

Neural Compensation Within the Human Triceps Surae During Prolonged Walking

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¹Neuromuscular Research Centre, Department of Biology of Physical Activity, University of Jyväskylä, Jyväskylä, Finland; ²School of Physiotherapy and Exercise Science, Griffith University, Gold Coast, Queensland, Australia; and ³Center for Sensory–Motor Interaction, Department of Health Science and Technology, Aalborg University, Aalborg, Denmark

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Cronin NJ, Peltonen J, Sinkjaer T, Avela J. Neural compensation within the human triceps surae during prolonged walking. *J Neurophysiol* 105: 548–553, 2011. First published December 15, 2010; doi:10.1152/jn.00967.2010. During human walking, muscle activation strategies are approximately constant across consecutive steps over a short time, but it is unknown whether they are maintained over a longer duration. Prolonged walking may increase tendinous tissue (TT) compliance, which can influence neural activation, but the neural responses of individual muscles have not been investigated. This study investigated the hypothesis that muscle activity is up- or down-regulated in individual triceps surae muscles during prolonged walking. Thirteen healthy subjects walked on a treadmill for 60 min at 4.5 km/h, while triceps surae muscle activity, maximal muscle compound action potentials, and kinematics were recorded every 5 min, and fascicle lengths were estimated at the beginning and end of the protocol using ultrasound. After 1 h of walking, soleus activity increased by $9.3 \pm 0.2\%$ ($P < 0.05$) and medial gastrocnemius activity decreased by $9.3 \pm 0.3\%$ ($P < 0.01$). Gastrocnemius fascicle length at ground contact shortened by $4.45 \pm 0.99\%$ ($P < 0.001$), whereas soleus fascicle length was unchanged ($P = 0.988$). Throughout the stance phase, medial gastrocnemius fascicle lengthening decreased by $44 \pm 13\%$ ($P < 0.001$), whereas soleus fascicle lengthening amplitude was unchanged ($P = 0.650$). The data suggest that a compensatory neural strategy exists between triceps surae muscles and that changes in muscle activation are generally mirrored by changes in muscle fascicle length. These findings also support the notion of muscle-specific changes in TT compliance after prolonged walking and highlight the ability of the CNS to maintain relatively constant movement patterns in spite of neuromechanical changes in individual muscles.

INTRODUCTION

During human walking, numerous muscles are activated at different stages of the step cycle to facilitate a smooth, fluent motion. This apparent fluidity belies the underlying complexity of the coordination of muscle activity. During unconstrained walking, the particular muscles that are activated, as well as the degree of activation of these muscles, may remain approximately constant across consecutive step cycles when walking for a short time (Winter and Yack 1987). However, it is unknown whether this activation strategy is maintained when walking for several minutes or longer.

In a previous study where subjects walked for about 75 min, we reported evidence of an increase in the compliance of the tendinous tissues (TTs) in the soleus muscle–tendon unit

(MTU), which resulted in less muscle fascicle lengthening during the stance phase. Concurrently, in several subjects, soleus muscle activation appeared to decrease as the walking duration increased (Cronin et al. 2009a). These data suggested that mechanical changes in the MTU led to neural changes in the soleus muscle.

However, this study raised further questions regarding the neuromechanics of other triceps surae muscles. We previously speculated that a decrease in the activation of an individual muscle may be compensated by an increase in activation of synergistic muscles (Cronin et al. 2009a). This kind of within-group compensation has been suggested to occur in muscles of the quadriceps (Akima et al. 2002), spine (Kavanagh et al. 2006), and hand (Duchateau and Hainaut 1993) after higher intensity, fatiguing exercise. In the present study, we sought to investigate the hypothesis that muscle activity may be up- or down-regulated in individual triceps surae muscles in response to a relatively low intensity, prolonged period of walking.

METHODS

Ethical approval

The study was approved by the local ethics committee and each subject provided written informed consent prior to participation. All testing was performed in accordance with the Declaration of Helsinki.

Subjects

Thirteen healthy subjects (5 males, 8 females; age: 27 ± 3 yr; height: 171 ± 8 cm; body mass: 67 ± 10 kg) with no history of neurological disorder volunteered to participate in this study. Prior to testing, subjects were fully informed of the procedures and risks.

Experimental procedures

Subjects initially walked on a custom-made motorized treadmill (Jyväskylä Olympic Research Center, Jyväskylä, Finland) for 5 to 10 min at 4.5 km/h for familiarization. At the end of this period, data were acquired from nearly 30 steps to generate a control profile of the ankle trajectory and ground contact signals. Average stance phase duration (mean $\pm$ SD) was then calculated from these steps based on ankle trajectory data and signals from a force-sensitive resistor placed inside the right shoe. Stance phase duration was used to determine the timing of maximal muscle stimulation (M-max; see following text). Subjects rested for 5–10 min prior to the actual walking experiment to prevent any possible effects of the familiarization period on performance.

After the rest period, subjects walked on the treadmill for 60 min at 4.5 km/h. During this time, muscle activity, ankle and knee joint kinematics, and M-max were recorded at 5-min intervals, resulting in

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the collection of 13 data sets per subject. Within each measurement interval, electromyographic (EMG) activity was recorded from an average of 49 ± 6 steps, which took about 1 min. M-max data were subsequently collected from 3 steps, whereby stimulation was elicited at midstance (see RESULTS for precise timing values). Within each interval, muscle activity data from medial gastrocnemius (MG) and soleus were later expressed relative to M-max measured from the same 5-min interval. During the first and last measurement intervals (0 and 60 min, respectively), ultrasound data were collected from 5 to 8 steps to enable MG and soleus fascicle length to be estimated. A schematic of the experimental setup is shown in Fig. 1.

Materials

Surface electromyography. During walking, surface EMG activity was recorded from the MG, lateral gastrocnemius, soleus, and tibialis anterior muscles of the right leg using bipolar surface electrodes (720; Ambu, Ølstykke, Denmark), with an interelectrode distance of 2 cm and a sampling frequency of 2 kHz.

Maximal muscle compound action potential (M-max). In a previous study, we reported evidence of an increase in TT compliance after a prolonged walking protocol (Cronin et al. 2009a). Because this could lead to a geometric artifact in the EMG signal, which could influence EMG amplitude (Gerilovsky et al. 1989), the present study was designed to enable normalization of the ongoing EMG to M-max elicited during walking. The use of M-max obtained during walking was used in preference to a standing value because the latter method may lead to erroneous conclusions (Ferris et al. 2001; Simonsen and Dyhre-Poulsen 1999).

To elicit M-max, the tibial nerve was stimulated using a circular 1-cm cathode (Unilect, Ag/AgCl; Unomedical, Redditch, UK) positioned in the popliteal fossa and a 40×60 mm oval-shaped self-adhesive anode (V-trodes; Mettler Electronics, Anaheim, CA) placed above the patella. The stimuli were 1-ms square pulses delivered by a constant-current stimulator (DS7A; Digitimer, Hertfordshire, UK). The optimum stimulation site was first determined using a handheld electrode. After locating the optimum site, M-max was determined during standing by gradually increasing the stimulation intensity until no further increase in peak-to-peak M-max amplitude was observed in

MG or soleus. The corresponding stimulus intensity was then increased by a factor of 1.5 and this intensity was used to elicit M-max during walking. Within each interval, stimuli were elicited randomly at midstance until three trials were obtained. For all M-max trials, the sampling frequency was 10 kHz. Despite attempts to also normalize lateral gastrocnemius data, it was not possible to consistently elicit M-max in this muscle during walking. Therefore normalized EMG data are reported for only MG and soleus.

Ultrasonography. An ultrasonographic device (Alpha-10; Aloka, Tokyo, Japan) was used to measure fascicle lengths in MG and soleus during walking at a scanning frequency of 78 frames/s. The probe, which weighed about 130 g, was positioned over the midbelly of MG, which also enabled soleus muscle fascicles to be visualized in the same image. The probe was secured over the skin surface with a custom-made support device to prevent movement of the probe relative to the skin. The ultrasound settings were individually adjusted to optimize the contrast between muscle fascicles and connective tissues, which greatly aids the analysis process. The ultrasound device was positioned at the side of the treadmill during the walking experiments. The reliability of the ultrasound method of fascicle length calculation was determined by calculating the coefficient of variation (CV) between all trials at each measurement interval, in each muscle, and for each subject. The mean ($\pm$ SD) CV values were 3 ± 1 and $6 \pm 1\%$ for the MG and soleus muscles, respectively. These values are similar to those reported previously during walking (Cronin et al. 2009a,b; Ishikawa et al. 2007).

Kinematics. Goniometers (M-series twin axis; Biometrics, Gwent, UK) were positioned on the lateral sides of the ankle and knee joints to calculate changes in joint angle during walking. Foot-ground contact was detected by a force-sensitive resistor placed under the right heel.

Data analysis

All M-max data were band-pass filtered at 10 Hz to 5 kHz. In each measurement interval and for each muscle, M-max was calculated as the highest peak-to-peak EMG value of the three stimulation trials. The ongoing locomotor EMG data were band-pass filtered (10 Hz to 1 kHz), rectified, low-pass filtered (40 Hz), and ensemble averaged (49 ± 6 trials per measurement interval) to produce mean EMG traces, which were then normalized to M-max recorded within that measurement interval. Mean background EMG was quantified as average EMG throughout the entire stance phase. In the RESULTS section, both the original (not normalized) and the normalized EMG data are shown.

For the ultrasound analysis, an individual fascicle was identified in each muscle and fascicle length was determined manually using a three-point tracking model (proximal, mid, and distal) with custom-made digitizing software. For each subject and muscle, the ultrasound data of three steps were averaged from the first and last measurement intervals after which data from all subjects were then pooled. The force-sensitive resistor in the right shoe was used to synchronize the EMG, joint trajectory, and ultrasound data.

Statistics

Repeated-measures ANOVA was used to test for differences between intervals (factors: measurement intervals 1–13). Paired samples *t*-tests were used to examine differences in fascicle length between the first and last measurement intervals. For all statistical tests, significant differences were determined based on a level of significance of $P < 0.05$. Results are presented as means $\pm$ SD.

RESULTS

Because the timing of electrically evoked contractions within the stance phase can influence the amplitude of the

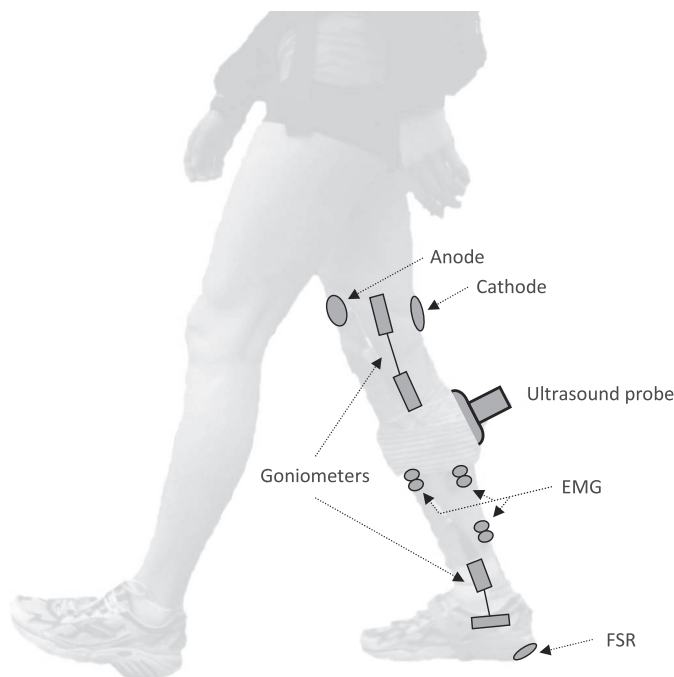


FIG. 1. Schematic of the experimental setup.

resulting EMG response (Simonsen and Dyhre-Poulsen 1999), M-max was elicited at the same relative time in the stance phase ($48 \pm 4\%$) at each interval; this timing did not differ throughout the protocol ($P > 0.9$). At each interval, three M-max trials were recorded and the mean variation in EMG amplitude between these trials was 7 ± 3 and $8 \pm 2\%$ for the soleus and MG muscles, respectively. M-max amplitude varied considerably throughout the walking protocol in both muscles, with a general decrease being apparent in MG and an increase in soleus (Fig. 3A).

Walking data from a single subject are shown in Fig. 2. Across the entire group ($n = 13$), mean stance phase duration was 810 ± 14 ms and did not change throughout the walking protocol [increased by $1.7 \pm 3.8\%$; $F_{(1,13)} = 2.070$; $P > 0.99$]. After 1 h of walking, the range of ankle rotation during the stance phase increased by $3.3 \pm 0.3^\circ$ [$F_{(1,13)} = 3.322$; $P < 0.05$], from 27.8 ± 7.1 to $31.1 \pm 7.0^\circ$. The range of knee rotation did not change significantly [increased by $1.1 \pm 0.2^\circ$; $F_{(1,13)} = 2.997$; $P = 0.705$; Fig. 3A]. However, in the swing phase, greater knee rotation was evident (Fig. 2).

After 1 h of treadmill walking, mean background EMG decreased across the group by $10.0 \pm 0.1\%$ [$F_{(1,13)} = 4.043$; $P < 0.05$] and $13.1 \pm 0.2\%$ [$F_{(1,13)} = 3.705$; $P < 0.01$] in soleus and MG, respectively. However, after normalizing the data to M-max measured during walking, soleus EMG actually increased by $9.3 \pm 0.2\%$ [$F_{(1,13)} = 2.941$; $P < 0.05$] and MG EMG decreased by $9.3 \pm 0.3\%$ [$F_{(1,13)} = 2.349$; $P < 0.01$; Fig. 3A]. Because the M-max responses evoked in lateral gastrocnemius were not consistent enough to allow normalization, only the original data are reported here. Between the first and last intervals, lateral gastrocnemius EMG did not change [$F_{(1,13)} = 5.440$; $P = 0.736$], nor were changes evident in tibialis anterior EMG [$F_{(1,13)} = 8.131$; $P > 0.99$].

In MG, fascicle length at the point of ground contact shortened between the first and last measurement intervals by $4.45 \pm 0.99\%$ [$t(12) = 5.582$, $P < 0.001$]. In soleus, fascicle length at ground contact was unchanged [increased by $2.05 \pm 0.82\%$; $t(12) = -5.546$, $P = 0.988$]. Between the first and last measurement intervals, MG fascicle lengthening amplitude, measured as the difference between the shortest length immediately after ground contact and peak length during the stance phase, decreased by $44 \pm 13\%$ [$t(12) = 33.477$, $P < 0.001$], whereas soleus fascicle lengthening amplitude was unchanged [increased by $1 \pm 6\%$; $t(12) = 0.467$, $P = 0.650$; Fig. 3B].

DISCUSSION

The results of this study demonstrate that muscle activity can be up- or down-regulated in individual triceps surae muscles after a prolonged walking protocol, despite the absence of major changes in knee and ankle joint kinematics. When failing to take into account nonphysiological changes in the EMG signal (e.g., due to geometric artifact), the data suggest that muscle activity decreased in soleus and MG. However, when normalizing the data to M-max measured during walking, MG activity actually decreased and this was compensated by a corresponding increase in soleus activation. These neural changes were also generally mirrored by mechanical data, in that MG fascicles were shorter and lengthened less during the stance phase at the end of the protocol, although no clear changes occurred in soleus fascicle behavior. These findings

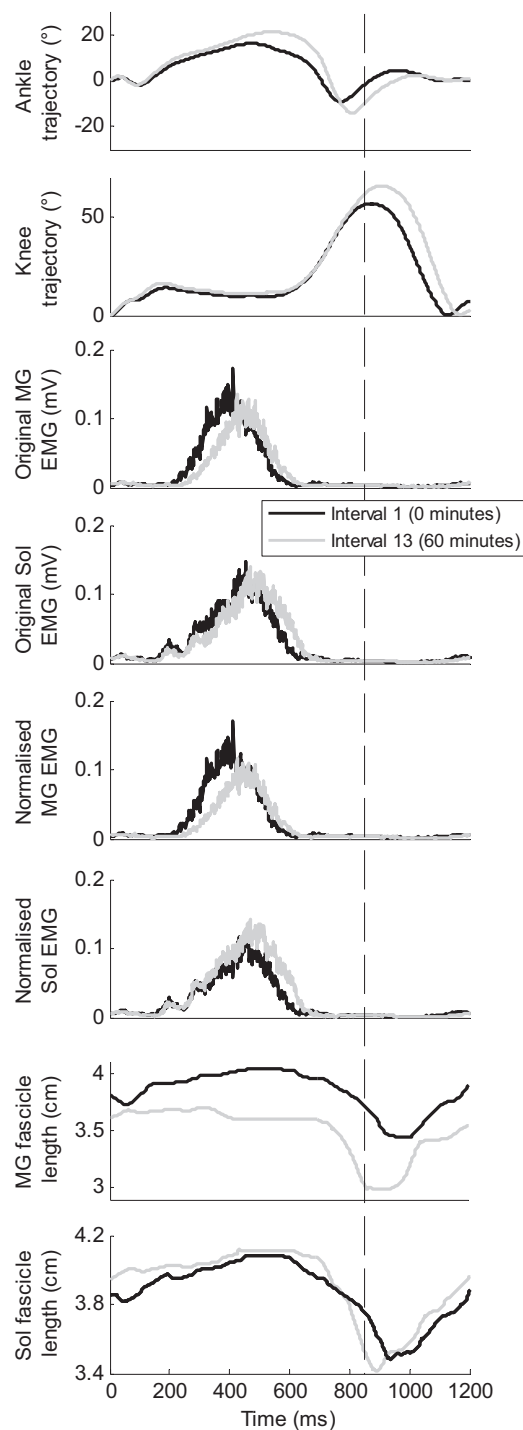
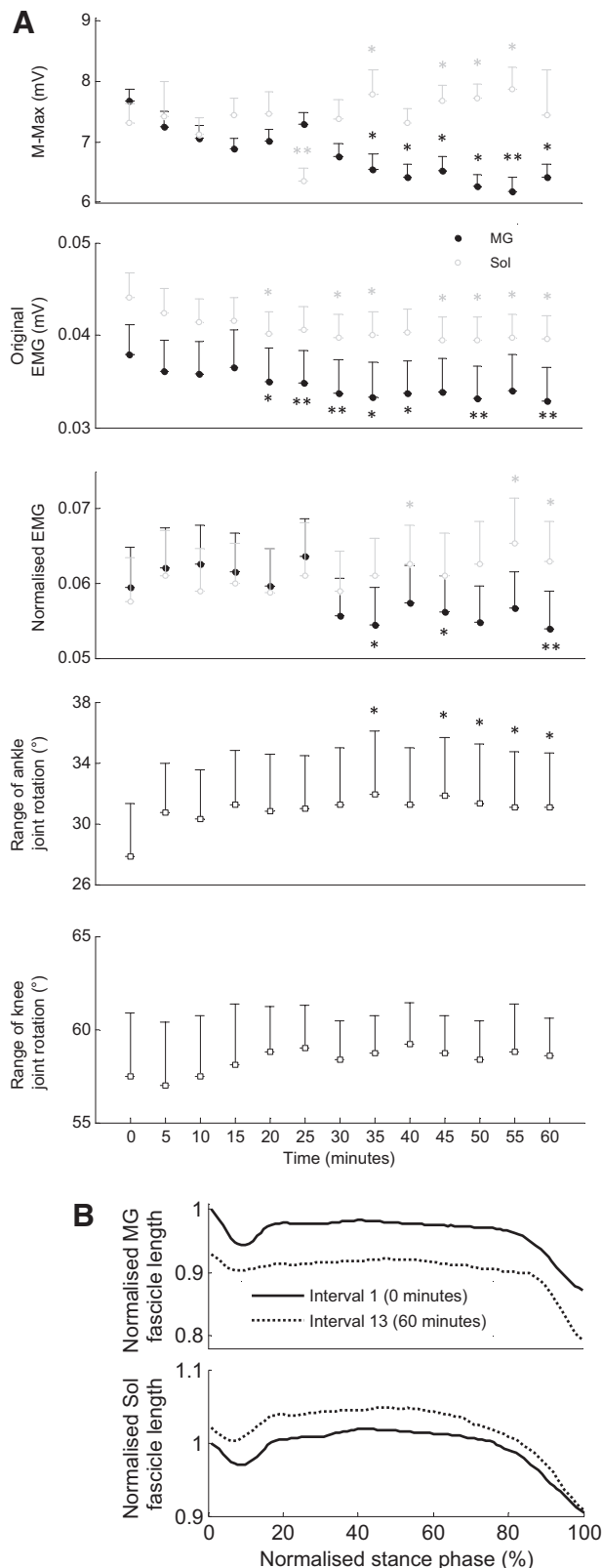


FIG. 2. Data from a single subject across one step cycle (ground contact to ground contact) showing changes in all parameters between the first and last measurement intervals. From top to bottom: ankle trajectory; knee trajectory; original MG EMG; original soleus EMG; normalized MG EMG; normalized soleus EMG; MG fascicle length; soleus fascicle length. In this particular subject, normalizing the EMG data had a minimal influence on MG EMG but a clear effect on soleus EMG. The vertical dashed line denotes the stance-swing transition. EMG, electromyography; MG, medial gastrocnemius.

support our previous data, whereby TT compliance was altered after prolonged walking (Cronin et al. 2009a), and suggest that these changes may be muscle specific. Because MG and soleus share a distal tendon but exhibited different neural and me-

chanical behavior, the site of change in compliance may be the aponeurotic tissues. These findings collectively highlight not only the influence of muscle–tendon mechanics on neural activation, but also the muscle specificity of these effects.



Before discussing the findings of this study in detail, some methodological issues should be addressed. One inherent limitation, albeit unavoidable, is the use of two-dimensional ultrasound techniques to study length changes of three-dimensional structures. Furthermore, potential errors that occur during dynamic conditions are not currently quantifiable and may not be consistent throughout the step cycle. The data from this study also suggest that TT compliance may have increased in MG, whereas no evidence of a change in soleus compliance was detected. This is in contrast to our previous data, where TT compliance increased in soleus (Cronin et al. 2009a). This may have been due to the use of incline walking in the previous study (3% vs. level walking in the present study), which could conceivably alter the activation strategy and thus the degree of activation of individual muscles (Lay et al. 2007; Lichtwark and Wilson 2006), particularly over a 1-h time course. Unfortunately, we were unable to measure MG fascicle length in our previous work. It should also be noted that EMG data were normalized to M-max at midstance and M-max may vary throughout the stance phase (Simonsen and Dyhre-Poulsen 1999). Therefore the normalizing technique used here may have yielded different results if M-max had been elicited in a different portion of the stance phase. Variation in M-max throughout stance is thought to be due to movement of the muscle fibers under the skin relative to the surface electrodes (Simonsen and Dyhre-Poulsen 1999). Accordingly, the degree of M-max variation is generally smaller in walking than that in running (see Table 1 and Fig. 2 in Simonsen and Dyhre-Poulsen 1999), since the latter activity involves larger joint excursions and length changes of muscle fascicles during stance (Ishikawa et al. 2007). Therefore the particular choice of M-max timing is unlikely to have influenced our results dramatically.

In the present study, normalized MG muscle activation started to decrease appreciably after about 35 min, with a concomitant increase in soleus activity at roughly 40 min. In a previous study we speculated that a decrease in muscle activation may be due to an increase in TT compliance, leading to a decrease in fascicle lengthening and a concomitant decrease in the excitation of muscle spindle afferents (Cronin et al. 2009a). Although this explanation may be valid in MG, muscle activation increased in soleus and no clear changes in fascicle behavior were evident, indicating a lack of change in TT compliance. If correct, this would suggest that changes in TT compliance can occur somewhat independently between muscles, even those with a common distal tendon. Differences in neural and mechanical behavior have been postulated between these muscles during walking (Ferris et al. 2001; Ishikawa et al. 2005). Furthermore, previous studies have reported shear at the aponeurotic boundaries between MG and soleus during isometric conditions (Bojsen-Moller et al. 2004), as well as

FIG. 3. Mean data for the whole group ($n = 13$). *A*, top to bottom: absolute maximal muscle stimulation (M-max) values; original average EMG values for MG and soleus; normalized average EMG values for MG and soleus; range of ankle joint rotation during the stance phase; range of knee joint rotation during the stance phase. *B*: mean MG and soleus fascicle length throughout the stance phase at the first (0 min; solid lines) and last (60 min; dotted lines) measurement intervals. Data are shown normalized to fascicle length at ground contact at the first interval. * and ** denote a significant difference from interval 1 (0 min) at the $P < 0.05$ and $P < 0.01$ levels, respectively; # and ## denote a significant difference from the previous interval at the same significance levels.

during hopping and walking (Cronin et al., unpublished observations). These findings suggest that these muscles are able to act somewhat independently in spite of a shared distal tendon (Maganaris et al. 2006). With regard to the cause of increased soleus activation, this may be explained by an increase in afferent feedback and/or increased supraspinal drive, both of which make important contributions to ongoing muscle activation (Akima et al. 2002; Sinkjaer et al. 2000). However, the precise site of neural modification cannot be determined from these results.

An important question related to the findings of this study concerns the site of change in TT compliance. The TTs can be subdivided into the outer tendon and aponeuroses and these structures differ to some extent in their function (Epstein et al. 2006; Magnusson et al. 2003). Several studies have suggested that outer tendon stiffness is unaffected by cyclic loading, at least within the time frame relevant to this study (De Zee et al. 2000; Peltonen et al. 2010). Furthermore, MG and soleus both attach to the outer Achilles tendon, so a change in outer tendon properties would presumably be evident in both muscles, which was not the case. Conversely, aponeurotic stiffness may be more acutely adaptable because these tissues are somewhat “anchored” to the muscle fascicles (Lieber et al. 2000), so their stiffness changes with variations in fascicle length/force (Azizi and Roberts 2009). Consequently, our findings of differential changes in TT compliance and muscle activation between MG and soleus may be due to muscle-specific changes in aponeurotic compliance in response to prolonged walking.

It should be noted that the observed changes are consistent with compositional differences between these muscles. The MG muscle is biarticular and contains nearly 50% slow-twitch fibers and is thus more prone to fatigue than soleus, which is monoarticular and contains roughly 88% slow-twitch fibers (Edgerton et al. 1975; Gollnick et al. 1974). Accordingly, prolonged walking may induce mild fatigue symptoms in MG, which are then compensated by the more fatigue-resistant soleus. Fatigue can lead to an increase in activity of type III and type IV afferents, which in turn may inhibit α -motoneuron activity in MG while simultaneously exciting the soleus α -motoneurons (Duchateau and Hainaut 1993), or indeed those of other muscles such as lateral gastrocnemius. Despite the relatively low intensity of prolonged walking and our previous finding of unchanged contractile properties after prolonged walking (Cronin et al. 2009a), it cannot be completely excluded that the presence of mild fatigue symptoms in MG contributed to the observed results.

In addition to the notion of intermuscular neural compensation, it is possible that compensation also occurs within a muscle. A single muscle can exhibit variations in mechanical action (Carrasco et al. 1999), fiber type (Wang and Kernell 2000), activation patterns (English 1984), and length changes (Ahn et al. 2003; Pappas et al. 2002; Soman et al. 2005). Furthermore, surface EMG recordings from the entire triceps surae area using matrix electrodes reveal that different parts of the triceps surae are activated at different times during muscle contraction (Staudenmann et al. 2009). It is therefore possible that the observed decrease in MG EMG was also compensated within the MG muscle, i.e., a different part of MG was activated after exercise (Higham et al. 2008). Such a change would not have been detectable using a bipolar electrode configuration focused on a relatively small portion of the

muscle. It is also possible that compensation occurs in other muscles, such as the more proximal knee extensors.

In this study, a low-intensity walking protocol led to neural and mechanical changes that differed between the MG and soleus muscles, in spite of their shared distal tendon. In MG, the walking intervention led to a shortening of the muscle fascicles, a decrease in fascicle lengthening during the stance phase, and a decrease in muscle activation of about 10%. In soleus, no clear changes in fascicle lengthening patterns were detected, but muscle activation increased by about 10%, suggesting a compensatory neural strategy between these muscles. We attribute these changes primarily to muscle-specific alterations in the compliance of aponeurotic tissues, although a moderate influence of MG fatigue cannot be completely excluded. These findings highlight the ability of the CNS to maintain a relatively constant movement pattern in spite of neural and mechanical changes in individual muscles.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

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