Title

The effect of cadence on the muscle-tendon mechanics of the gastrocnemius muscle during walking.

Short Title

Cadence effects on walking ankle mechanics.

Authors & affiliations

Scott F Brennan[1], Andrew G Cresswell[1], Dominic J Farris[1], Glen A Lichtwark[1]

[1]School of Human Movement & Nutrition Sciences, The University of Queensland, Brisbane, QLD 4072, Australia.

Corresponding author

Mr Scott Brennan
School of Human Movement and Nutrition Sciences
Building 26 - Level 2 - Room 213
Cnr Blair & Union Rd
University of Queensland
T: +61 3365 6482
E: s.brennan@uq.edu.au

Abstract

Humans naturally select a cadence that minimises metabolic cost at a constant walking velocity. The aim of this study was to examine the effects of cadence on the medial gastrocnemius (MG) muscle and tendon interaction, and examine how this might influence lower limb energetics. We hypothesised that cadences higher than preferred would increase MG fascicle shortening velocity because of the reduced stride time. Furthermore, we hypothesised that cadences lower than preferred would require greater MG fascicle shortening to achieve increased muscle work requirements. We measured lower limb kinematics and kinetics, surface electromyography (EMG) of the *triceps surae* and MG fascicle length, via ultrasonography, during walking at a constant velocity at the participants' preferred cadence and offsets of ±10%, ±20% and ±30%. There was a significant increase in MG fascicle shortening with decreased cadence. However, there was no increase in the MG fascicle shortening velocity at cadences higher than preferred. Cumulative MG muscle activation per minute was significantly increased at higher cadences. We conclude that low cadence walking requires more MG shortening work, while MG muscle and tendon function changes little for each stride at higher cadences, driving up cumulative activation costs due to the increase in steps per minute.

Keywords: Human, locomotion, power, work

Introduction

Humans will automatically select a combination stride length and stride duration that minimises the rate of energy expenditure for a constant walking velocity. The preferred stride rate or cadence for a given walking velocity results in the least energy expenditure (Zarrugh & Radcliffe 1978; Holt et al. 1991; Minetti et al. 1995). Humans may have to use small variations in cadence to adapt to specific conditions, such as walking in a crowded space. However the more pertinent issue is why humans gravitate to a narrow range of preferred cadences. While it is clear in the literature that non-preferred walking patterns result in increased rates of energy expenditure, the link to neuromuscular mechanisms is less clear.

The amount of energy consumed during gait is related to the amount of force and work muscles must generate and the contractile conditions under which force and work are generated. The inverted pendulum model of walking suggests that muscle forces are predominantly generated to support body weight and propel the body forward between steps (Cavagna et al. 1977). This can be achieved with seemingly low metabolic cost because of the out of phase exchange of gravitational potential and kinetic energies. More recent models adapted the basic inverted pendulum with that of a spring-mass model that would normally be associated with running or hopping (Geyer et al. 2006). In this way the model better represents the centre of mass (COM) trajectory (which is not perfectly circular) and reflects the compliant nature of the leg, which is able to compress and recoil during the gait cycle. This is particularly important during the transition period from late stance until opposite limb heel strike. The coordination of collision and push off work is necessary for reducing metabolic cost of walking, where the COM trajectory must be redirected from downward in late stance to upward for the consecutive step (Donelan et al. 2002). These step-to-step transition models suggest that walking with longer stride lengths increases the negative collision work and corresponding positive push-off work that must be done to transition between consecutive steps and that this makes walking at slow cadences energetically costly. Such analyses provide evidence for why mechanical work requirements vary with spatiotemporal gait parameters, but they do not provide much information about how lower limb muscle function is modulated to meet these changing mechanical demands.

An inverse dynamics approach allows for calculation of joint level mechanical work, which may provide insight into what muscle groups are contributing to mechanical work. Umberger & Martin (2007) measured the effect of cadence on joint level mechanical powers for a constant walking velocity. They found minimal mechanical power at cadences 12% below preferred and maximal efficiency at cadences 8% above preferred. Total limb positive mechanical power increased at cadences above preferred, largely due to an increased hip positive power. At cadences slower than preferred, the ankle contributed a greater proportion of the total positive power requirements. The authors attributed the selection of preferred cadence to be a compromise between work and efficiency. However, one of the limitations of analysing work at the joint level is that one cannot account for transfer of power via biarticular muscles or torque due to co-contraction of antagonist muscles. It also fails to distinguish between work provided actively by contractile elements within the muscle and energy that has been elastically cycled in aponeuroses and tendons. For example, approximately forty percent of positive leg joint work during walking occurs about the ankle joint (Farris & Sawicki 2011) but over half of this is estimated to be elastic energy returned by the Achilles tendon that was stored earlier in stance (Sasaki et al. 2009; Farris & Sawicki 2012).

In walking, the compliant nature of the Achilles tendon and aponeuroses allows the active contractile tissues of the *triceps surae* muscles to shorten at relatively slow velocities while rapid shortening of the muscle-tendon unit is achieved through high velocity recoil of the series elastic tissues (Lichtwark et al. 2007). This is beneficial for force production and energetic cost because the muscles may act at more favourable lengths and shortening velocities while performing little mechanical work (Lichtwark & Wilson 2007). However, it has been shown that when walking at speeds above preferred, the velocity of MG fascicle shortening increases (Farris & Sawicki 2012), presumably requiring increased activation of MG to meet the required levels of MG force. Fascicle velocity may be a factor in the selection of preferred gait parameters because of its influence on force production and might change with varied cadence.

The aim of the present study was to investigate the effect of manipulating cadence on MG muscle mechanics while walking at a constant velocity. We hypothesised that MG fascicle shortening velocity would be greater at cadences faster than preferred due to the increased stride rate and consequently, decreased stride time to produce the required work. We also predicted that activation of the plantar flexors would increase because of an impaired force producing capacity at faster shortening rates in accordance with the force-velocity relationship. We also hypothesised that stride rates lower than preferred would result in greater MG fascicle shortening and peak activation because of increased positive power requirements at the ankle (Umberger & Martin 2007).

Material & Methods

Participants

Fifteen healthy participants (9 male, 6 female), age 24 ± 3.5 (mean ± S.D.) years, height 175 ± 8.5 cm and mass 72 ± 9.3 kg gave written consent to participate in this study. The study was approved by the University of Queensland Human Movement & Nutrition Studies ethics committee. Kinematic data was collected from 7 participants walking on a motorized treadmill (Austredex AC190, Doncaster, VIC, Australia) while kinematic and kinetic data were collected from 8 participants walking on an instrumented treadmill (AMTI DBCEEWI, Watertown, MA, USA). Participants were recruited from the staff and students of the University of Queensland.

Protocol

Height, body mass and right leg length (taken from the most prominent points of the greater trochanter and lateral malleolus) were recorded for each participant. Participants were asked to walk at the same normalised speed for all movement trials while cadence was randomised across conditions. A standardised walking speed adjusted for leg length was used for each participant. The walking speed was based on a Froude number of 0.25 [$Fr = v^2/gL$, where v is the speed of locomotion, g is gravitational acceleration and L is limb length], which is close to the preferred walking speed that minimises cost of transport (Minetti 2001). Participants were asked to walk for one minute while the preferred cadence was calculated as the total number of steps taken divided by time. All of the participants had prior experience with walking on motorized treadmills at the moderate walking velocities prescribed in this protocol. Participants completed the protocol barefoot, to reduce any footwear effects. For the other experimental conditions, the preferred cadence was offset by ±10%, ±20% and ±30% to manipulate the normal velocity-cadence relationship. Participants were required to match the target cadence for a minimum of one minute before data collection. Representative fascicle length data requires approximately 6 strides of data (Aggeloussis et al. 2010), therefore the data collection period allowed for a minimum of 6 strides. The absolute time of data collection varies for each participant due to the different speed and cadence in each trial. During trials that required a non-preferred cadence, participants received step frequency feedback via visual (LED's and pendulum) and auditory (beats for left and right heel strike) cues from a metronome (Boss TU-80, Roland Corp., Los Angeles, CA, USA) positioned on the treadmill control panel. Data collection was synchronised using a TTL pulse from the ultrasound unit to signal the motion capture and electromyography systems to start/stop capture.

Kinetics and kinematics

An 8 camera motion analysis system (Qualysis, Gothenburg, Sweden) was used to capture the position of 19 passive, reflective markers (200 Hz). A static capture of the markers was used to define the thigh, shank and foot in a standing position with hands crossed to opposite shoulder. Individual markers were placed on the greater trochanter, medial and lateral condyles of the knee, medial and lateral malleoli at the ankle, calcaneus and 1st and 5th metatarsal heads. During dynamic trials, marker clusters were positioned laterally on the mid thigh and mid shank as well as superiorly on the foot. Raw marker positions were filtered using a 15 Hz, low-pass, 2nd order Butterworth filter, performing one bidirectional pass to remove high frequency movement artefact. All data were exported for analysis in Visual 3D software (C-motion Inc., Germantown, MD, USA). An inverse kinematic model of the right lower limb was developed and applied to the data. Force signals were filtered using the same frequency as marker position data (15 Hz)(Kristianslund et al. 2012). An inverse dynamics analysis was then used to compute the ankle joint moments and mechanical powers. Mechanical work and joint moment calculations were normalized to the participants body mass. Metrics of ankle mechanics were calculated during the phase of positive ankle power production associated with push-off.

Muscle-tendon measures

Musculotendinous unit (MTU) length for the MG was estimated using Grieve's regression equation (Grieve et al. 1978). Muscle fascicle length of the medial gastrocnemius was measured using B-mode ultrasound imaging. A flat ultrasound transducer (LV7.5/60/96Z, TELEMED, Vilnius, Lithuania) was positioned over the mid-belly of the medial gastrocnemius to show the muscle fascicles as well as deep and superficial aponeuroses, using a similar technique to previous research (Lichtwark et al. 2007). The ultrasound transducer was secured to the skin using an adhesive bandage to reduce rotation or translation of the transducer during movement trials. Ultrasound images were recorded at 6 MHz frequency, image depth of 50 mm and a frame rate of 80 Hz (Logicscan 128, TELEMED, Vilnius, Lithuania). Measurements of fascicle length and pennation angle were made offline using a custom Matlab script (MathWorks Inc., Natick, USA). The custom Matlab script uses a semi-automatic tracking algorithm, which has been shown to provide valid and reliable measurements during gait studies (Cronin et al. 2011). Fascicle and MTU lengths were normalised to the respective mean length during the preferred walking condition. It is assumed that the difference in length changes between the MTU and fascicles is reflective of the contributions of the tendon and associated connective tissue. MG fascicle length change and velocity measurements were made during the period of positive ankle power production for the participants that completed the protocol on the instrumented treadmill. For those participants without force data, the onset of positive ankle joint velocity was used as a marker for the onset of positive ankle power and toe-off used as the marker for cessation of positive power. To correctly scale the fascicle and MTU lengths for the fascicle shortening:MTU shortening ratio, the MTU lengths were normalised to the mean fascicle length of the preferred condition. Fascicle velocity was calculated as the derivative of the normalised length signal. Fascicle length change was calculated as the amount of shortening during the period of right ankle positive power.

Muscle activation

Electromyography was used to measure the electrical activity of the MG, LG, SOL and TA muscles (MA-300, Motion Lab Systems inc. Baton Rouge, LA, USA). The recording sites were prepared by shaving, cleaning the skin using an abrasive gel and sterilized with alcohol. The fibular head was used to position the ground electrode. Surface EMG electrodes were placed on the belly of the muscle following SENIAM guidelines (Hermens et al. 2000), with an inter-electrode distance of 2 cm. EMG signals were collected at 2 kHz and processed using a moving root mean square (RMS) with a time window of 0.05 seconds to create an EMG envelope. The EMG envelope for each participant was normalized across conditions to the mean of the maximal activation per stride during preferred walking. Therefore the EMG values presented are shown as arbitrary units (au) relative to the activation during preferred walking. The time integral of the EMG envelope was used to calculate the area under the EMG curve, quantifying the amount of muscle activation, referred to as the integrated EMG. In addition to analysing the data per stride, the integrated EMG was also adjusted to account for the different cadences used in each condition. To do this we calculated cumulative muscle activation per minute (au/min) by multiplying the mean integrated EMG per step (au/step) by the mean cadence (steps/min) for each condition (Carrier et al. 2011).

Data for each condition was averaged across every full stride cycle from right heel strike. Since kinetic data was not available for all of the participants, the sagittal plane kinematics of the right calcaneus marker was used to determine the time of heel strike. All data was exported for statistical analysis using Graphpad Prism. A one-way repeated measures ANOVA was performed. A Holm-Sidak multiple comparisons test was also performed, comparing the preferred condition versus percentage cadence offsets. Two participants had lower than preferred image quality during the -30% condition and hence could not be tracked. To accommodate this, multiple imputations were performed for the missing fascicle data points, re-digitising the missing data. The pooled multiple imputations data was then used to run the repeated measures ANOVA. Alpha was set to 0.05 for all statistical tests.

Results

The mean limb length for the 15 participants was 82.8 ± 4.2 cm (mean ± S.D.) and mean walking velocity was 1.43 ± 0.04 m/s. The preferred cadence used by the participants was 124 ± 3.6 steps/min. The actual cadence was calculated offline from the kinematic data, to determine how successful the participants were at matching the cadence set by the metronome. The mean differences between target and actual cadence (strides/min) were -0.44 ± 1.6, -0.60 ± 1.3, -0.07 ± 0.36, 1.5 ± 2.2, -0.1 ± 0.49, 0.42 ± 1.1 and 0.47 ± 1.7 respectively, from slowest to fastest cadence.

Kinetics and kinematics

Average right ankle moment, normalised to body mass, was significantly different across cadences (Fig. 1B). While there was no significant post hoc differences versus preferred, there was a trend for greater average ankle moments at slower cadence. A significant main effect of cadence was found on average positive ankle velocity, with greater average velocities found at slower cadences (Fig. 1C). Post hoc comparisons found significant differences between preferred cadence and all other conditions except the +30% cadence. Ankle average positive power was significantly different across conditions, with greater positive power at slower stride rates compared to the preferred condition and similar work rates between the preferred condition and increased stride rates (Fig. 1D). Post hoc tests found significant differences between the -20% cadence offset and the preferred cadence. There was a systematic decrease in ankle joint range of motion as cadence increased, showing a significant main effect of cadence as well as significant differences between all conditions versus preferred walking. Peak vertical ground reaction force per stride was not significantly different across conditions or compared to preferred walking. The group mean force (normalised to body mass) was 10.94 ± 1.10, 11.79 ± 0.49, 11.97 ± 0.45, 11.89 ± 0.38, 12.03 ± 0.24, 11.63 ± 0.79 and 11.27 ± 0.95 N/kg respectively, from slowest to fastest cadence.

Fascicle mechanics

Group mean MTU length, MG muscle fascicle length and fascicle shortening velocity are shown in Fig. 2. Throughout early stance, the MTU lengthens while the fascicles remain relatively isometric (Fig. 2A). Between mid stance and push off the fascicles then shorten rapidly, during the period of positive power production at the ankle (Fig. 2B, C). Although the absolute time of a single stride is different, when normalised to the same time scale (% stride) the pattern of length changes in the MTU and muscle fascicles remained relatively consistent across cadence conditions (Fig. 2A, B). A significant effect of cadence was found on the amount of MG fascicle shortening during positive ankle power production. The amount of MG fascicle shortening increased as cadence decreased (Fig. 3A). Post hoc tests showed significant differences for the -30% cadence, but no other conditions. There was also a significant main effect of cadence on MTU shortening during ankle positive power, with greater amounts of MTU shortening occurring as cadence decreased (Fig. 3A). Significant differences in MTU shortening were found between all conditions and the preferred stride rate. As an indication of fascicle work relative to MTU work, we also calculated the fascicle shortening:MTU shortening ratio (Fig. 3B). There was a significant main effect of cadence where the ratio generally increased as cadence decreased. The average fascicle shortening velocity during positive power production was not significantly different across conditions (Fig. 3C).

Muscle activation

The maximal muscle activation per stride was significantly different to the preferred cadence across conditions for all muscles except MG (Fig. 4). Peak activation was significantly higher at the slowest cadences in SOL, LG and TA. In these muscles, there was no significant change in the peak EMG between preferred cadence and faster cadences. However, cadence did have a significant main effect on cumulative integrated EMG of the MG and LG with significant increases at higher cadences compared to the preferred cadence for MG.

Discussion

In this study we examined the effect of stride rate on MG fascicle mechanics, ankle mechanics and the activation of *triceps surae* and TA muscles during walking. Our data provides novel insight into how ankle muscle and tendon function varies with walking cadence and therefore can help us understand why humans prefer to walk at a particular cadence. As hypothesised, walking at slower cadences increased average ankle positive power and MG fascicle shortening during positive power production. An increased amount of fascicle shortening, with apparent increases in the load supported by the muscle (as indicated by an increase in the average ankle moment during power production) at slower cadences suggested that there were greater muscular work requirements for MG at slow cadences. There were also increases in peak EMG of LG and SOL muscles at slow cadences, suggesting greater activation costs associated with producing the additional force and work requirements. Contrary to our other hypothesis, cadences faster than preferred did not produce increases in MG fascicle shortening velocity or peak MG EMG. While there was increased cumulative activation of the MG at faster cadences (therefore requiring more total activation), it appears that MG fascicle mechanics were not modulated to meet the increasing limb power requirements at cadences above preferred.

Slower than preferred cadence

Humans may prefer not to utilise slow stride rates because of the greater ankle positive mechanical power and plantar flexor moment requirement compared to preferred (Fig 1B, D). Umberger & Martin (2007) showed that the ankle provides a significant proportion of the summed limb positive power at slow cadences (approximately 55% of summed power at -20% cadence). Similarly, our results demonstrate that walking with slower cadences resulted in increased ankle moment, increased ankle joint velocity and increased ankle joint power (Fig. 1). An increased average ankle moment would suggest greater force requirements of the plantar flexor muscles, which likely comes at a greater energetic cost. The energetic cost of increased ankle power is, however, dependent on the fascicle length and velocity conditions under which the muscles produce force and these may be influenced by the role of elastic tissues.

Our results demonstrated that walking at a slower cadence resulted in increased fascicle shortening (and presumably work) as well as MTU shortening. These changes were not proportional and resulted in a significant increase in the fascicle shortening to MTU shortening ratio at slower than preferred cadences, showing that fascicle shortening comprised a greater proportion of total MTU shortening with decreasing cadence (Fig. 3B). The requirement for increased fascicle shortening, relative to MTU shortening, at slower cadences is evidence that the increased ankle joint power production is not fully accounted for by increased energy cycled in the tendon. The muscle contractile tissue must have produced the extra positive work (rather than the elastic tissues) at slow cadences because there was no increase in the negative ankle joint power available to stretch the tendon in early stance (Figure 1D). The increased amount of force required by the plantar flexors and the increased shortening required may contribute to the increase in energetic cost at reduced stride rates that has previously been reported by Umberger & Martin (2007).

Faster than preferred cadence

In contrast to slow stride rates, where ankle work requirements increased, faster cadences did not result in concomitant changes in average ankle moment and positive power, despite the increased movement rate. We found less MG fascicle shortening during ankle joint positive power production at cadences higher than preferred and no net changes in the fascicle shortening velocities (Fig. 3A, C). This is in contrast to our initial hypothesis that average fascicle shortening velocity would increase at faster than preferred cadences. It is apparent that the ankle range of motion becomes progressively smaller at higher cadences in order to reduce contact time. This pattern of movement may make it difficult to use the plantar flexors for propulsion at high cadences.

While elasticity may assist in producing positive power and reducing collision losses (Zelik et al. 2014), the reduced stance time at faster cadences may limit the capacity for generating force and storing elastic energy that can be used to power push-off. We observed similar average ankle joint moments with much shorter stance time at high cadences compared to the preferred cadence. Therefore, it seems like there is a limit to the amount energy stored in series elastic structures (which is proportional to the forces applied) as cadence increased and this may have constrained the capacity for power production at the ankle. While it is conceivable that the muscle fibres might be able to contribute more work during elastic recoil of the tendon, increasing muscle activation during this propulsive period would only serve to reduce the rate at which energy is released from the tendon and hence it is unlikely that this would enable greater power production at the ankle. This would be consistent with the findings of Umberger & Martin (2007) that showed the total limb (hip, knee and ankle) joint positive power increased at higher than preferred cadences, largely because of an increase in hip joint positive power. The knee joint primarily absorbs energy, exhibiting greater negative power at higher than preferred cadence. The ankle joint does not show a large increase in positive power, despite the increase in overall limb power. Therefore, because of the force constraints and the reliance on elastic energy storage and return in the Achilles tendon, it may become increasingly difficult to generate power at the ankle with cadences higher than preferred.

The preceding rationale provides a thesis based on mechanical power requirements. However, one might also consider that ankle and gastrocnemius mechanics are dictated by work requirements for individual steps. As cadence increases, step length decreases and this has been shown to reduce external positive work requirements per stride, owing to smaller collisional energy losses in the step-to-step transition (Donelan et al. 2002). From this perspective, it could be postulated that ankle work requirements actually decrease with increased cadence and therefore an alternate hypothesis could be formed that there should be no need to increase gastrocnemius fascicle shortening, fascicle velocity or elastic recoil. This might explain the present results showing that fascicle velocity (Fig 2C) and ankle power (Fig 1D) did not increase at cadences above preferred. However, the additional external power requirement of maintaining speed at higher cadences must be met somehow and this will ultimately be important for the cost of transport for walking. Therefore, our initial consideration of why the ankle is not used to increase power requirements remains pertinent.

There was not a decrease in peak muscle activation of the plantar flexors at high cadence compared to preferred walking. This may suggest that the cost of generating force *per stride* remained similar to preferred walking for the plantar flexor muscles, since the average ankle moment also remained similar to preferred. However the costs of plantar flexor activation are summative for a given distance or time, and the higher *cumulative* activation that we report may be a source of increased metabolic cost with increasing cadence. The increased plantar flexion cumulative activation is likely the result of having similar joint moment and muscle shortening requirements for each stride, and therefore similar peak muscle activation requirements per stride, whilst the number of strides taken over a period of time increases. The greater quantity of short duration contractions may also result in an increased energetic cost for the plantar flexors. In-situ muscle preparations that varied the contraction duration while maintaining a constant total time of contraction have shown that short duration contractions significantly increase muscle O_2 cost of force development, ATP utilization and muscle lactate concentration (Hogan et al. 1998). This indicates that contraction duration can significantly affect the metabolic cost of repetitive contractions such as those found in walking. In addition, the shift in power production to the hip (Umberger & Martin 2007) and an increased requirement to swing the leg at higher rates (Doke & Kuo 2007) will also increase the required muscle activation levels of the hip musculature and is likely to contribute to the increased energetic rate for the entire body at high cadences.

Limitations

There are a large number of muscles that actuate individual joints during walking. In this study we recorded and tracked fascicle length changes in MG across conditions, and assumed that this was similar to the other muscles of the triceps surae. It is likely that changes in cadence resulted in changes to SOL fascicle length or shortening velocity during walking, since SOL is also mechanically decoupled from the MTU via the series elastic tissues (Rubenson et al. 2012). Fascicle length changes do differ slightly between MG and SOL during walking at the preferred cadence (Cronin et al. 2013; Cronin et al. 2013), with SOL experiencing slightly slower maximum shortening speeds. However the pattern and timing of fascicle shortening is very similar, as this is dictated primarily by the stretch and recoil of the common tendon that is generating force around the ankle. Therefore, with the changes in force requirements at different cadences and limited knee flexion during most of the stance phase, we would expect to see similar trends in the length changes of SOL, MG and LG. However, further experimental work is required to confirm this hypothesis.

The focus of this study was the ankle joint and a key muscle that crosses this joint. However, changes in the contributions of leg joints to overall power production during walking make it difficult to draw strong conclusions regarding the links between muscle mechanics of muscles crossing the ankle and energetic cost of the entire body based on data for ankle muscle only. It is not clear whether unfavourable energetic costs are due primarily to the shift in power contribution from proximal muscles that may also affect the economy of movement. The muscle lengths used in this study were calculated using a kinematics based equation (Grieve et al. 1978). This allowed for estimation of muscle length based on segment lengths and joint angles, although it does not account for individual variations in joint geometry that may influence muscle length changes. However these kinematic models remain our best descriptive method of determining muscle length changes in vivo. We are also assuming that the preferred cadence condition is the most economical because of the abundance of published literature that relates energetics to variations of stride rate

(Zarrugh & Radcliffe 1978; Holt et al. 1991).

Conclusions

In conclusion, previous research shows the naturally selected cadence is the most cost effective method of transport for a given walking velocity (Zarrugh & Radcliffe 1978; Holt et al. 1991). Here we have shown that walking at a slower stride rate than preferred increased maximal muscle activation of LG and SOL and increased shortening of MG fascicles during positive ankle power production. This reflects energetically less favourable muscle mechanics that may contribute to the commonly observed increase in energetic costs associated with slower cadence walking. At faster stride rates than preferred we observed greater cumulative activation of plantar flexors, in the absence of increased fascicle shortening or shortening velocities. We suggest that the ankle joint capacity to significantly increase energy storage and return is constrained at high cadences because of the plateau in joint moment that reflects force in the tendon. This results in a shift in power production from the ankle to the more proximal muscles that can produce more power but may be less economical. Our results provide new evidence of muscular level mechanisms that may help understand how humans select preferred cadence.

Perspectives

This study provides valuable new information about how the gastrocnemius muscle functions when humans walk with energetically non-optimal cadences. It highlighted that knowledge of external mechanics is often insufficient for understanding optimal movement strategies. At all cadences, the same net goal was achieved (walking at a given velocity) but gastrocnemius muscle mechanics adapted in ways that could not be easily predicted from joint mechanics because of the influence of tendon elasticity. This had implications for muscle activations and, ultimately, will influence which strategy is optimal for minimising the energetic cost of locomotion. Such considerations are important for human movement, sports performance and sports medicine because each of these fields seeks to understand optimal movement strategies for purposes such as maximising performance and minimising injury risk. This research emphasises the need to examine movement at the muscular level when trying to understand how forces for movement are generated and how we can optimise muscle function, particularly for muscles with significant tendon elasticity. It remains to be seen whether tendon compliance can be tuned to minimise energetic cost or injury risk in trained movements or whether the nervous system can use feedback from the muscle-tendon system to optimise movement efficiency.

Acknowledgements

Scott Brennan is supported by an Australian Postgraduate Scholarship. Dominic Farris is supported by the Australian Sports Commission.

Conflict of Interest

The authors have no conflict of interest to declare in the publication of this manuscript.

References

Aggeloussis N, Giannakou E, Albracht K, Arampatzis A. Reproducibility of fascicle length and pennation angle of gastrocnemius medialis in human gait in vivo. *Gait & posture*. 2010: **31**: 73-77.

Carrier DR, Anders C, Schilling N. The musculoskeletal system of humans is not tuned to maximize the economy of locomotion. *Proc Natl Acad Sci USA*. 2011: **108**: 18631-18636.

Cavagna GA, Heglund NC, Taylor CR. Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am J Physiol*. 1977: **233**: R243-R261.

Cronin NJ, af Klint R, Grey MJ, Sinkjaer T. Ultrasonography as a tool to study afferent feedback from the muscle-tendon complex during human walking. *Journal of Electromyography and Kinesiology*. 2011: **21**: 197-207.

Cronin NJ, Avela J, Finni T, Peltonen J. Differences in contractile behaviour between the soleus and medial gastrocnemius muscles during human walking. *J Exp Biol*. 2013: **216**: 909-914.

Cronin NJ, Prilutsky BI, Lichtwark GA, Maas H. Does ankle joint power reflect type of muscle action of soleus and gastrocnemius during walking in cats and humans? *J Biomech*. 2013: **46**: 1383-1386.

Doke J, Kuo AD. Energetic cost of producing cyclic muscle force, rather than work, to swing the human leg. *J Exp Biol*. 2007: **210**: 2390-2398.

Donelan JM, Kram R, Kuo AD. Mechanical work for step-to-step transitions is a major determinant of the metabolic cost of human walking. *J Exp Biol*. 2002: **205**: 3717-3727.

Farris DJ, Sawicki GS. The mechanics and energetics of human walking and running: a joint level perspective. *JR Soc Interface*. 2011: **9**: 110-118.

Farris DJ, Sawicki GS. Human medial gastrocnemius force-velocity behavior shifts with locomotion speed and gait. *Proc Natl Acad Sci USA*. 2012: **109**: 977-982.

Geyer H, Seyfarth A, Blickhan R. Compliant leg behaviour explains basic dynamics of walking and running. *Proceedings of the Royal Society B-Biological Sciences*. 2006: **273**: 2861-2867.

Grieve DW, Pheasant S, Cavanagh PR. Prediction of gastrocnemius length from knee and ankle joint posture. In: Asmussen E, Jorgensen K, eds. *Proceedings of the Sixth International Congress of Biomechanics*. Baltimore: University Park Press, 1978:405-412.

Hermens HJ, Freriks B, Disselhorst-Klug C, Rau G. Development of recommendations for SEMG sensors and sensor placement procedures. *Journal of Electromyography and Kinesiology*. 2000: **10**: 361-374.

Hogan MC, Ingham E, Kurdak SS. Contraction duration affects metabolic energy cost and fatigue in skeletal muscle. *Am J Physiol-Endoc M*. 1998: **274**: E397-E402.

Holt KG, Hamill J, Andres RO. Predicting the minimal energy costs of human walking. *Med Sci Sports Exerc*. 1991: **23**: 491-498.

Kristianslund E, Krosshaug T, van den Bogert AJ. Effect of low pass filtering on joint moments from inverse dynamics: implications for injury prevention. *J Biomech*. 2012: **45**: 666-671.

Lichtwark GA, Bougoulias K, Wilson AM. Muscle fascicle and series elastic element length changes along the length of the human gastrocnemius during walking and running. *J Biomech*. 2007: **40**: 157-164.

Lichtwark GA, Wilson AM. Is Achilles tendon compliance optimised for maximum muscle efficiency during locomotion? *J Biomech*. 2007: **40**: 1768-1775.

Minetti AE. Walking on other planets. *Nature*. 2001: **409**: 467, 469.

Minetti AE, Capelli C, Zamparo P, di Prampero PE, Saibene F. Effects of stride frequency on mechanical power and energy expenditure of walking. *Med Sci Sports Exerc*. 1995: **27**: 1194-1202.

Rubenson J, Pires NJ, Loi HO, Pinniger GJ, Shannon DG. 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*. 2012: **215**: 3539-3551.

Sasaki K, Neptune RR, Kautz SA. The relationships between muscle, external, internal and joint mechanical work during normal walking. *J Exp Biol*. 2009: **212**: 738-744.

Umberger BR, Martin PE. Mechanical power and efficiency of level walking with different stride rates. *J Exp Biol*. 2007: **210**: 3255-3265.

Zarrugh MY, Radcliffe CW. Predicting Metabolic Cost of Level Walking. *Eur J Appl Physiol*. 1978: **38**: 215-223.

Zelik KE, Huang TWP, Adamczyk PG, Kuo AD. The role of series ankle elasticity in bipedal walking. *J Theor Biol*. 2014: **346**: 75-85.

Figure 1.

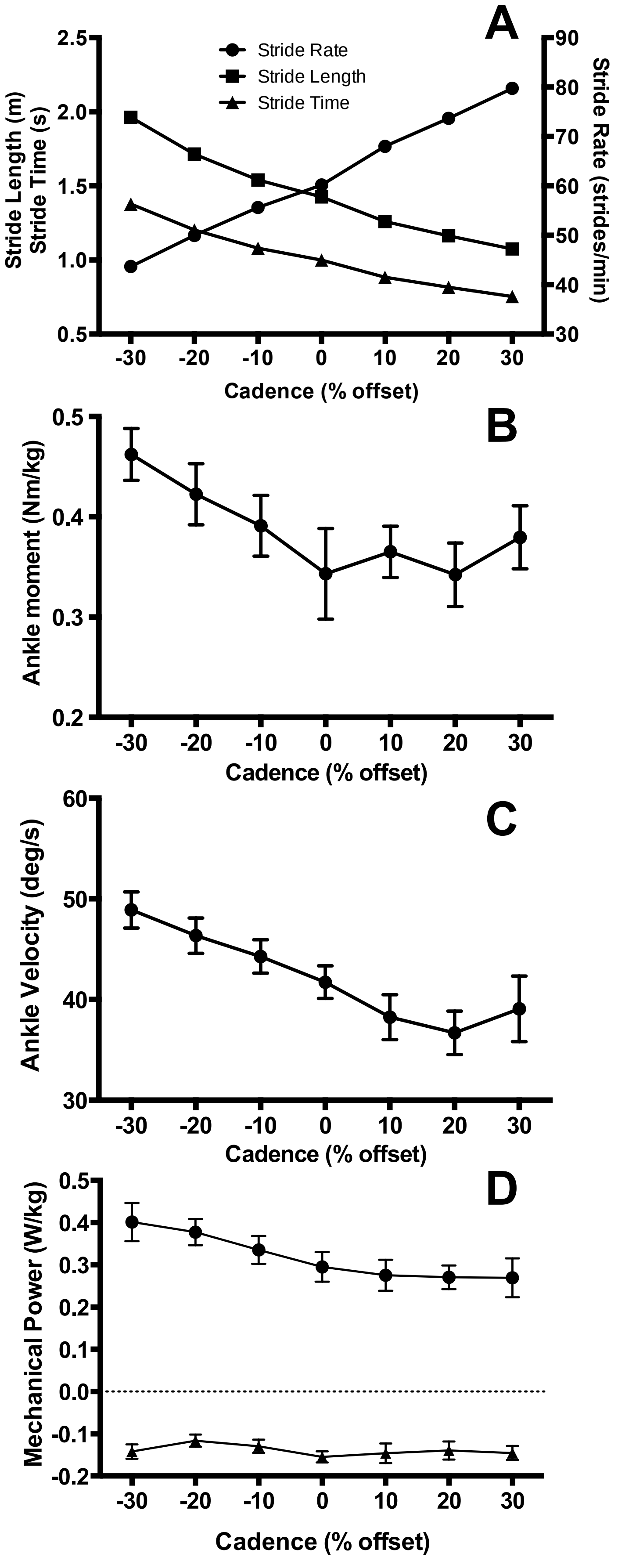
A
Stride Rate
Stride Length
Stride Time
Stride Length (m)
Stride Time (s)
Stride Rate (strides/min)
2.5
2.0
1.5
1.0
0.5
90
80
70
60
50
40
30
-30
-20
-10
0
10
20
30
Cadence (% offset)
B
Ankle moment (Nm/kg)
0.5
0.4
0.3
0.2
-30
-20
-10
0
10
20
30
Cadence (% offset)
C
Ankle Velocity (deg/s)
60
50
40
30
-30
-20
-10
0
10
20
30
Cadence (% offset)
D
Mechanical Power (W/kg)
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-30
-20
-10
0
10
20
30
Cadence (% offset)

Figure 2.

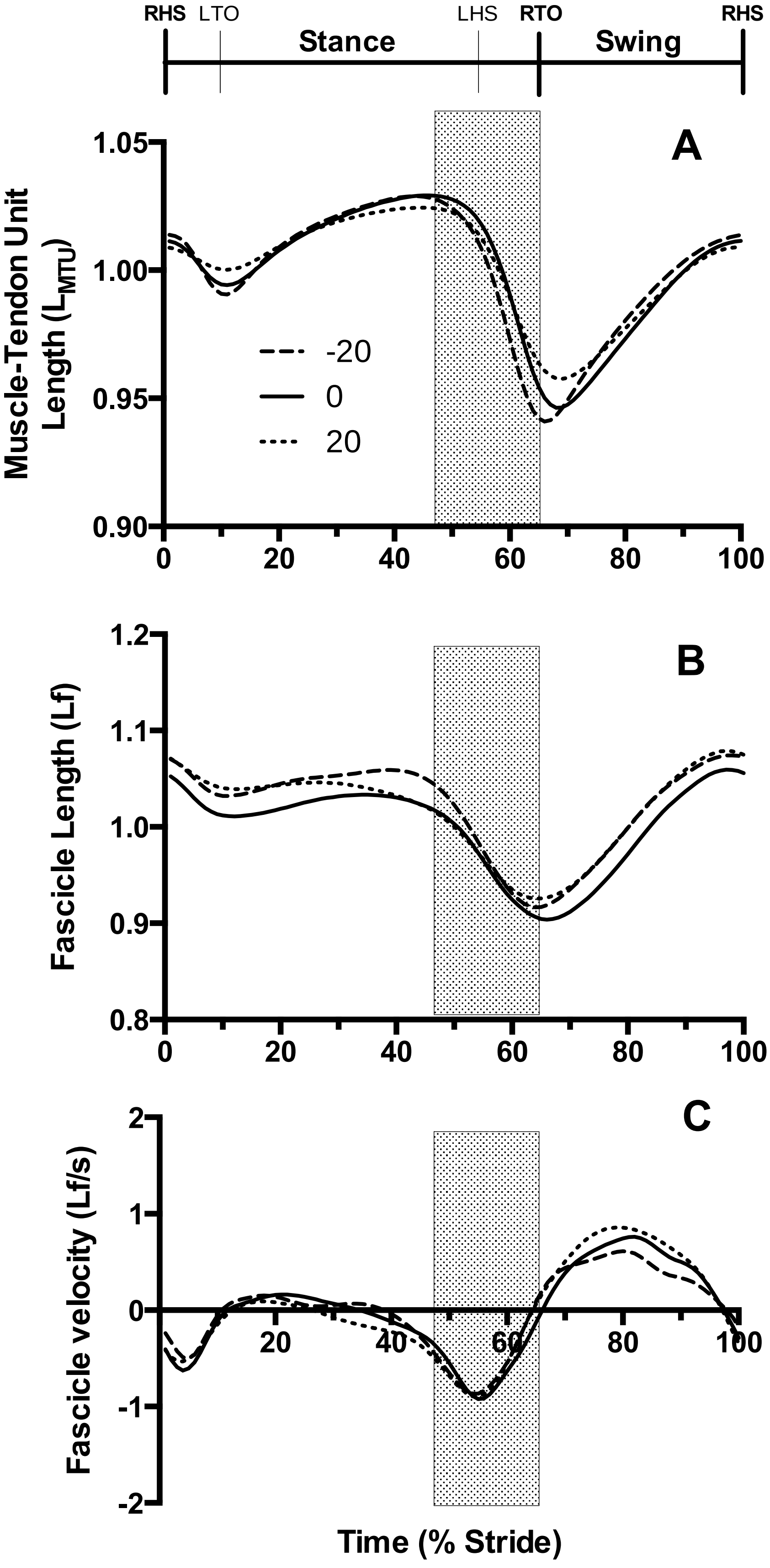
RHS
LTO
Stance
LHS
RTO
Swing
RHS
A
Muscle-Tendon Unit Length (L_{MTU})
1.05
1.00
0.95
0.90
-20
0
20
0
20
40
60
80
100
B
Fascicle Length (Lf)
1.2
1.1
1.0
0.9
0.8
0
20
40
60
80
100
C
Fascicle velocity (Lf/s)
2
1
0
-1
-2
20
40
60
80
100
Time (% Stride)

Figure 3.

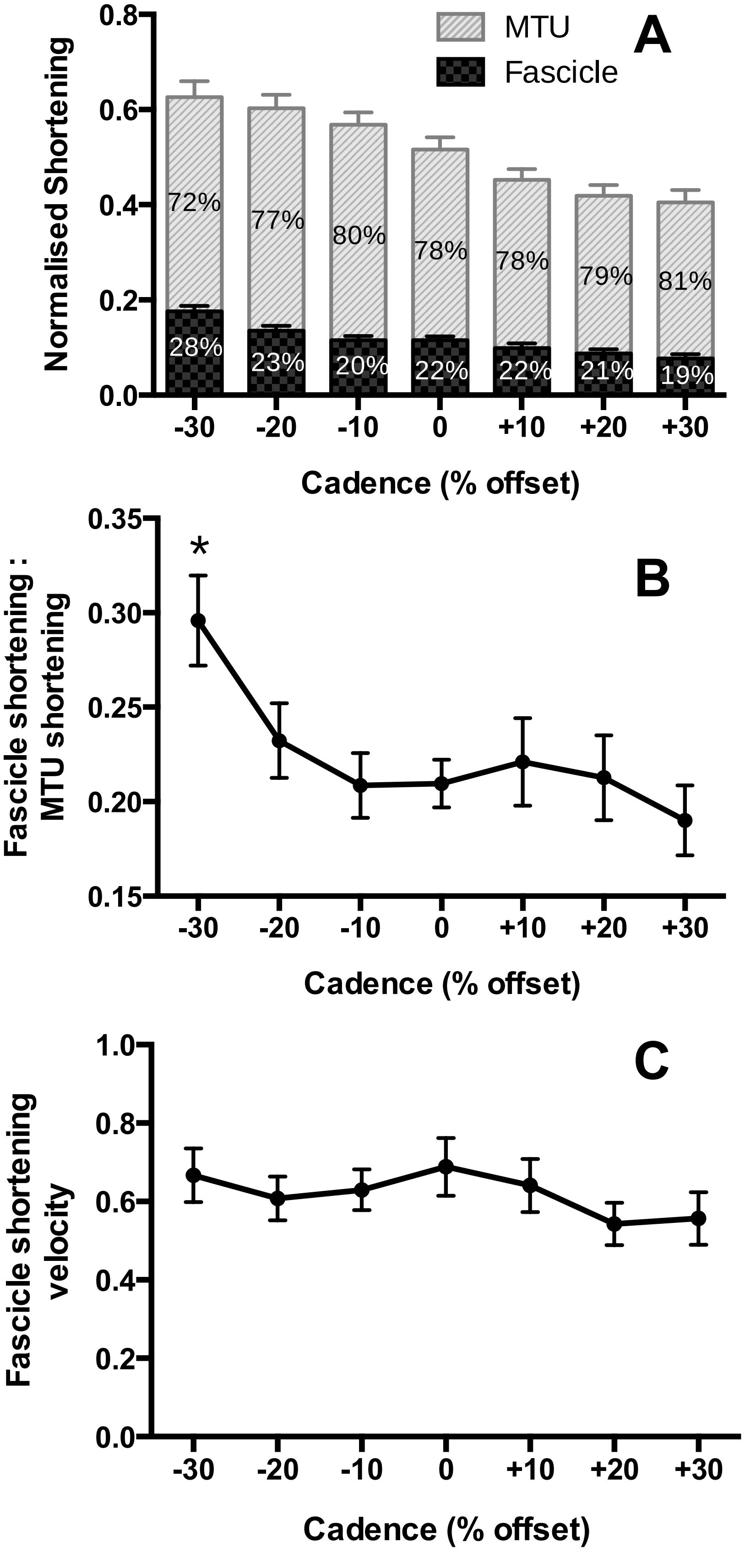
A
MTU
Fascicle
Normalised Shortening
0.8
0.6
0.4
0.2
0.0
72%
77%
80%
78%
78%
79%
81%
28%
23%
20%
22%
22%
21%
19%
-30
-20
-10
0
+10
+20
+30
Cadence (% offset)
B
*
Fascicle shortening : MTU shortening
0.35
0.30
0.25
0.20
0.15
-30
-20
-10
0
+10
+20
+30
Cadence (% offset)
C
Fascicle shortening velocity
1.0
0.8
0.6
0.4
0.2
0.0
-30
-20
-10
0
+10
+20
+30
Cadence (% offset)

Figure 4.

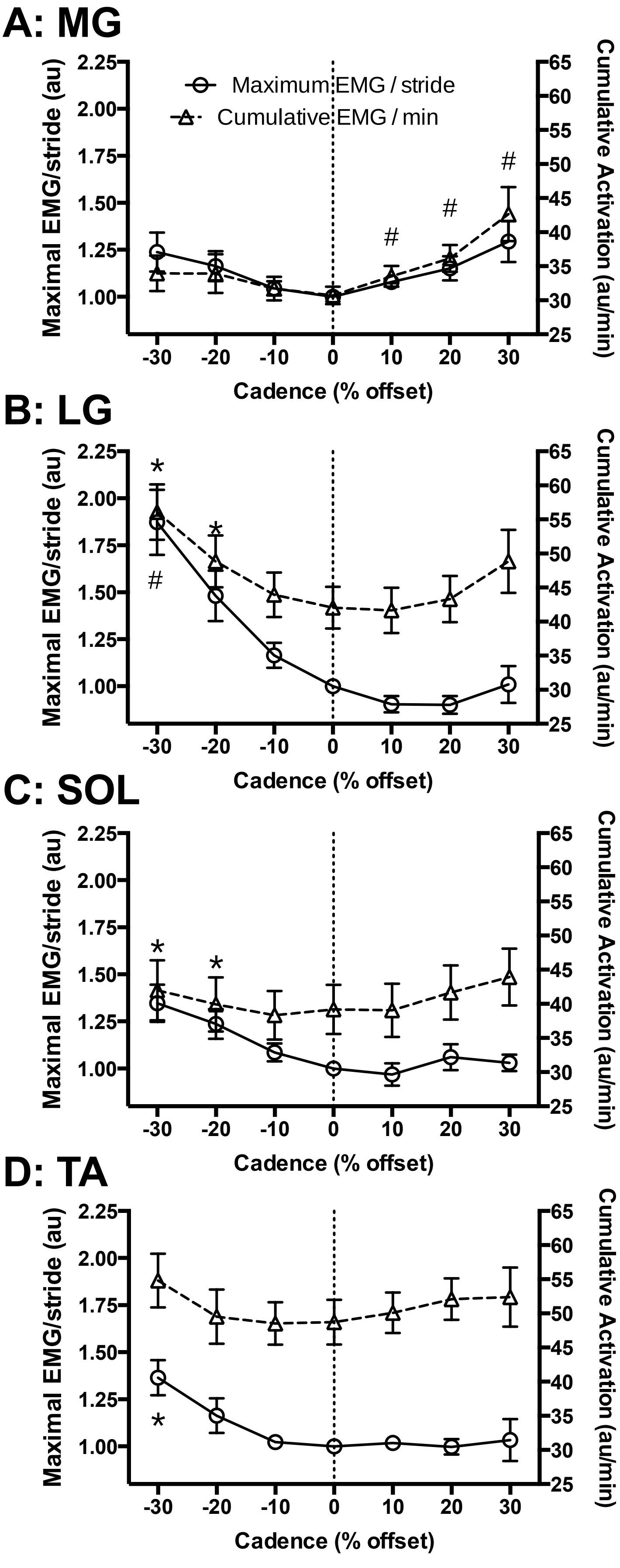
A: MG
Maximum EMG / stride
Cumulative EMG / min
#
#
#
B: LG
*
*
#
C: SOL
*
*
D: TA
*
Maximal EMG/stride (au)
2.25
2.00
1.75
1.50
1.25
1.00
Cumulative Activation (au/min)
65
60
55
50
45
40
35
30
25
-30
-20
-10
0
10
20
30
Cadence (% offset)

Figure 1. **Stride metrics (A), average ankle joint moment (B), velocity (C) and mechanical power (D) during positive power production at the ankle**. Stride length and time (left axis) show a systematic decrease as stride rate increases (right axis). Normalised ankle joint moment (B) and velocity (C) showed an increase for stride rates slower than the preferred cadence (0% offset), while faster stride rates remained similar to the preferred. Average ankle positive power (circles) was greater at slower stride rates whereas negative ankle power (triangles) was not significantly affected by cadence. Normalisation for joint moment and power is by participant's body mass. Error bars show mean ± s.e.m. Annotations (B-D) show significant differences versus preferred cadence (0) where $p = < 0.05$.

Figure 2. **Muscle-tendon unit length, muscle fascicle lengths and muscle fascicle shortening velocities for MG.** MTU length and fascicle length are normalised to their respective means during the preferred cadence condition. The MTU stretches during stance phase (20-50%) and recoils rapidly near push off (60-65%). Fascicle length remains relatively isometric during stance while the MTU stretches, utilising elastic energy storage in the SEE. Elasticity in the MTU then contributes to push-off during late stance. The fascicles also shorten during late stance, but account for a much smaller percentage of overall length change (approximately 20%). Fascicle velocity is calculated as the first derivative of the normalised fascicle length**.** The preferred (solid), +20% (dot) and -20% (dash) cadence conditions are shown for clarity. Annotations for stance and swing phases, right heel strike (RHS) and toe off (RTO) are shown at the top of the figure. The shaded region represents the period of positive ankle mechanical power.

Figure 3. **Group mean MG MTU and fascicle shortening amplitudes and fascicle shortening velocity.** (A) MTU shortening during positive ankle power (grey) with superimposed fascicle shortening amplitude (black). Percentages within columns show the contributions of fascicle shortening as a proportion of total MTU shortening. MTU and Fascicle lengths were normalised to the mean fascicle length of the preferred walking condition. Both MTU and MG fascicle shortening increased as cadence decreased. (B) Fascicle shortening to MTU shortening ratio shows slower cadence resulted in greater fascicle shortening contributions to overall length change. (C) Average fascicle shortening velocity was taken as the first derivative of the

normalised fascicle length. Fascicle shortening velocity during positive ankle power was not significantly affected by cadence. Error bars show mean ± s.e.m. Annotations indicate statistical significance versus the preferred condition where p = < 0.05.

Figure 4. **Group mean normalised maximal muscle activations for the triceps surae (A-C) and tibialis anterior (D) muscles.** Muscle activations per stride were normalised to the mean maximal activation per stride, of the preferred stride rate. The LG (B), SOL (C) and TA (D) muscles showed a significant main effect of cadence on maximal muscle activation (circles), whereas the MG (A) did not reach statistical significance. Cumulative muscle activation (triangles) represented the amount of normalised muscle activation per minute of walking, equal to the mean integrated EMG per stride multiplied by the mean cadence. The MG (A) and LG (B) showed significant main effects of cadence on cumulative activation. Error bars show mean ± s.e.m. Significant differences between the relevant cadence offset and the preferred stride rate for maximal muscle activation (*) and cumulative activation (#) are also shown where p = < 0.05.