

RESEARCH ARTICLE

Differences in contractile behaviour between the soleus and medial gastrocnemius muscles during human walking

Neil J. Cronin*, Janne Avela, Taija Finni and Jussi Peltonen

Neuromuscular Research Centre, Department of Biology of Physical Activity, University of Jyväskylä, Finland

*Author for correspondence (neil.j.cronin@jyu.fi)

SUMMARY

The functional roles of individual lower limb muscles during human walking may differ depending on walking speed or duration. In this study, 11 volunteers walked on a treadmill for 60 min at speeds corresponding to both optimal and 20% above optimal energetic cost of transport whilst oxygen consumption and medial gastrocnemius (MG) and soleus fascicle lengths were measured. Although energetic cost of transport was ~12% higher at the faster speed, it remained constant over 60 min at both speeds, suggesting that humans can walk for prolonged periods at a range of speeds without compromising energetic efficiency. The fascicles of both muscles exhibited rather 'isometric' behaviour during the early to mid stance phase of walking, which appears to be independent of walking speed or movement efficiency. However, several functional differences were observed between muscles. MG exhibited time- and speed-dependent decreases in operating length, and shortened faster during the pushoff phase at the faster walking speed. Conversely, soleus exhibited consistent contractile behaviour regardless of walking speed or duration, and always shortened slower than MG during pushoff. Soleus appears to play a more important functional role than MG during walking. This may be especially true when walking for prolonged periods or at speeds above the most energetically efficient, where the force potential and thus the functional importance of MG appears to decline.

Key words: muscle fascicle, human locomotion, efficiency, ultrasound, automatic tracking.

Received 23 July 2012; Accepted 13 November 2012

INTRODUCTION

During human walking, movement efficiency is greatest at intermediate walking speeds, where the exchange between kinetic and potential energy is greatest and thus the total mechanical work requirement of the muscles is minimised (Cavagna and Kaneko, 1977). This is reflected in measurements of energetic cost of transport (COT), which is essentially a measure of the cumulative metabolic rates of the muscles that power locomotion, and is defined as the energetic cost of moving a unit mass a unit distance. In human walking, COT exhibits a U-shaped curve when plotted against speed; it is lowest at intermediate speeds of ~4.5 kmh⁻¹ and increases at speeds faster or slower than this optimum (Margaria, 1938).

Triceps surae muscle fascicles operate essentially isometrically during the early to mid stance phase of walking (Cronin et al., 2011b), thus minimising muscular work. During the subsequent pushoff phase, the fascicles shorten at velocities associated with high efficiency (Farris and Sawicki, 2012b; Krishnaswamy et al., 2011). However, as walking speed increases above the speed corresponding to optimal efficiency (i.e. minimal COT), the fascicles of the medial gastrocnemius (MG) muscle have been shown to shorten faster during pushoff in humans and cats, resulting in a decrease in force production due to the force-velocity relationship of muscle (Farris and Sawicki, 2012b; Prilutsky et al., 1996). Similar findings have been reported after prolonged walking for 1 h (Cronin et al., 2011b). Decreased MG force production would, in turn, require the activation of a larger proportion of MG motor units and/or an increase in activation of synergistic muscles (e.g. soleus) to maintain sufficient ankle joint torque (Cronin et al., 2011b; Lichtwark and Wilson, 2008). As

well as complicating motor control, such changes could affect movement efficiency.

It is currently unknown whether and to what extent soleus may be able to compensate for a decrease in MG force production during human walking. This is due in part to the small number of studies that have examined soleus fascicle behaviour during walking, which in turn can be attributed to the relative difficulty of imaging soleus compared with gastrocnemius muscles. Recent advances in both imaging and analysis techniques enable the simultaneous study of MG and soleus fascicle length changes during dynamic tasks such as walking (Cronin and Lichtwark, 2012). Rubenson et al. (Rubenson et al., 2012) recently reported that the soleus muscle's operating length is highly conserved between walking and running, and suggested that soleus is preferentially selected for stable, rather than optimal, force output. It has also been suggested that soleus is more metabolically efficient and shortens at a lower velocity than MG (Krishnaswamy et al., 2011). Thus, despite the fact that MG and soleus are functionally synergistic, their roles and relative importance within this synergy may differ.

Accordingly, we have previously hypothesised that a decrease in MG force output could be compensated by an increase in soleus force in order to maintain appropriate ankle joint torque. This hypothesis was based on data obtained during walking for 1 h at 4.5 kmh⁻¹ (Cronin et al., 2011b). However, as the speed corresponding to optimal COT is individual-specific (Weyand et al., 2010), and as MG operates less efficiently at speeds that do not correspond to optimal COT (Farris and Sawicki, 2012b), the use of a standardised speed is unlikely to have corresponded to optimal efficiency for all subjects in our previous study. The present study

was thus designed to examine the effects of walking at individually determined energetically optimal and sub-optimal walking speeds, as well as the effects of prolonged walking (up to 60 min), on fascicle behaviour of the soleus and MG muscles. These tasks were chosen as they are frequently encountered by humans, and because they have both been found to induce disadvantageous changes in MG fascicle behaviour and/or a decrease in MG force potential (Cronin et al., 2011b; Farris and Sawicki, 2012b). It was thus expected that this paradigm could shed light on the functional importance of the soleus muscle when contractile conditions are sub-optimal in the synergistic gastrocnemius. Two hypotheses were tested: (1) walking at a faster than optimal speed will increase muscle fascicle shortening amplitude and/or shortening velocity in MG but not soleus; and (2) time-dependent changes in muscle fascicle behaviour will be more evident in MG than in soleus.

MATERIALS AND METHODS

Participants

Eleven healthy volunteers (six males, five females; age 28 ± 5 years; height 172 ± 7 cm; body mass 67 ± 8 kg) with no history of neurological disorder took part in the study. Participants were instructed to abstain from caffeine consumption and food intake 2 h prior to testing. All experimental procedures had received prior approval by the local ethics committee and were conducted in accordance with the Declaration of Helsinki. All volunteers provided written informed consent.

Experimental protocol

Participants attended the laboratory on three separate occasions. In the first session, COT was measured while participants walked on a motorised treadmill (OJK-1; Telineyhtymä, Kotka, Finland) at seven speeds between 3.5 and 6.5 km h^{-1} in a randomised order. Each speed was maintained for 4 min and oxygen consumption was recorded during the fourth minute. In the second session, which was at least 24 h after the first, participants walked on the treadmill for 60 min at the speed corresponding to their lowest COT in session one (hereafter referred to as 'optimal condition') whilst oxygen consumption and MG and soleus fascicle lengths were measured. In the third session, which was always at least 1 week after the second, the protocol was repeated but at a speed 20% faster than the individually determined optimal speed ('fast condition'). All sessions were performed at the same time of day within ± 2 h.

Methodology and analysis

Cost of transport

Breath-by-breath O_2 consumption was measured using open circuit indirect calorimetry. Participants wore a face mask through which air was inspired, and the gas content of the inspired air was analysed (SensorMedics v_{max} 229, Yorba Linda, CA, USA). COT was determined as the mass-specific rate of O_2 consumption divided by walking speed ($\text{ml O}_2 \text{ kg}^{-1} \text{ km}^{-1}$) and values were averaged over 1 min intervals. Rates of O_2 consumption recorded during quiet standing were subtracted from the values recorded during walking to calculate the O_2 consumption attributable to walking.

Ultrasound

An ultrasonographic device (Alpha-10; Aloka, Tokyo, Japan) was used to measure fascicle lengths in the MG and soleus of the right leg during walking at a scanning frequency of 95 Hz. The probe was positioned over the medio-lateral centre of MG to facilitate comparisons between sessions and to allow soleus muscle fascicles to be visualised in the same image. The repeatability of fascicle

lengths measured on separate days has been found to be high using similar methodology (Aggeloussis et al., 2010). The probe was secured over the skin surface with a custom-made support device to prevent movement of the probe relative to the skin. MG and soleus muscle fascicle lengths were determined throughout the step cycle using an automated fascicle tracking algorithm validated previously (Cronin et al., 2011a; Gillett et al., 2012). Data were sampled at 10 min intervals and analysed from four to five steps per interval for all participants and then averaged. Fascicle velocities were determined by differentiating fascicle length with respect to time. The onset of fascicle shortening in the pushoff phase was determined as the first incidence where five consecutive data points exhibited a negative instantaneous velocity.

Additional measures

Foot-ground contact was detected by a force-sensitive resistor placed under the right heel, and these signals were used to determine temporal stride parameters.

Statistics

Differences in COT between speeds in the first session were tested with repeated-measures ANOVA. Two-way repeated-measures ANOVA was used to assess the effects of speed (optimal *versus* fast) and measurement interval (0, 10, 20, 30, 40, 50 and 60 min) on all outcome measures. Mauchly's test of sphericity was applied, and where the assumption of sphericity was violated, Geisser-Greenhouse (GG) adjustments were used. Where significant main effects were observed, *post hoc* Bonferroni corrections were used to identify the location of differences. For all tests, the minimum level of statistical significance was set at $P < 0.05$.

RESULTS

Cardio-respiratory parameters

Walking speed had a significant effect on COT in the first session ($F_{GG} = 4.556$, $P = 0.034$; Fig. 1A). On average, COT was lowest at 4.5 km h^{-1} , although three subjects showed optimal COT at 4, 5 or 5.5 km h^{-1} . In the 60 min walking sessions, COT was significantly different between speeds ($F = 4.295$, $P = 0.042$) but not measurement intervals ($F = 1.389$, $P = 0.230$; Fig. 1B). Respiratory quotient (RQ), calculated as the ratio of CO_2 production to O_2 consumption, was not significantly different between speeds ($F = 2.649$, $P = 0.155$), but was influenced by measurement interval ($F = 13.951$, $P < 0.001$; Fig. 1C).

Muscle fascicle behaviour

In soleus, there was no effect of speed ($F = 0.001$, $P = 0.983$) or measurement interval ($F = 0.371$, $P = 0.890$) on fascicle length at the instant of ground contact, whereas in MG, fascicle length at ground contact decreased between the first and last measurement intervals at both speeds ($F = 4.005$, $P = 0.01$), and was shorter in the fast condition at all intervals ($F = 2.576$, $P = 0.035$). There was no effect of speed or measurement interval on the range of fascicle length changes throughout the mean stride in soleus ($F = 0.039$, $P = 0.851$), but the range of length changes decreased in MG at both speeds between the first and last measurement intervals ($F = 3.551$, $P = 0.048$; Fig. 2). The timing within the stance phase when fascicle shortening began was unaffected by speed or measurement interval in both muscles ($F = 0.087$ – 0.608 , $P = 0.599$ – 0.995). Soleus shortening velocity during the pushoff phase was unaltered by speed ($F = 0.855$, $P = 0.539$) or measurement interval ($F = 0.620$, $P = 0.564$). In MG, there was a main effect of speed ($F = 3.148$, $P = 0.033$) but not measurement interval ($F = 0.170$, $P = 0.983$) on shortening velocity (Fig. 3).

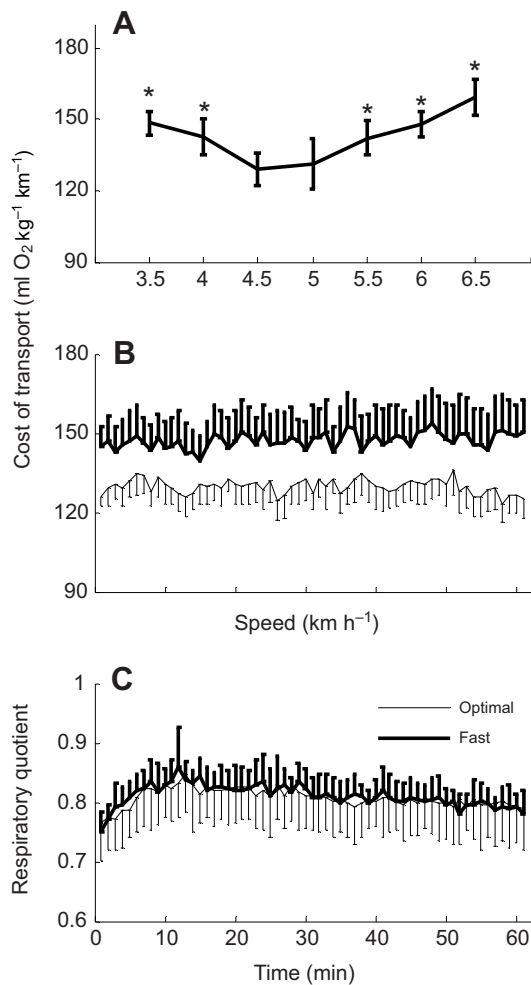


Fig. 1. (A) Group mean cost of transport (COT) data obtained from the first session at seven walking speeds ($N=11$). Asterisks denote a significant difference from 4.5 km h^{-1} . (B) Group mean COT data averaged per minute from the optimal and fast sessions. COT was significantly higher at each 10 min interval in the fast condition. (C) The corresponding values for respiratory quotient (RQ), which was always below 1.0, indicating aerobic conditions. RQ increased significantly between 0 and 10 min at both speeds, but showed no other significant changes. In all plots, error bars denote ± 1 s.d. Note that the 0 time interval began ~ 3 min after the treadmill started to allow steady state to be reached. Key in C also applies to B.

Gait characteristics

Stride duration was shorter at all intervals in the fast condition ($F=12,165$, $P=0.018$; grand mean: 1123 versus 1020 ms), and also increased at the optimal speed between the first and last measurement intervals from 1108 ± 17 to 1127 ± 17 ms ($F=3.553$, $P=0.009$).

DISCUSSION

This study demonstrates several novel findings. Firstly, even when walking at inefficient speeds, COT remained constant over 60 min, highlighting the human capability to walk for prolonged periods at a relatively wide range of speeds without a decline in energetic efficiency. In addition, MG fascicle length decreased over 60 min at both walking speeds by $\sim 5\text{--}6\%$, suggesting a speed-independent increase in MG tendinous compliance, which was not evident in soleus at either speed, despite the shared distal outer tendon of these muscles. At the faster speed, the MG fascicles operated at an even shorter length and shortened $\sim 20\%$ faster during pushoff, neither of which occurred

in soleus. These results suggest that when walking for prolonged periods and/or at faster than optimal speeds, the force potential of MG decreases due to exercise-induced changes in its force-length and force-velocity relationships. Because of the consistency of soleus behaviour across walking speed and duration, we hypothesised that an increase in soleus activation may be one mechanism by which decreased MG force is compensated in the conditions studied. As well as potentially indicating a more important functional role of soleus in these conditions, the findings have important implications for motor control, implying that the motor commands to MG and soleus must be continuously and independently modulated to maintain appropriate joint torques, despite the apparently synergistic function of these muscles. Interestingly, although COT is a measure of the cumulative metabolic rates of the locomotor muscles, changes in MG fascicle behaviour (and presumably also efficiency) did not affect COT values.

The evolutionary origins of human walking

In this study, COT remained constant over 60 min when walking at the most efficient speed. In light of the long evolutionary history of human locomotion, it is perhaps unsurprising that humans can maintain the optimal speed for an extended period of time without detectable changes in COT. For example, oxygen consumption has also been found to remain constant when running for an equivalent period of time (Finni et al., 2003). In addition, at walking speeds where COT is minimised, Achilles tendon storage and return of elastic energy (Neptune et al., 2008) and muscular efficiency (Cavagna and Kaneko, 1977) have been suggested to be maximal. Knee joint flexion in the stance phase is also minimal around optimal COT, which is associated with decreased cost of muscle work (Winter, 1983). It thus seems that humans are both biomechanically and metabolically tuned to walk at intermediate speeds efficiently. Our results provide indirect evidence for some of these claims, because the rate and amplitude of MG fascicle shortening increased at the faster, non-optimal speed, implying decreased efficiency due to the force-velocity relationship and increased contractile work, respectively.

When walking at a speed faster than optimal, COT was $\sim 12\%$ higher on average (Fig. 1B) but still remained constant over 60 min. The consistency of COT at both speeds cannot be attributed to a training effect because humans tend to select speeds that coincide closely with those that are most energetically efficient (Martin et al., 1992), and are thus unaccustomed to walking 20% faster than optimal for prolonged periods. The fast speed was $\sim 1 \text{ km h}^{-1}$ faster than optimal, which was sufficient to produce significantly higher COT values. However, the U-shaped curve of COT versus speed for human walking is quite flat within the narrow range of walking speeds that humans tend to naturally select, whereby large changes in speed result in relatively small increases in COT (Fig. 1A) (see also Willis et al., 2005). Our data show that humans are capable of walking for prolonged periods of time at a relatively wide range of speeds without a decline in energetic efficiency, even when the initial COT is sub-optimal (see also Carrier et al., 2011).

Effects of prolonged walking on triceps surae contractile behaviour

When the duration of walking exceeds ~ 30 min, the repeated muscle-tendon unit length changes that occur with every step can lead to an increase in the compliance of the MG tendinous tissues, but this effect is not evident in soleus during level walking (Cronin et al., 2011b). In the present study, MG fascicle length decreased over the course of 60 min at both walking speeds by $\sim 5\text{--}6\%$, supporting the notion of increased MG tendinous compliance, which

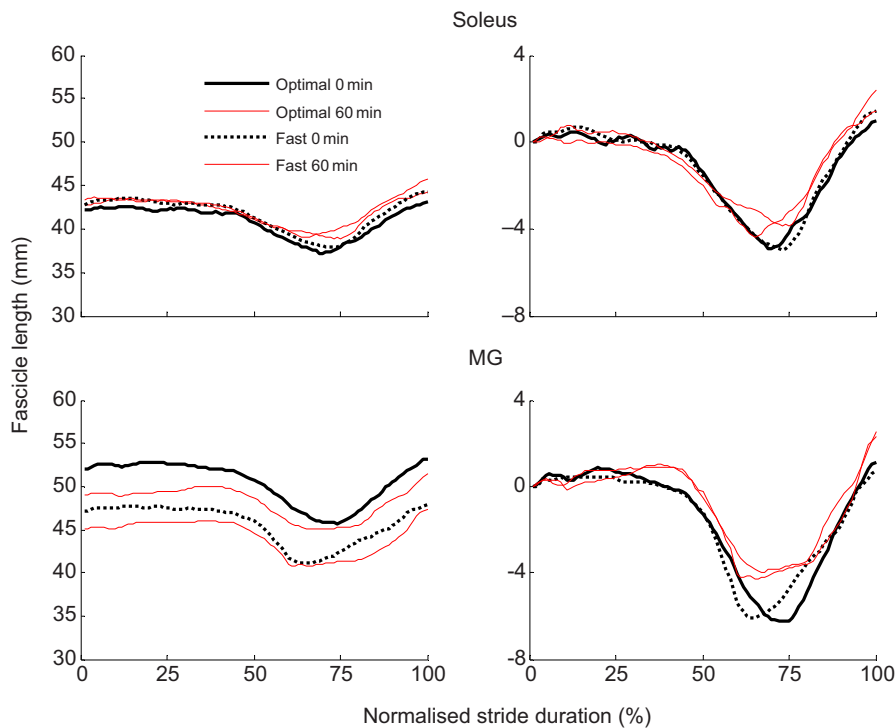


Fig. 2. Mean soleus and medial gastrocnemius (MG) fascicle lengths from the first (0 min) and last (60 min) measurement intervals ($N=11$). Each trace represents the average of four to five steps per subject and interval, which were then normalised to 100 data points and group averaged. In the left column, the averaged data are shown, and in the right column each trace has been corrected for differences in length at ground contact to facilitate comparisons. Note that stride duration differed between speeds, which is not evident in this figure due to normalisation.

appears to be independent of walking speed and thus movement efficiency. This effect was not evident in soleus at either speed, implying that changes in tendinous compliance can occur in individual muscles, presumably in the aponeurotic tissues because MG and soleus share a distal outer tendon. Despite time- and speed-dependent changes in MG behaviour, both muscles exhibited rather 'isometric' behaviour during the early to mid stance phase of walking. Our results suggest that this phenomenon is independent of walking speed or movement efficiency.

Consequences of changes in MG fascicle behaviour

It has been suggested that MG operates primarily on the plateau region of the force-length relationship in walking (Fukunaga et al., 2001). Therefore, when the MG fascicles operate at a shorter length, as observed here during prolonged walking and even more so at the faster speed (~ 4.3 mm shorter compared with the optimal speed), MG force output may decrease due to a shift of the MG fibres towards the ascending limb of the force-length relationship. Furthermore, at the faster speed, our results showed that the MG muscle also shortened $\sim 20\%$ faster in the pushoff phase, which would theoretically further decrease MG force because of the force-velocity relationship (Farris and Sawicki, 2012b; Prilutsky et al., 1996). Our results thus lend support to the suggestion that the MG muscle experiences less favourable contractile conditions at faster walking speeds (Farris and Sawicki, 2012b; Neptune and Sasaki, 2005; Prilutsky et al., 1996) and when walking for prolonged periods (Cronin et al., 2011b), which can decrease its ability to produce force.

Increases in walking speed within the range studied here are associated with similar peak Achilles tendon forces but an increase in the rate of force development in the stance phase (Finni et al., 1998). Therefore, a decrease in MG force must be compensated within the triceps surae group in order to maintain the required Achilles tendon force level. Within the MG muscle, higher forces could be achieved by activating a larger muscle volume, which would involve recruitment of faster motor units, but this increases

energy consumption (Roberts et al., 1998). Alternatively, activation of synergistic muscles such as soleus may be increased (Cronin et al., 2011b; Lichtwark and Wilson, 2008). Although this would still increase energy consumption, the additional cost is likely smaller in soleus because it is more suited to relatively slow, prolonged movements than MG (see below). Our data show that soleus exhibited consistent contractile behaviour when walking for up to 60 min, as well as when walking at inefficient speeds. This is consistent with recent data showing that soleus operates over a similar region on its force-length curve in both walking and running, thus conserving a near-optimal ($\sim 95\%$) length-dependent force-generating capacity around the time the highest forces are required (Rubenson et al., 2012). Furthermore, in the pushoff phase, we observed that soleus always shortened at lower velocities than MG, implying lower metabolic energy consumption (Hill, 1938). We therefore suggest that when walking for prolonged periods or at faster speeds, the decrease in MG force capacity is compensated by an increase in soleus force. This phenomenon is presumably more evident at faster walking speeds due to the decrease in fascicle operating length and increase in shortening velocity of MG at faster speeds. It should be noted that in the case of prolonged walking at a constant speed, a decrease in MG force could be compensated by a change in the distribution of relative torque between joints. Relative joint powers have been shown to remain constant with changes in walking speed (Farris and Sawicki, 2012a), but it is not known whether this mechanism is involved in prolonged walking. However, our previous finding of neural compensation within the triceps surae in prolonged walking (Cronin et al., 2011b) suggests that this is unlikely.

It is noteworthy that changes in the contractile behaviour of MG (and presumably also MG efficiency) did not appear to affect COT values. As COT is a measure of the cumulative metabolic rates of the muscles that power locomotion, this apparent discrepancy may be due to the relatively low importance of MG in the overall efficiency of walking. Alternatively, compensatory mechanisms within the triceps surae group (e.g. increased soleus activation) may

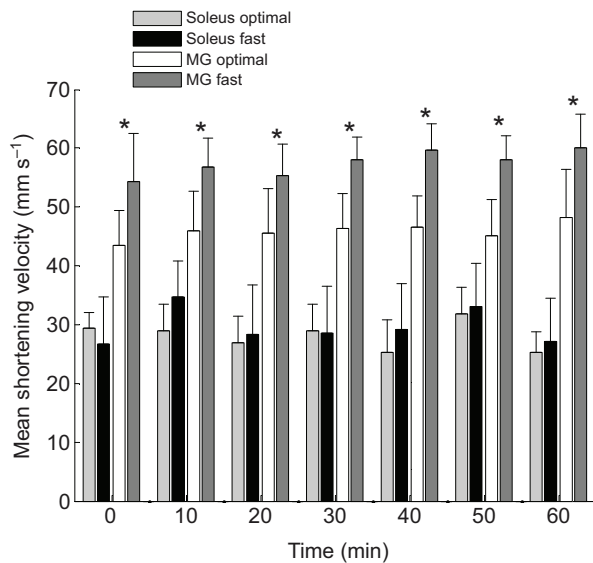


Fig. 3. Mean fascicle shortening velocities calculated during the pushoff phase ($N=11$). Error bars denote ± 1 s.d. Asterisks denote a significant difference between speeds in MG.

occur at sufficiently small energetic cost that there is no observable net effect on COT. Future studies should examine the contribution of individual muscles to total COT during locomotion.

Conclusions

The results of this study may be indicative of a more important functional role for soleus than MG in human walking, particularly when walking for prolonged periods or at faster speeds. In addition to the lower shortening velocities of soleus observed here, this monoarticular muscle has been suggested to make a larger contribution to ankle torque, make greater use of elastic energy storage and reuse, and be metabolically more efficient than the biarticular MG in walking (Krishnaswamy et al., 2011; Neptune et al., 2008). Soleus also has a larger cross-sectional area (Ward et al., 2009) and shorter fascicles than either gastrocnemius head (Maganaris et al., 1998), reducing the required activation volume for a given force. Furthermore, soleus contains $\sim 88\%$ slow-twitch fibres compared with $\sim 50\%$ in MG (Edgerton et al., 1975; Gollnick et al., 1974), and thus relies more on slower fibres with a lower maximal shortening velocity (V_{\max}). Therefore, soleus is probably able to function at higher activation levels more economically than MG, particularly over prolonged periods. Interestingly, in the pushoff phase, soleus shortened at velocities between 0.12 and $0.16V_{\max}$ [based on a resting fascicle length of 35.4 mm (Maganaris et al., 1998) and a V_{\max} for soleus of 6 lengths s^{-1} (Geyer and Herr, 2010)], which is close to the predicted optimum efficiency (Hill, 1964), and was independent of walking speed and duration. Based on these findings, it is more energetically sensible that decreases in MG force would be compensated by increased recruitment of soleus, rather than increased recruitment of MG. We thus hypothesise that during walking, soleus acts as the primary force generator in the triceps surae group by providing efficient propulsion, while MG is more metabolically demanding and less important in this context (Krishnaswamy et al., 2011). The functional importance of MG likely declines with increasing walking speed, whereby MG operates at a progressively shorter length and shortens faster, and thus the contribution of MG force to total ankle torque decreases (Farris and

Sawicki, 2012b). However, it should be noted that the functional roles of the individual muscles may differ between walking and running (Carrier et al., 2011; Farris and Sawicki, 2012b).

LIST OF SYMBOLS AND ABBREVIATIONS

COT	cost of transport
GG	Geisser–Greenhouse
MG	medial gastrocnemius
RQ	respiratory quotient
V_{\max}	maximal shortening velocity

FUNDING

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors.

REFERENCES

- Aggeloussis, N., Giannakou, E., Albracht, K. and Arampatzis, A. (2010). Reproducibility of fascicle length and pennation angle of gastrocnemius medialis in human gait in vivo. *Gait Posture* **31**, 73–77.
- Carrier, D. R., Anders, C. and Schilling, N. (2011). The musculoskeletal system of humans is not tuned to maximize the economy of locomotion. *Proc. Natl. Acad. Sci. USA* **108**, 18631–18636.
- Cavagna, G. A. and Kaneko, M. (1977). Mechanical work and efficiency in level walking and running. *J. Physiol.* **268**, 467–481.
- Cronin, N. J. and Lichtwark, G. (2012). The use of ultrasound to study muscle-tendon function in human posture and locomotion. *Gait Posture* [Epub ahead of print] doi: 10.1016/j.gaitpost.2012.07.024.
- Cronin, N. J., Carty, C. P., Barrett, R. S. and Lichtwark, G. A. (2011a). Automatic tracking of medial gastrocnemius fascicle length during human locomotion. *J. Appl. Physiol.* **111**, 1491–1496.
- Cronin, N. J., Peltonen, J., Sinkjaer, T. and Avela, J. (2011b). Neural compensation within the human triceps surae during prolonged walking. *J. Neurophysiol.* **105**, 548–553.
- Edgerton, V. R., Smith, J. L. and Simpson, D. R. (1975). Muscle fibre type populations of human leg muscles. *Histochem. J.* **7**, 259–266.
- Farris, D. J. and Sawicki, G. S. (2012a). The mechanics and energetics of human walking and running: a joint level perspective. *J. R. Soc. Interface* **9**, 110–118.
- Farris, D. J. and Sawicki, G. S. (2012b). Human medial gastrocnemius force-velocity behavior shifts with locomotion speed and gait. *Proc. Natl. Acad. Sci. USA* **109**, 977–982.
- Finni, T., Komi, P. V. and Lukkariniemi, J. (1998). Achilles tendon loading during walking: application of a novel optic fiber technique. *Eur. J. Appl. Physiol. Occup. Physiol.* **77**, 289–291.
- Finni, T., Kyroläinen, H., Avela, J. and Komi, P. V. (2003). Maximal but not submaximal performance is reduced by constant-speed 10-km run. *J. Sports Med. Phys. Fitness* **43**, 411–417.
- Fukunaga, T., Kubo, K., Kawakami, Y., Fukashiro, S., Kanehisa, H. and Maganaris, C. N. (2001). In vivo behaviour of human muscle tendon during walking. *Proc. Biol. Sci.* **268**, 229–233.
- Geyer, H. and Herr, H. (2010). A muscle-reflex model that encodes principles of legged mechanics produces human walking dynamics and muscle activities. *IEEE Trans. Neural Syst. Rehabil. Eng.* **18**, 263–273.
- Gillett, J. G., Barrett, R. S. and Lichtwark, G. A. (2012). Reliability and accuracy of an automated tracking algorithm to measure controlled passive and active muscle fascicle length changes from ultrasound. *Comput. Methods Biomech. Biomed. Engin.* [Epub ahead of print] doi:10.1080/10255842.2011.633516.
- Gollnick, P. D., Sjödin, B., Karlsson, J., Jansson, E. and Saltin, B. (1974). Human soleus muscle: a comparison of fiber composition and enzyme activities with other leg muscles. *Physiol. Arch.* **348**, 247–255.
- Hill, A. V. (1938). The heat of shortening and the dynamic constants of muscle. *Proc. R. Soc. Lond. B* **126**, 136–195.
- Hill, A. V. (1964). The efficiency of mechanical power development during muscular shortening and its relation to load. *Proc. R. Soc. Lond. B* **159**, 319–324.
- Krishnaswamy, P., Brown, E. N. and Herr, H. M. (2011). Human leg model predicts ankle muscle-tendon morphology, state, roles and energetics in walking. *PLoS Comput. Biol.* **7**, e1001107.
- Lichtwark, G. A. and Wilson, A. M. (2008). Optimal muscle fascicle length and tendon stiffness for maximising gastrocnemius efficiency during human walking and running. *J. Theor. Biol.* **252**, 662–673.
- Maganaris, C. N., Baltzopoulos, V. and Sargeant, A. J. (1998). In vivo measurements of the triceps surae complex architecture in man: implications for muscle function. *J. Physiol.* **512**, 603–614.
- Margaria, R. (1938). Sulla fisiologica e specialmente sul consumo energetico della corsa a varie velocità ed inclinazioni del terreno. *Atti Accad. Naz. Lincei Memorie* **7**, 299–368.
- Martin, P. E., Rothstein, D. E. and Larish, D. D. (1992). Effects of age and physical activity status on the speed-aerobic demand relationship of walking. *J. Appl. Physiol.* **73**, 200–206.
- Neptune, R. R. and Sasaki, K. (2005). Ankle plantar flexor force production is an important determinant of the preferred walk-to-run transition speed. *J. Exp. Biol.* **208**, 799–808.
- Neptune, R. R., Sasaki, K. and Kautz, S. A. (2008). The effect of walking speed on muscle function and mechanical energetics. *Gait Posture* **28**, 135–143.

- Prilutsky, B. I., Herzog, W. and Allinger, T. L.** (1996). Mechanical power and work of cat soleus, gastrocnemius and plantaris muscles during locomotion: possible functional significance of muscle design and force patterns. *J. Exp. Biol.* **199**, 801-814.
- Roberts, T. J., Kram, R., Weyand, P. G. and Taylor, C. R.** (1998). Energetics of bipedal running. I. Metabolic cost of generating force. *J. Exp. Biol.* **201**, 2745-2751.
- Rubenson, J., Pires, N. J., Loi, H. O., Pinniger, G. J. and Shannon, D. G.** (2012). On the ascent: the soleus operating length is conserved to the ascending limb of the force-length curve across gait mechanics in humans. *J. Exp. Biol.* **215**, 3539-3551.
- Ward, S. R., Eng, C. M., Smallwood, L. H. and Lieber, R. L.** (2009). Are current measurements of lower extremity muscle architecture accurate? *Clin. Orthop. Relat. Res.* **467**, 1074-1082.
- Weyand, P. G., Smith, B. R., Puyau, M. R. and Butte, N. F.** (2010). The mass-specific energy cost of human walking is set by stature. *J. Exp. Biol.* **213**, 3972-3979.
- Willis, W. T., Ganley, K. J. and Herman, R. M.** (2005). Fuel oxidation during human walking. *Metabolism* **54**, 793-799.
- Winter, D. A.** (1983). Knee flexion during stance as a determinant of inefficient walking. *Phys. Ther.* **63**, 331-333.