a maximal isometric contraction for the MG (Narici et al., 1996; Maganaris et al., 1998). However, this study utilized twitches that would not reach a full activation state and so we would expect more modest increases in pennation angle: and the increases in pennation angle of 4–6 degrees are in accordance with this. The initial fascicle lengths for the loaded states in this study (mean of 68 mm) were longer than resting fascicle lengths from previous studies of 45 mm (Maganaris et al., 1998; knee angle of 90 degrees), and 57 mm (Narici et al., 1996; extended knee), suggesting that the transverse load caused a lengthening of the fascicles (Table 1) in addition to a reduction in the pennation angle.

We suggest that it is unlikely that the changes to fascicle length and pennation angle are responsible for the decreases in the muscle twitch force with transverse loading *per se*. The transverse load causes the pennation angle to decrease and the fascicles to lengthen. The decreases in pennation angle would increase the component of (longitudinal) fascicle force in the line of action in the muscle, and this would actually counter any decreases in muscle twitch force. The increases in fascicle length would extend the fascicles down the descending limb of their force-length relationship for their initial states (Maganaris, 2003; Kawakami and Fukunaga, 2006); so the muscle twitches would consequently shorten the fascicles to be closer to their optimal length, this would tend to increase the muscle force and thus counter the reductions resulting from the transverse load. Instead, it is possible that the reductions in muscle force are due to transverse mechanisms working within the muscle.

Intramuscular pressure within muscle increases during contraction, and has been reported in the range of 100–300 mm Hg in frog gastrocnemius (Hill, 1948), and similar pressures should be found in muscles across size ranges provided they share similar shape and intrinsic strength (Hill, 1948). Indeed, intramuscular pressures, at maximum voluntary contraction, of 200 mm Hg and 225 mm Hg have been reported for the tibialis anterior and soleus in man, respectively (Aratow et al., 1993; Ateş et al., 2018). Based on the contact area of the indenter, the pressures exerted by the transverse load in this study ranged from 43 to 218 mm Hg, and so span the range of expected intramuscular pressures. There would thus be sufficient intramuscular pressure generated during the contraction to lift the transverse load, and this is seen by the increases in muscle thickness during the twitches.

A combination of experimental and modelling work has shown a link between longitudinal and transverse forces during muscle contraction (Siebert et al., 2014b, 2018). A Hill-type model was adapted to include an external mass, and a spring-damper component (Siebert et al., 2014b). The external mass represented the transverse load on the muscle, and the spring-damper was used to represent the viscoelastic properties of the muscle tissue. An energy balance was used to link the work of the contractile component and energy in the series elastic component with the work done through the lifting of the mass and the deformation of the spring-damper. By doing so the model was able to replicate reductions in muscle force and increases in muscle thickness found in both previous observations (Siebert et al., 2014a) and our study. These ideas parallel a recent model of dynamic muscle contractions in which the energy state within the muscle is made up of kinetic, volumetric, base material, and contractile components (Ross et al., 2018). Transverse deformation of the muscle results in strain energy within the base material and this base material and the volumetric components (from the intramuscular fluid) redistribute the forces across all three-dimensions. Thus, transverse work done against the volumetric and base material components and to lift the transverse load result in a reduction of the work that can be done in the line-of-action of the muscle belly.

The nerve stimulation excited several muscles in the lower leg. A maximal stimulus intensity was selected that achieved maximum twitch torque, where higher intensities resulted in decreased torque due to co-contractions. This study applied pressure and reported the architectural changes in one localized region of the lower leg, the MG; however, adjacent muscles that were not tested may impinge on and influence each other and the net joint torque (Fontana et al., 2018).

The subject rotation and ultrasound probe placement were set to provide the clearest views of the fascicles within the muscle belly. Probe misalignments cause only minor errors in the estimation of pennation angle for the MG (Rana et al., 2013), however, the compression from the probe resulted in lower pennation and longer fascicle lengths than in unloaded muscle Narici et al., 1996; Maganaris et al., 1998). These lower pennations increase the extent to which fascicles extend beyond the scanned images, and so their length must be obtained by extrapolation and are more sensitive to errors. Nonetheless, changes in fascicle length were observed during the twitches and between compressive loads, however the additional variability in the length measurements contributed to the lack of significant differences being found for the fascicle lengths between conditions.

In this study, we have shown that transverse loading has an effect on human MG contraction. We have shown that greater transverse loads result in lower contraction force, as well as changes in muscle architecture. However, architectural changes cannot completely explain muscle force reduction and it seems that intramuscular pressure and internal work play a significant role in muscle shape and force production. Thus, analysis of intramuscular pressure in relation to muscle architecture might lead to a better understanding of the effects of transverse loading and muscle forces in general.

Conflict of interest statement

The authors have no conflicts of interest to disclose.

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