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Lilian Lacourpaille, Antoine Nordez, François Hug. The nervous system does not compensate for an acute change in the balance of passive force between synergist muscles. *Journal of Experimental Biology*, 2017, 220 (Pt19), pp.3455-63. 10.1242/jeb.163303 . hal-03347462

HAL Id: hal-03347462

<https://hal.science/hal-03347462>

Submitted on 30 Aug 2023

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The nervous system does not compensate for an acute change in the balance of passive force between synergist muscles

Lilian Lacourpaille¹, Antoine Nordez^{1,2} and François Hug^{1,3,4,*}

ABSTRACT

It is unclear how muscle activation strategies adapt to differential acute changes in the biomechanical characteristics between synergist muscles. This issue is fundamental to understanding the control of almost every joint in the body. The aim of this human experiment was to determine whether the relative activation of the heads of the triceps surae [gastrocnemius medialis (GM), gastrocnemius lateralis (GL) and soleus (SOL)] compensates for differential changes in passive force between these muscles. Twenty-four participants performed isometric ankle plantarflexion at 20 N m and 20% of the active torque measured during a maximal contraction, at three ankle angles (30 deg of plantarflexion, 0 and 25 deg of dorsiflexion; knee fully extended). Myoelectric activity (electromyography, EMG) provided an index of neural drive. Muscle shear modulus (elastography) provided an index of muscle force. Passive dorsiflexion induced a much larger increase in passive shear modulus for GM (+657.6±257.7%) than for GL (+488.7±257.9%) and SOL (+106.6±93.0%). However, the neural drive during submaximal tasks did not compensate for this change in the balance of the passive force. Instead, when considering the contraction at 20% MVC, GL root mean square (RMS) EMG was reduced at both 0 deg (−39.4±34.5%) and 25 deg dorsiflexion (−20.6±58.6%) compared with 30 deg plantarflexion, while GM and SOL RMS EMG did not change. As a result, the GM/GL ratio of shear modulus was higher at 0 deg and 25 deg dorsiflexion than at 30 deg plantarflexion, indicating that the greater the dorsiflexion angle, the stronger the bias of force to GM compared with GL. The magnitude of this change in force balance varied greatly between participants.

KEY WORDS: Electromyography, Elastography, Shear modulus, Plantar flexors

INTRODUCTION

The torque produced by a muscle results from the interplay between its activation by the nervous system and several biomechanical characteristics such as its moment arm, physiological cross-sectional area, force–length and force–velocity relationships, specific tension and passive force. When multiple muscles act on a single joint, the nature of the relationship between the distribution

of activation among the synergist muscles and their biomechanical characteristics is largely unknown. This issue is fundamental to understanding how the nervous system coordinates the activation of synergist muscles, which is necessary to understand the control of almost every joint in the body.

There is some evidence that muscle activation is biased by muscle torque-generating capacity (Hudson et al., 2009; Hug et al., 2015b). In a population of healthy participants, Hug et al. (2015b) showed that the greater the physiological cross-sectional area of the lateral head of the quadriceps (vastus lateralis) compared with that of the medial head (vastus medialis), the stronger the bias of activation to the vastus lateralis. However, it remains unclear how muscle coordination strategies adapt to differential acute changes in the mechanical properties of individual synergist muscles. When the force-generating capacity of one synergist muscle is acutely reduced (through isolated electrically induced damage to this muscle), no systematic redistribution of activation between this muscle and its synergists is observed (Bouillard et al., 2014; de Rugy et al., 2012). This may be because of: (i) the relative difficulty of disassociating the activation of the quadriceps muscles in Bouillard et al. (2014) and the forearm muscles in De Rugy et al. (2012), and (ii) a testing period that was too short to observe an adaptation to a selective decreased force-generating capacity of one muscle that could be considered as a non-physiological situation.

The triceps surae muscle group, which is pivotal for functional tasks such as walking (Neptune et al., 2001; Sutherland, 1966), is an ideal model to understand how muscle activation adapts to differential changes in mechanical characteristics between synergist muscles. First, the three heads of the triceps surae can be independently controlled (Duysens et al., 1996; Nardone and Schieppati, 1988). For example, when isometric activation of knee extensors is added to voluntary isometric plantar flexion, a decreased gastrocnemius medialis (GM) activation and increased soleus (SOL) activation is observed, while gastrocnemius lateralis (GL) activation does not change (Suzuki et al., 2014). Second, the three heads of the triceps surae exhibit differential changes in passive mechanical characteristics during passive dorsiflexion. Taking advantage of elastography, our group (Le Sant et al., 2017) and others (Hirata et al., 2015) have shown that passive dorsiflexion induces a much larger increase in shear modulus (stiffness) of GM than GL and SOL when the knee is fully extended. As a strong linear relationship exists between muscle shear modulus and muscle force (Bouillard et al., 2011; Hug et al., 2015a; Maïsetti et al., 2012) and because GM cross-sectional area is 2 times larger than that of GL (Fukunaga et al., 1996), these results provide strong evidence that ankle dorsiflexion induces a much larger increase in GM passive force than in GL passive force. It is unknown whether this change in passive force balance is compensated by a change in activation or by a change of the active force-generating capacity of the muscles, due to the muscles operating over different regions of their force–length curve. In such a case, the same distribution of force between GM

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DOI: 10.1002/0002-6432-558X

and GL would be used during contraction, regardless of ankle angle. This maintenance of the same force-sharing strategy over the full range of ankle angles would aim to maintain similar deformation of the Achilles tendon (Magnusson et al., 2003) into which the three muscle heads are inserted.

The aim of this study was to determine how the relative activation of the three heads of the triceps surae (GM, GL and SOL) during submaximal contractions adapts to differential changes in passive mechanical properties between these muscles. These changes in passive properties were induced by modifying the ankle angle. Muscle activation was assessed using surface electromyography (EMG) and we used elastography to estimate an index of change in individual muscle force (Hug et al., 2015a). The advantage of elastography is the ability to account for both passive and active muscle force, allowing us to provide an accurate index of change in force sharing as a function of ankle angle. We hypothesized that the distribution of neural drive would be modified to maintain the force balance between muscles such that the ratio of shear modulus between GM and GL would be unchanged across ankle angles.

MATERIALS AND METHODS

Participants

Twenty-four young healthy volunteers (12 males and 12 females; Table 1) participated in this study. This sample size was chosen to ensure adequate power (0.80) for the main outcomes. Participants had no history of ankle injury that had limited function or required them to seek intervention from a health care professional. Participants provided informed written consent. The experimental procedures were approved by the local ethics committee (Rennes Ouest V – CPP-MIP-010) and all procedures adhered to the declaration of Helsinki.

Measurements

Experimental set-up

Participants were positioned lying prone (hip and knee fully extended) on a Con-Trex® isokinetic dynamometer (CMV AG, Dübendorf, Switzerland). The ankle of the dominant leg (the leg used to kick a ball) was fixed to the dynamometer’s accessory with non-compliant straps. All mechanical signals were collected at 1000 samples s⁻¹ with an analog/digital converter (ADInstruments, Colorado Springs, CO, USA).

Surface electromyography

Myoelectrical activity was recorded from the test leg with surface EMG electrodes placed over the GM, GL and SOL. For each muscle, a pair of self-adhesive Ag/AgCl electrodes (Kendall Medi-Trace™, Mansfield, MA, USA) was attached to the skin with an inter-electrode distance of 20 mm (centre-to-centre). B-mode ultrasound (v6.0, Aixplorer, Supersonic Imagine, Aix-en-Provence, France) was used to facilitate placement of the electrodes

longitudinally with respect to the muscle fascicle alignment, away from the borders of the neighbouring muscles (position of the electrodes is shown in Fig. 1). Prior to electrode application, the skin was shaved and cleaned with alcohol. Raw EMG data were amplified 1000 times, band-pass filtered between 10 Hz and 500 Hz and sampled at 5000 samples s⁻¹ (MP36, Biopac, Goleta, CA, USA). Mechanical and EMG data were synchronized using transistor-transistor logic pulses.

Shear wave elastography

An Aixplorer ultrasound scanner (v6.0, Supersonic Imagine) coupled with a linear transducer array (2–10 MHz, SuperLinear 10-2, Vermon, Tours, France) was used in shear wave elastography mode (musculoskeletal preset). This technique provides a 2D map of shear modulus (index of stiffness) at 1 sample s⁻¹ (Fig. 1). The optimal ultrasound transducer location and orientation was determined such that several fascicles could be observed. For SOL, the ultrasound probe was placed over the distal aspect of the GL (Fig. 1). These locations were marked on the skin using a waterproof marker so that the transducer location remained constant for all the measurements for each participant. Because there is a strong linear relationship between muscle shear modulus and muscle force, we considered changes in shear modulus as an index of changes in muscle force (reviewed in Hug et al., 2015a). Note that this technique has very good reliability when measuring shear modulus of both superficial and deep muscles (Dieterich et al., 2017), at rest and during contraction.

B-mode ultrasound

The aforementioned ultrasound scanner was used in B-mode to measure the thickness of each plantar flexor muscle. The measurement site was defined as the thickest muscle region after moving the ultrasound transducer slowly along the midline of each muscle belly in a transverse orientation (Hodges et al., 2003; Reeves et al., 2004). This was repeated twice, and the maximum thickness that was recorded with either sweep was used for further analysis.

Protocol

After a standardized warm-up, participants underwent five slow (10 deg s⁻¹) passive loading/unloading cycles between 15 deg of plantarflexion and 15 deg of dorsiflexion to account for the possible effect of conditioning (Nordez et al., 2008). Immediately after, a series of measurements was performed at three ankle angles in a random order [30 deg of plantarflexion (PF 30 deg), 0 deg and 25 deg of dorsiflexion (DF 25 deg)]. A constant 1 min period was kept between ankle positioning and the start of the elastography measurements to account for any potential stretch-relaxation effects. At each ankle angle, the passive shear modulus was first measured twice for each muscle (GM, GL and SOL; in a random order) while the participants were instructed to remain as relaxed as possible. Then, two maximal isometric voluntary plantarflexions were performed. Each maximal voluntary contraction (MVC) was maintained for 3 s and separated by 120 s rest. The experimental task involved matching two target net plantarflexion torque levels during short (10 s) isometric plantarflexion using a visual feedback displayed on a monitor placed in front of the participants. The first target torque was set at 20% of the MVC torque achieved at the tested ankle angle. This ensures the same relative effort across ankle angles. However, because MVC torque increases with dorsiflexion, the absolute target torque differed between ankle angles. To account for this possible confounding factor, a second target torque was set at 20 N m, such that the same absolute torque was produced at the

Table 1. Participants (n=24)

	Mean±s.d.
Age (years)	23.8±4.0
Sex (males/females)	12/12
Height (cm)	172.6±10.2
Body mass (kg)	67.7±12.8
MVC at PF 30 deg (N m)	47.5±16.5
MVC at 0 deg (N m)	109.4±49.3
MVC at DF 25 deg (N m)	142.1±78.3

MVC, maximal voluntary contraction, measured at 30 deg of plantarflexion (PF 30 deg), 0 deg and 25 deg of dorsiflexion (DF 25 deg).

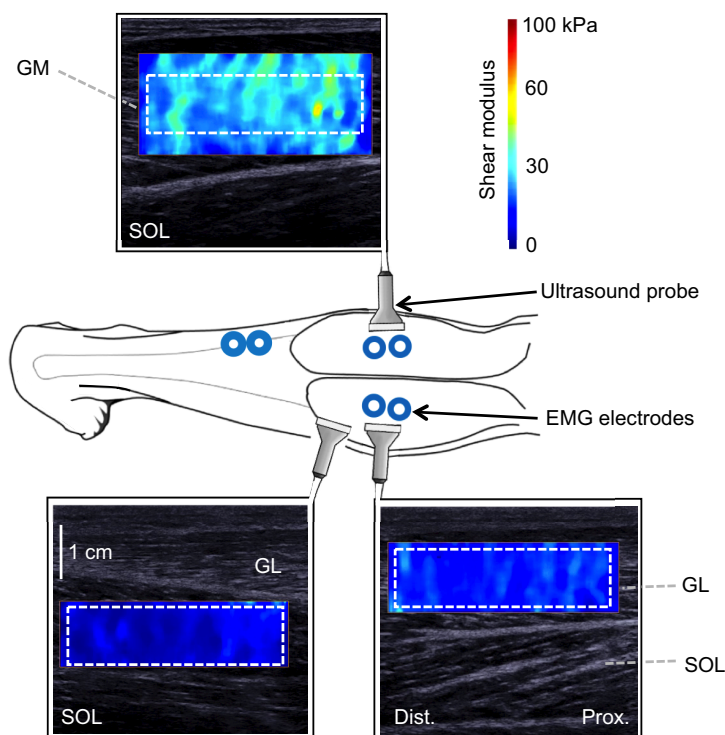


Fig. 1. Schematic representation of electromyography (EMG) electrodes and ultrasound probe positioning on the plantar flexor muscles. A map of shear elastic modulus (i.e. index of stiffness) is superposed onto the B-mode image, with the colour scale depicting graduation of shear elastic modulus (scale in kPa, blue being soft and red being stiff). To obtain a representative value, the shear modulus was averaged over the region of interest (outlined by white dashed lines). Dist., distal; Prox., proximal; GM, gastrocnemius medialis; GL, gastrocnemius lateralis; SOL, soleus.

three ankle angles. The order of the conditions was randomized. During each force-matched submaximal contraction, either myoelectrical activity or shear modulus of the GM, GL and SOL was measured. Note that because elastography measurements induced noise within the EMG signal, there were no elastography measurements performed when myoelectrical activity was recorded. Each of these measurements was performed twice, such that 16 contractions were performed per ankle angle with 30 s rest between each repetition. Measurements and contraction intensities were performed in a random order. At the end of the protocol, a smooth linear torque ramp from 0 to 50% of MVC over 10 s was also performed at 0 deg for another purpose; data are not presented here.

Data analysis

All torque, EMG and elastography data were processed using Matlab (The Mathworks, Natick, MA, USA).

Plantarflexion torque

Plantarflexion MVC torque was calculated from the two maximal contractions as the difference between the maximal torque measured over a 300 ms time window and the baseline that corresponded to the passive torque. To verify that the participants accurately matched the torque during the submaximal isometric contractions, we calculated the mean torque over 5 s at the middle of the torque plateau. As for MVC, the baseline torque was systematically subtracted from the produced torque. This was done to ensure that the participants produced the same effort between the three ankle angles.

Myoelectrical activity

To determine the maximal EMG amplitude achieved during the two maximal contractions, the root mean square (RMS) of the EMG signal was calculated over a time window of 300 ms and the maximal value was considered as the maximal activation level ($\text{RMS EMG}_{\text{max}}$). During the submaximal contractions, we

calculated the RMS EMG over the same 5 s window as that used for torque. These values were normalized to the $\text{RMS EMG}_{\text{max}}$ values.

Shear modulus

The data processing was partially blinded (the experimenter was not aware of the ankle angle/muscle state when viewing the images) and was performed using Matlab. Videos of shear modulus maps were exported in mp4 format and sequenced into jpeg images (i.e. 10 images for a 10 s recording). First, a region of interest was defined for each map as the largest muscle area. Each region of interest was then inspected for artefacts (saturation or void areas). If artefacts were present in any of the images to be analysed within a recording (i.e. passive or contraction), the region of interest was reduced in size to exclude the area of artefact from all images within that recording. On average, the area of the region of interest used for the analysis was 38 mm². Image processing converted each pixel of the colour map into a value of the shear modulus based on the recorded colour scale (MacDonald et al., 2016; Tucker et al., 2014). Passive shear modulus was averaged over 5 s. For each submaximal contraction, the shear elastic modulus values were averaged over the same 5 s window as that used for torque and EMG data analysis, so that one representative value was obtained per contraction.

Ratio of shear modulus

As muscle shear modulus is strongly linearly related to both passive and active muscle force, previous reports suggest that the change in shear modulus can be used to estimate an index of the change in muscle force (reviewed in Hug et al., 2015a). Compared with myoelectrical activity, which only relates to active force, shear modulus has the advantage of accounting for changes in both passive and active force. To determine the effect of ankle joint angle on force balance between synergist muscles during submaximal contractions, we calculated a ratio of shear modulus (in kPa) between each muscle pair (GM–GL, GM–SOL and GL–SOL) as

follows:

$$\text{Ratio of shear modulus} = \frac{\text{shear modulus muscle 1}}{\text{shear modulus muscle 1} + \text{shear modulus muscle 2}} \quad (1)$$

Because shear modulus provides information about the change in muscle force rather than information about muscle force (in N) itself, only the changes in the ratio of shear modulus between ankle angles were interpreted.

Statistics

All analyses were performed using Statistica v7.0 (StatSoft, Tulsa, OK, USA). Normality testing (Kolmogorov–Smirnov) and sphericity assumption (Mauchly's test) were consistently passed and values are reported as means±s.d. The level of significance was set at $P<0.05$.

To assess intra-session reliability of the activation strategies during submaximal contractions, the intra-class correlation coefficient (ICC) and the standard error of measurement (s.e.m.) of the RMS EMG values were calculated.

A repeated measures analysis of variance (ANOVA) was used to determine the differences in thickness between muscles [within-subject factor: muscle (GM, GL and SOL)]. To test the effect of ankle angle on resting muscle shear modulus, we performed a repeated measures ANOVA [within-subject factor: muscle (GM, GL and, SOL) and angle (PF 30 deg, 0 deg and DF 25 deg)]. To determine whether the RMS EMG or muscle shear modulus was influenced by changes in ankle angle during submaximal contractions, a repeated measures ANOVA was performed for each contraction intensity (20% of MVC and 20 N m) [within-subject factor: muscle (GM, GL and SOL) and angle (PF 30 deg, 0 deg and DF 25 deg)]. For each ratio of shear modulus [GM/(GM+GL), GL/(GL+SOL) and GM/(GM+SOL)], the potential for a difference between ankle angles at each contraction intensity (20% of MVC and 20 N m) was tested using a repeated measures ANOVA [within-subject factor: angle (PF 30 deg, 0 deg and DF 25 deg)]. When appropriate, *post hoc* analyses were performed using the Newman–Keuls test.

Finally, the relationship between the change in the ratio of activation and the change in the ratio of passive shear modulus between PF 30 deg and both 0 deg and DF 25 deg was tested using Pearson's correlation coefficient.

RESULTS

Muscle thickness

A significant main effect of muscle was observed for muscle thickness ($P<0.001$). Muscle thickness was greater for GM (1.82 ± 0.3 cm) than for GL (1.48 ± 0.4 cm, $P<0.001$) and thickness was greater for SOL (1.72 ± 0.4 cm) than for GL ($P=0.007$). There was no difference between GM and SOL ($P=0.25$).

Passive muscle shear modulus

Note that passive plantarflexion torque at DF 25 deg was 15.9 ± 7.0 N m (i.e. 56.3% of the active torque produced at 20% of MVC). We observed a significant angle×muscle interaction on resting shear modulus ($P<0.001$). Shear modulus increased at 0 deg ($P<0.001$) and DF 25 deg ($P<0.001$) compared with that at PF 30 deg, regardless of the muscle. In addition, the shear modulus measured at DF 25 deg was higher for GM (57.2 ± 11.4 kPa) than for both GL (34.9 ± 6.0 kPa, $P<0.001$) and SOL (16.1 ± 5.3 kPa, $P<0.001$) (Fig. 2); and GL shear modulus was higher than SOL shear

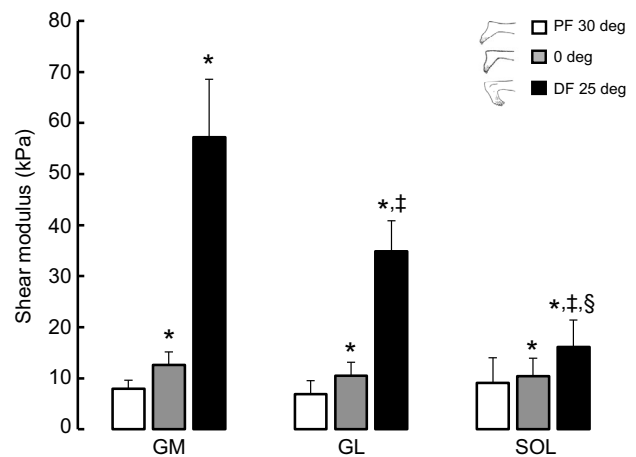


Fig. 2. Passive shear modulus of the gastrocnemius medialis (GM), gastrocnemius lateralis (GL) and soleus (SOL) measured at 30 deg of plantarflexion (PF 30 deg), 0 deg and 25 deg of dorsiflexion (DF 25 deg). $n=24$. *Significant difference from PF 30 deg ($P<0.05$). ‡Significant difference from GM ($P<0.05$). §Significant difference between GL and SOL ($P<0.05$).

modulus ($P<0.001$). No significant difference between muscles was observed at PF 30 deg and 0 deg (all $P>0.10$; Fig. 2).

Intra-session reliability of RMS EMG values

For submaximal contractions performed at both 20% of MVC and 20 N m, the intra-session reliability of the RMS EMG was good (all ICC>0.84; Table 2), indicating that the participants adopted a robust coordination strategy between these synergist muscles. Based on this good reliability, RMS EMG values were averaged between the two trials to obtain a representative value for each ankle angle and contraction intensity.

Submaximal contractions at 20% of MVC

The mean net torque at 20% of MVC was 9.5 ± 3.3 , 21.8 ± 9.8 and 28.4 ± 15.6 N m, for PF 30 deg, 0 deg and DF 25 deg, respectively.

Myoelectrical activity

We observed a significant angle×muscle interaction in RMS EMG ($P=0.010$, Fig. 3). The RMS EMG value was significantly lower for

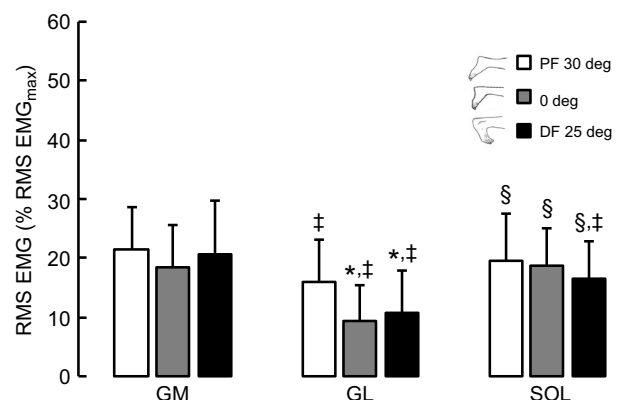


Fig. 3. Myoelectrical activity of the GM, GL and SOL measured at PF 30 deg, 0 deg and DF 25 deg during an isometric plantarflexion performed at 20% of maximal voluntary contraction (MVC). Myoelectrical activity [root mean square (RMS) EMG] is expressed as a percentage of the maximal RMS EMG recorded during a maximal isometric voluntary contraction ($n=24$). *Significant difference from PF 30 deg ($P<0.05$). ‡Significant difference from GM ($P<0.05$). §Significant difference between GL and SOL ($P<0.05$).

Table 2. Intra-session reliability of myoelectrical activity (RMS EMG) measured during the isometric plantarflexion tasks (20% of MVC and 20 N m)

		PF 30 deg		0 deg		DF 25 deg	
		ICC	s.e.m. (% RMS EMG _{max})	ICC	s.e.m. (% RMS EMG _{max})	ICC	s.e.m. (% RMS EMG _{max})
20% MVC	GM	0.89	2.6	0.88	2.7	0.85	2.9
	GL	0.91	2.3	0.85	2.6	0.87	2.5
	SOL	0.96	2.1	0.85	3.5	0.84	2.7
20 N m	GM	0.96	3.0	0.90	2.4	0.93	2.1
	GL	0.97	2.8	0.96	1.3	0.99	1.3
	SOL	0.95	3.9	0.95	2.0	0.98	1.2

RMS, root mean square; EMG, electromyography; ICC, intra-class coefficient correlation; s.e.m., standard error of measurement (% of RMS EMG_{max}); MVC, maximum voluntary contraction; PF, plantarflexion; DF, dorsiflexion; GM, gastrocnemius medialis; GL, gastrocnemius lateralis; SOL, soleus.

GL at both 0 deg ($9.3 \pm 6.2\%$ of RMS EMG_{max}, $P < 0.001$) and DF 25 deg ($10.6 \pm 6.5\%$ of RMS EMG_{max}, $P < 0.005$) compared with that at PF 30 deg ($15.9 \pm 7.1\%$ of RMS EMG_{max}). There was no significant difference for GM (all $P > 0.16$) and SOL (all $P > 0.08$) at any ankle angle (Fig. 3). RMS EMG of GL was lower than that for GM (all $P < 0.001$) and SOL (all $P < 0.046$) at the three tested ankle angles. The RMS EMG of SOL was lower than that of GM only at DF 25 deg ($P = 0.02$) (Fig. 3).

Ratio of shear modulus

We considered a change in the ratio of shear modulus between muscles as a change in force balance. There was a main effect of angle for both GM/(GM+GL) and GL/(GL+SOL) ratios at 20% of

MVC (all $P < 0.002$), but not for GM/(GM+SOL) ratio ($P = 0.22$). The GM/(GM+GL) ratio was higher at 0 deg ($+30.3 \pm 48.8\%$; $P = 0.002$) and DF 25 deg ($+30.1 \pm 48.3\%$; $P < 0.001$) than at PF 30 deg (Fig. 4A), indicating that the greater the dorsiflexion angle, the stronger the bias of force to GM compared with GL. There was no difference in ratios between 0 deg and DF 25 deg ($P = 0.86$). The GL/(GL+SOL) ratio was lower at both 0 deg ($-13.9 \pm 24.6\%$; $P = 0.002$) and DF 25 deg ($-9.5 \pm 20.4\%$; $P = 0.012$) than at PF 30 deg, indicating that the greater the dorsiflexion angle, the stronger the bias of force to SOL compared with GL. There was no difference between ratios at 0 deg and DF 25 deg ($P = 0.34$). Notably, the magnitude of change in GM/(GM+GL) and GL/(GL+SOL) ratios varied greatly between participants (individual data are depicted in Fig. 4A).

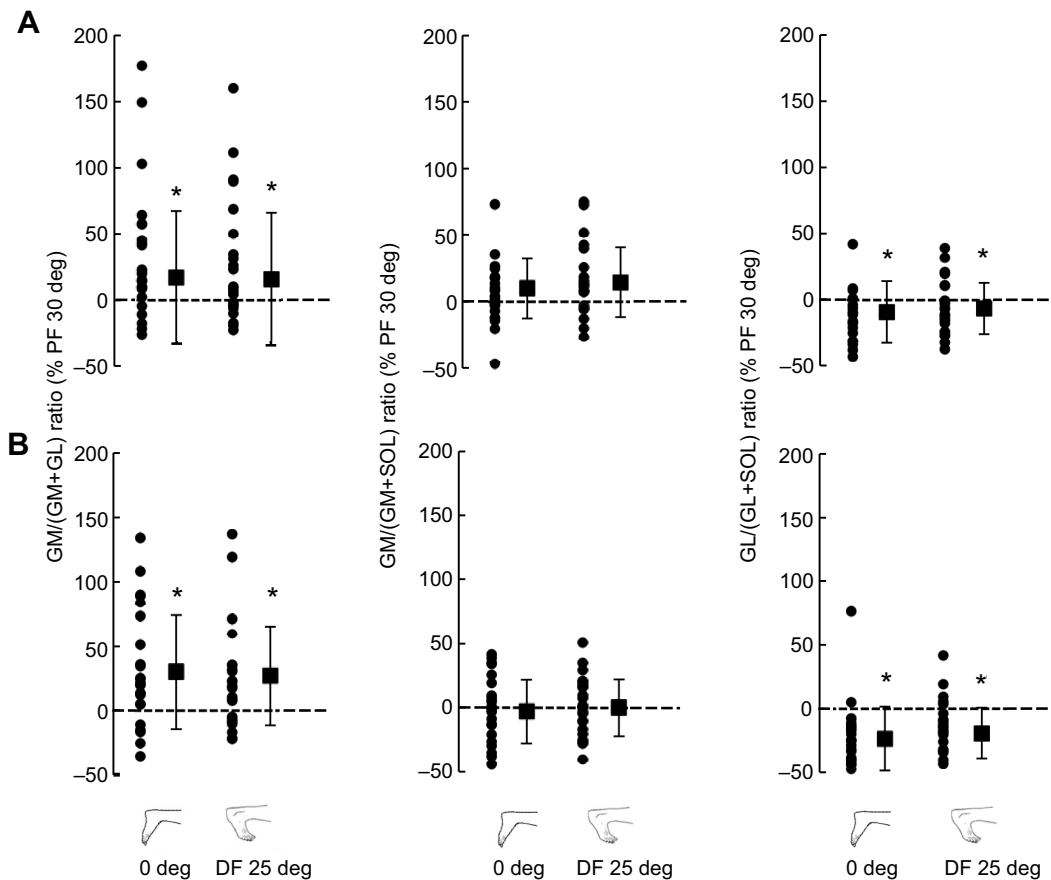


Fig. 4. Scatterplot of the changes in the ratios of shear modulus (index of force) between ankle angles. Individual data points (circles), mean (square; $n = 24$) and s.d. are shown. These ratios were calculated during an isometric plantarflexion performed at (A) 20% of MVC and (B) 20 N m between each muscle pair (GM–GL, GM–SOL and GL–SOL) as the change in the ratio of shear modulus between PF 30 deg and 0 deg, and between PF 30 deg and DF 25 deg. *Significant difference from PF 30 deg ($P < 0.05$).

There was no significant correlation between the change in the ratio of activation and the change in the ratio of passive shear modulus between PF 30 deg and both 0 deg and DF 25 deg ($0.01 < r < 0.36$).

Submaximal contractions at 20 N m

The isometric plantarflexion performed at 20 N m represented $48.1 \pm 18.9\%$, $23.2 \pm 9.8\%$ and $19.1 \pm 10.5\%$ of MVC for PF 30 deg, 0 deg and DF 25 deg, respectively.

Myoelectrical activity

Although no significant muscle \times angle interaction was observed ($P=0.15$), there were significant main effects of muscle ($P<0.001$) and angle ($P<0.001$) for RMS EMG values. GL RMS EMG ($14.8 \pm 13.7\%$ of RMS EMG_{max}) was lower than that of GM ($21.7 \pm 12.4\%$ of RMS EMG_{max}, $P<0.001$) and SOL ($19.4 \pm 13.0\%$ of RMS EMG_{max}, $P<0.003$), and no difference was found between GM and SOL ($P=0.10$) (Fig. 5). RMS EMG values measured at 0 deg ($15.8 \pm 6.9\%$ of RMS EMG_{max}, $P<0.001$) and DF 25 deg ($17.1 \pm 8.1\%$ of RMS EMG_{max}, $P<0.001$) were lower than that measured at PF 30 deg ($32.2 \pm 13.7\%$ of RMS EMG_{max}) (Fig. 5). There was no difference between values at 0 deg and DF 25 deg ($P=0.89$).

Ratio of shear modulus

A main effect of angle was found for both GM/(GM+GL) and GL/(GL+SOL) ratios (all $P<0.001$), but not for the GM/(GM+SOL) ratio ($P=0.74$). The GM/(GM+GL) ratio was higher at 0 deg ($+28.9 \pm 43.2\%$, $P<0.001$) and DF 25 deg ($+26.7 \pm 39.4\%$, $P=0.002$) than at PF 30 deg, indicating that the greater the dorsiflexion angle, the stronger the bias of force to GM compared with that to GL. There was no difference between 0 deg and DF 25 deg ($P=0.50$) (Fig. 4B). Similarly, the GL/(GL+SOL) ratio was lower at both 0 deg ($-21.8 \pm 25.8\%$, $P<0.001$) and DF 25 deg ($-13.7 \pm 20.0\%$, $P<0.001$) than at PF 30 deg, indicating that the greater the dorsiflexion angle, the stronger the bias of force to SOL compared with that to GL. There was no difference between 0 deg and DF 25 deg ($P=0.08$). As observed for the plantarflexion performed at 20% of MVC, the difference in the magnitude of change in GM/(GM+GL) and GL/(GL+SOL) ratios between participants is noteworthy (Fig. 4B).

There was no significant correlation between the change in the ratio of activation and the change in the ratio of passive shear

modulus between PF 30 deg and both 0 deg and DF 25 deg ($-0.04 < r < 0.20$).

DISCUSSION

The novel finding of this study is that the neural drive during submaximal plantarflexion tasks did not compensate for an acute change in the balance of the passive mechanical properties between the individual heads of the triceps surae. This led to a change in force balance between synergist muscles, the magnitude of which varied greatly between participants. These results provide a deeper understanding of the complex interplay between neural drive and muscle mechanical characteristics. These results also have clinical relevance as they may provide a basis on which to consider the potential for force sharing between synergist muscles as a contributing factor to the development of Achilles tendon problems.

Methodological considerations

This experiment requires consideration of four methodological aspects. First, we cannot rule out methodological issues that may have influenced the EMG signal, such as crosstalk and signal cancellation. However, to limit crosstalk, we checked the appropriate electrode location using B-mode ultrasound. Further, EMG results were confirmed by elastography, which is not prone to the limitations inherent to EMG. Second, because the muscle volume under the recording area changes with changes in muscle length (and thus ankle angle), it was important to normalize the RMS EMG values measured during the submaximal tasks to those measured during MVC at the corresponding ankle angle (Cechetto et al., 2001; Mesin et al., 2006). For this normalization procedure to be correct, it is important that the maximal voluntary activation can be reached at every tested ankle angle. In this way, a recent study reported no changes in maximal voluntary activation level from 20 deg in plantarflexion to 10 deg in dorsiflexion (Kluka et al., 2016). It is therefore unlikely that the normalization procedure influenced the RMS EMG results obtained in the present study. Third, the effect of muscle contraction on passive force is unknown. Considering classical biomechanical models where the series elastic component (tendon and aponeurosis) and the contractile element (actin and myosin filaments) lie in parallel to the parallel elastic component (cytoskeletal proteins, sarcolemma, connective tissue), muscle contraction would have minimal influence on passive muscle force. Considering an alternative model where only the contractile element lies in parallel to the parallel elastic component (Hoffman et al., 2012), one would expect that passive force in the muscles would drop upon contraction, depending on how much they shorten. For our hypothesis to be tested, it was important that passive muscle force was still present during contraction in the dorsiflexed position. To confirm the presence of passive force, we measured the fascicle length of the GM from the B-mode images obtained during elastography measurements (Table 3). The fascicle length of the GM measured during the submaximal contractions at DF 25 deg (7.0 ± 1.4 cm and 7.0 ± 1.3 cm for 20% of MVC and 20 N m, respectively) was significantly greater than that measured at rest at PF 30 deg (4.7 ± 0.7 cm, $P<0.001$). Considering that muscle fascicles are slack at PF 30 deg (Maïsetti et al., 2012), this result provides evidence that passive muscle force was still present during the submaximal contractions at DF 25 deg. Fourth, because shear modulus cannot be normalized to that measured during maximal contraction and because shear modulus does not account for muscle architecture (i.e. volume, fibre length), it is not possible to directly interpret a difference in shear modulus between muscles as a difference in force. To account for this limitation, we only

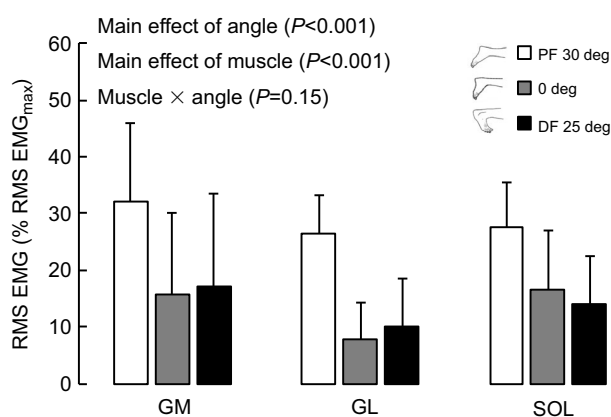


Fig. 5. Myoelectrical activity (RMS EMG) of the GM, GL and SOL measured at PF 30 deg, 0 deg and DF 25 deg during an isometric plantarflexion performed at 20 N m. RMS EMG is expressed as a percentage of the maximal RMS EMG recorded during MVC. $n=24$.

Table 3. Fascicle length of the GM measured at rest and during the isometric plantarflexion tasks (20% of MVC and 20 N m)

	Fascicle length (cm)		
	PF 30 deg	0 deg	DF 25 deg
Rest	4.7±0.9	6.2±0.8	7.9±1.1
20% of MVC	3.5±0.8	4.9±0.8	7.0±1.4
20 N m	3.2±1.0	5.1±0.9	7.0±1.3

Data are means±s.d. PF, plantarflexion; DF, dorsiflexion.

interpreted the changes in the ratio of shear modulus between ankle angles. Overall, we believe that the strength of our study is that similar results are obtained from both EMG and elastography, making us confident that the changes in force sharing observed in the present study reflect physiological changes rather than methodological artefacts.

Acute change in the balance of passive muscle force

The present study confirmed previous observations (Hirata et al., 2015; Le Sant et al., 2017) that passive dorsiflexion induces a much larger increase in shear modulus (stiffness) for GM (+657.6±257.7%) than for GL (+488.7±257.9%) and SOL (+106.6±93.0%) (Fig. 2). As a strong linear relationship between changes in muscle shear modulus and changes in passive muscle force exists (Koo et al., 2013; Maïsetti et al., 2012), this result strongly suggests that the distribution of passive force across the heads of the triceps surae is different when the ankle is dorsiflexed versus plantarflexed. However, this interpretation requires two methodological considerations. First, the measurement of shear modulus is sensitive to the angle between the muscle fibres and the ultrasound transducer, and therefore to the pennation angle (Eby et al., 2013; Gennissou et al., 2010; Koo and Hug, 2015). As such, differential changes in pennation angle between the muscles during passive dorsiflexion could have induced differential changes in shear modulus for the same change in passive force. However, the change in pennation angle during passive dorsiflexion is of low magnitude (between 2 and 12 deg; Abellana et al., 2008; Maganaris et al., 1998; Rana et al., 2013), with negligible differences between muscles (Maganaris et al., 1998; Rana et al., 2013). Therefore, we are confident that the different changes in shear modulus between the three muscles are strongly related to different changes in passive force. Second, the quantification of the balance of passive force between muscles requires the consideration of muscle cross-sectional area. For instance, if two muscles exhibit the same change in shear modulus during stretching, the bigger muscle will exhibit the larger change in passive force. In the present study, we found a greater thickness for GM than for GL, which is in accordance with magnetic resonance imaging studies showing that GM cross-sectional area is 2 times larger than that of GL (Fukunaga et al., 1996). Together with the larger increase in shear modulus for GM, we are confident that there is a higher imbalance of passive force between GM and GL when the ankle is dorsiflexed versus plantarflexed. It is more challenging to interpret the balance of force between SOL and gastrocnemii because the volume of SOL is 2.6 and 5.4 times larger than that of GM and GL, respectively (Albracht et al., 2008), but its increase in shear modulus during passive dorsiflexion was much smaller than that of GM and GL (6.2 and 4.6 times for GM and GL, respectively). Therefore, we cannot determine whether the force was more or less balanced between SOL and gastrocnemii at the dorsiflexed position but we can reasonably conclude that this balance was modified towards a higher proportion of gastrocnemii passive force. In the present

study, we were interested in this change in the balance of passive force across ankle angles, rather than in the absolute balance of force, which could not be measured.

Changes in the distribution of muscle activation

The good intra-session reliability of the GM, GL and SOL EMG RMS values (Table 2) indicates that the activation strategies were robust. As GM exhibited a much larger increase in passive force than GL and SOL when the ankle was dorsiflexed versus plantarflexed, a relatively lower activation of GM than GL and SOL was required at DF 25 deg to maintain the force balance between these muscles. However, this was not observed. Instead, when considering the contraction at 20% MVC, GL RMS EMG was reduced at both 0 deg (−39.4±34.5%) and DF 25 deg (−20.6±58.6%) compared with that at PF 30 deg, while GM and SOL RMS EMG did not change (Fig. 3). When considering the contraction at 20 N m, a lower activation of the three muscles was logically observed at both 0 deg and DF 25 deg than at PF 30 deg. This was expected, as 20 N m represents a lower relative percentage of MVC at 0 deg (~23%) and DF 25 deg (~19%) compared with that at PF 30 deg (~48%). But again, the redistribution of activation that would be required to maintain the force balance between muscles was not observed (no significant interaction involving the ‘muscle’ factor). This was further confirmed by the absence of correlation between the change in activation and the change in passive force. Consequently, the results do not support our hypothesis that neural drive compensates for differential changes in passive force between synergist muscles such that the force-sharing strategy is preserved over the ankle angle range. Instead the change in neural drive accentuates these differences by driving the GL muscle less. In contrast to previous studies where the activation strategies were maintained in the presence of differential acute changes in force-generating capacity between synergist muscles (Bouillard et al., 2014; De Rugy et al., 2012), here the dissociation of activation between the synergist muscles was observed between the heads of the triceps surae.

The underlying mechanisms are unknown for two reasons. First, although a change in reflex pathways may be proposed, Alrowayeh et al. (2011) showed that the H reflex is similarly affected by changes in ankle angle across the plantar flexor muscles. Second, Héroux et al. (2014) observed an absence of GL activation in standing balance and proposed that GL has higher threshold motor units, leading to a later recruitment. However, this cannot explain the ankle angle effect, and specifically why a selective decreased GL activation was observed at 0 deg and DF 25 deg compared with PF 30 deg for the contraction at 20% of MVC, while the torque logically increased from 9.5±3.3 N m at PF 30 deg to 21.8±9.8 N m at 0 deg and 28.4±15.6 N m at DF 25 deg, respectively. Additional experiments are needed to determine the role of both spinal and supra-spinal pathways in observed redistribution of activation with changes in ankle angle. Importantly, regardless the origin of changes in muscle activation, our results demonstrate that they have crucial mechanical consequences.

Ankle angle dependency of the force balance between the synergist muscles

It is important to note that the observed redistribution of activation estimated using EMG with a change in ankle angle does not provide direct evidence that force sharing was altered. This is because each muscle could have operated at a different length relative to its optimal length. Here, we took advantage of elastography to estimate an index of individual muscle force through the measurement of muscle shear modulus (Hug et al., 2015a). Because muscle shear

modulus is linearly related to both passive (Koo et al., 2013; Maïsetti et al., 2012) and active muscle force (Bouillard et al., 2011; Sasaki et al., 2014), this modulus has the advantage of accounting for changes in total force, i.e. active and passive force. As an illustration, Sasaki et al. (2014) showed that the muscle force–length relationship can be estimated by measuring muscle shear modulus using elastography. This means that a muscle that would receive the same drive at a more optimal length would exhibit a higher shear modulus, reflecting higher force. This technique also allowed us to interpret our finding without making any assumptions about the relative force-generating capacity of GM, GL and SOL. Overall, these elastography results reinforce the EMG results. In particular, the GM/(GM+GL) ratio was higher at both 0 deg and DF 25 deg (Fig. 4). As discussed above, because the cross-sectional area of GM is much higher than that of GL (Fukunaga et al., 1996), this increased shear modulus ratio probably reveals a large imbalance of force between these muscles at both 0 deg and DF 25 deg compared with PF 30 deg. Smaller, but significant changes in the GL/(GL+SOL) ratio were observed at 0 deg and DF 25 deg (Fig. 4). Note that the change in the index of force varied greatly between participants, especially for the GM/(GM+GL) ratio at 0 deg (i.e. ranging from –25.8% to +176.1% and –35.2% to +133.4% at 20% of MVC and 20 N m, respectively) and at DF 25 deg (i.e. ranging from –18.9% to +165.0% and –16.2% to +135.6% at 20% of MVC and 20 N m, respectively) (Fig. 4).

To the best of our knowledge, this is the first study to demonstrate an ankle angle dependency for the force-sharing strategies between the heads of the triceps surae. Considering that these muscles are all attached onto the Achilles tendon, and therefore have theoretically similar biomechanical advantage in plantarflexion, such a change in force balance was not expected. As suggested by Magnusson et al. (2003), this change in force balance may induce a different distribution of loads within the Achilles tendon. It is unclear whether this joint-angle dependency of force-sharing strategies has a biomechanical advantage. Indeed, it seems paradoxical with respect to the evolutionary process that the nervous system would retain a suboptimal strategy. We believe that the observed ankle angle dependency of the force balance between the heads of the triceps surae should be beneficial to some aspects. For example, the GM and GL muscles have been identified as contributors to frontal plane actions (Lee and Piazza, 2008; Vieira et al., 2013). As the ankle axis of rotation is inclined laterally during dorsiflexion and medially during plantarflexion (Barnett and Napier, 1952), it is possible that the nervous system takes advantage of these different mechanical advantages in the frontal plane to optimize force production. Measurements of joint configuration along with 3D torque are needed to test this hypothesis.

Significance

Our results demonstrate that the force balance between the three heads of the triceps surae changes as the ankle angle changes between PF 30 deg, 0 deg and DF 25 deg. This range of ankle angles is similar to that observed during maximal running (~PF 35 deg to ~DF 23 deg; Struzik et al., 2015). Interestingly, the change in the balance of force between the ankle positions varied greatly between participants (Fig. 4). This variability might have a clinical significance. Indeed, the Achilles tendon is composed of three mechanically separate fascicles that originate from each of the three heads of the triceps surae (Cummins and Anson, 1946). As such, an imbalance of force produced between the three heads of the triceps surae might lead to heterogeneous loading of the Achilles tendon, as previously suggested in cadaver preparations (Arndt et al., 1999)

and experimental work (Franz et al., 2015; Franz and Thelen, 2016). Although it has been proposed that the level of heterogeneous load within the tendon contributes to the development of Achilles tendinopathy (Bojsen-Møller and Magnusson, 2015), this has not yet been demonstrated. It is possible that a change in force-sharing strategies, as a result of use or disuse, would change the load distribution within the tendon, placing the subject at more risk of developing Achilles tendinopathy.

Finally, biomechanical models often consider the GL and GM muscles as a single muscle (Herzog et al., 1991; Hoang et al., 2005). Yet, the present work demonstrates that these muscles behave differently in both passive and active conditions and that they should be considered as distinct muscles.

Conclusion

This study provides evidence that the nervous system does not compensate for an acute change in the balance of passive force between the heads of triceps surae in humans. As such, the force balance changes as the ankle rotates, the magnitude of which varied greatly between participants in our experiment. As the three heads are attached distally onto the Achilles tendon, such a change in force balance probably creates a change in load distribution within the tendon. These results provide a deeper understanding of the complex interplay between neural drive and muscle mechanical characteristics. They also provide a basis on which to consider the potential for an imbalance of force between synergist muscles as a contributing factor to the development of Achilles tendon problems.

Acknowledgements

The authors thank Dr Kylie Tucker (University of Queensland, Australia) for editing the manuscript.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: L.L., A.N., F.H.; Methodology: L.L., A.N., F.H.; Software: L.L., F.H.; Formal analysis: L.L.; Investigation: L.L.; Resources: A.N., F.H.; Writing - original draft: L.L., F.H.; Writing - review & editing: L.L., A.N., F.H.; Supervision: F.H.; Project administration: L.L., A.N., F.H.; Funding acquisition: A.N., F.H.

Funding

This study was supported by a grant from the Région Pays de la Loire (QUETE project, no. 2015-09035). François Hug is supported by a fellowship from the Institut Universitaire de France (IUF).

Data availability

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.6ch89>

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