

RESEARCH ARTICLE

Elastic ankle muscle–tendon interactions are adjusted to produce acceleration during walking in humans

Dominic James Farris^{1,*} and Brent James Raiteri^{1,2}

ABSTRACT

Humans and other cursorial mammals have distal leg muscles with high in-series compliance that aid locomotor economy. This muscle–tendon design is considered sub-optimal for injecting net positive mechanical work. However, humans change speed frequently when walking and any acceleration requires net positive ankle work. The present study unveiled how the muscle–tendon interaction of human ankle plantar flexors are adjusted and integrated with body mechanics to provide net positive work during accelerative walking. We found that for accelerative walking, a greater amount of active plantar flexor fascicle shortening early in the stance phase occurred and was transitioned through series elastic tissue stretch and recoil. Reorientation of the leg during early stance for acceleration allowed the ankle and whole soleus muscle–tendon complex to remain isometric while its fascicles actively shortened, stretching in-series elastic tissues for subsequent recoil and net positive joint work. This muscle–tendon behaviour is fundamentally different from constant-speed walking, where the ankle and soleus muscle–tendon complex undergo a period of negative work to store energy in series elastic tissues before subsequent recoil, minimizing net joint work. Muscles with high in-series compliance can therefore contribute to net positive work for accelerative walking and here we show a mechanism for how in human ankle muscles.

KEY WORDS: Mechanical work, Fascicle, Acceleration, Gait, Ultrasound, Muscle mechanics

INTRODUCTION

Accelerative movements increase the velocity of a body and require net positive mechanical work. In animal and human movement, this net positive work usually requires muscles to actively produce net positive mechanical work. Much research has focused on the muscle contractile mechanics behind extreme accelerations in animals, ranging from insect (Bennet-Clark, 1975) and anuran species jumping (Astley and Roberts, 2012, 2014), to dogs (Walter and Carrier, 2009), wallabies (McGowan et al., 2005) and turkeys (Roberts and Scales, 2002, 2004) galloping, bounding or running. There is also a body of work on how humans generate muscular power to jump (Bobbert et al., 1986; Bobbert and van Ingen Schenau, 1988; Anderson and Pandy, 1993; Alexander, 1995) and accelerate during high-speed running (Van Caekenbergh et al.,

2013a,b; Lai et al., 2016). However, less research has focused on how muscle contractile behaviour is adjusted to produce net positive mechanical work for acceleration during human walking, which is our most commonly employed gait.

During accelerative walking, it has been shown that humans retract the swing leg further under the body centre of mass prior to ground contact and orient the ground reaction force vector more anteriorly compared with constant-speed walking (Orendurff et al., 2008; Peterson et al., 2011; Farris, 2016). At the individual leg-joint level, concurrent adjustments are made to leg posture at ground contact by flexing the hip and knee joints more and dorsiflexing the ankle joint more than when walking at a constant speed (Qiao and Jindrich, 2016; Farris and Raiteri, 2017). The hip and ankle joints then extend through a greater range of motion during the stance phase of accelerative walking and this leads to greater amounts of net positive work at these joints (Qiao and Jindrich, 2016; Farris and Raiteri, 2017). Thus it seems that the hip and ankle musculature are primarily responsible for generating net positive work to accelerate during walking. This additional use of hip and ankle joint work is consistent with findings for human running (Van Caekenbergh et al., 2013a) and other bipedal species such as turkeys (Roberts and Scales, 2004) and wallabies (McGowan et al., 2005).

Muscles crossing the hip seem well-equipped to modulate work output as they have long parallel fibres and short, stiff tendons (Roberts, 2002). Thus it is unsurprising that accelerative and incline locomotion in humans (Roberts and Belliveau, 2005), goats (McGuigan et al., 2009) and wallabies (McGowan et al., 2007) relies on increased net mechanical work output from proximal limb muscles. *In vivo* studies using sonomicrometry in turkeys (Roberts et al., 2007) and wallabies (McGowan et al., 2007) have shown that these species increase active fibre shortening in proximal limb muscles when net positive work is required for ambulating uphill. Conversely, distal limb (e.g. ankle) muscle groups commonly have short, pennate fibres and long compliant tendons (Roberts, 2002). These features favour economical force production rather than active muscle work (Biewener and Roberts, 2000; Lichtwark and Wilson, 2008). Furthermore, compliant tendons decouple muscle fascicle length change and work from ankle joint rotation and work, allowing the series elastic components of the muscle–tendon unit (MTU) to store and return energy in a spring-like manner during stance (Biewener and Baudinette, 1995; Lichtwark and Wilson, 2006; McGuigan et al., 2009; Farris and Sawicki, 2012). It is therefore no surprise that the human plantar flexors heavily utilize elastic energy storage and return during walking (Lichtwark and Wilson, 2006; Farris and Sawicki, 2012) and that many studies have characterized human ankle joint mechanics during constant-speed locomotion as spring-like (Farley and Morgenroth, 1999; Hansen et al., 2004; Sawicki et al., 2009; Qiao and Jindrich, 2016). However, recent analyses of ankle joint mechanics have shown that the ankle joint function switches during accelerative walking, where it exhibits large amounts of net positive work (Qiao and Jindrich,

¹School of Human Movement and Nutrition Sciences, The University of Queensland, Building 26B, Blair Drive, St Lucia, QLD 4072, Australia. ²Human Movement Science, Faculty of Sport Science, Ruhr-University Bochum, Bochum 44801, Germany.

*Author for correspondence (d.farris@uq.edu.au)

 D.J.F., 0000-0002-6720-1961

2016). This switch in function poses the question: how can ankle joint mechanics be switched from spring-like to injecting significant net positive work, when its primary extensors are architecturally suited to work like a spring? Some of the net positive ankle joint work is likely to be work transported from more proximal muscles, but there is also scope for input from the ankle plantar flexors.

Roberts and Azizi (2011) have presented a diverse range of functions that are performed by elastic tendons in distal limb muscles, including energy absorption and power amplification. Simulations and experiments involving humans jumping have shown that, in a squat jump with no preceding countermovement, the plantar flexors contribute to positive ankle work by active shortening of the contractile element while the ankle joint is isometric, which pre-stretches the series elastic component prior to shortening of the MTU (Anderson and Pandey, 1993; Bobbert et al., 1996). The series elastic component then recoils during MTU shortening (ankle plantar flexion) when the fascicles also shorten (Anderson and Pandey, 1993; Bobbert et al., 1996). More recently, simulations of plantar flexor mechanics have predicted the same muscle–tendon interaction during maximal running accelerations (Lai et al., 2016). Such a mechanism is similar to that used by jumping frogs (Astley and Roberts, 2014) and insects (Bennet-Clark, 1975), although humans appear to be much less effective at harnessing the power of elastic recoil as we cannot make use of mechanical advantage or the physical catch mechanisms that these animals use (Farris et al., 2016). It is clear that series elasticity in a muscle dictates that any positive work done by active contraction of the plantar flexors must be transiently stored as elastic potential energy by the tendon, and that producing net positive mechanical work at the ankle joint is not simply a case of increasing contractile element shortening coupled to joint extension. Investigating the plantar flexor muscle–tendon interactions during accelerative walking should therefore provide fundamental insight into how muscles with significant in-series compliance can contribute to the production of net positive mechanical work in human gait and more generally.

Based on our previous (Farris and Raiteri, 2017) analysis of accelerative walking, ankle joint mechanics are particularly modulated during a period of the gait cycle previously termed the ‘transition phase’ (Frigo et al., 1996), ‘late rising phase’ (Crenna and Frigo, 2011) or ‘dual flexion’ (Shamaei et al., 2013). This period starts at approximately 30% of the stride cycle, where there is a clear increase in the slope of the ankle joint moment–angle loop, and ends at approximately 50%, with the occurrence of the peak ankle joint moment. In accelerative walking, we have observed that the increase in slope was greater or that the ankle joint was ‘stiffened’ in the transition phase. Therefore, we believe that important changes in ankle muscle mechanics for acceleration will occur during this period.

The aim of the present study was to examine how plantar flexor muscle–tendon interaction is adjusted to meet the net positive ankle joint work demands of accelerative walking. We first hypothesized that compared with constant-speed walking, accelerative walking would require greater active shortening of muscle fascicles to generate more positive work. Furthermore, we hypothesized that the increased shortening of fascicles and associated greater fascicle work would occur prior to shortening of the muscle–tendon unit and ankle plantar flexion. The occurrence of fascicle shortening work before MTU shortening would indicate that energy is transitioned through stretch of the series elastic elements, before it is released to do positive work to extend the ankle joint. Because the previously highlighted transition phase precedes positive ankle joint work, we

also hypothesized that it is during the transition period that there would be increased activation of the plantar flexors and the related shortening and positive work of plantar flexor fascicles would be greater for accelerative walking.

MATERIALS AND METHODS

Experimental protocol

Six male participants (mean±s.d. age 26±2 years, mass 77±5 kg, height 1.79±0.05 m) gave written, informed consent to participate in the present study, which was approved by an institutional ethical review committee at The University of Queensland. Participants walked on a tandem-belt treadmill that is instrumented to measure three-dimensional forces (Tandem treadmill, AMTI, Watertown, MA, USA) under two conditions: constant speed (CS) and emulated acceleration (ACC). The treadmill had two belts arranged one in front of the other and each was separately instrumented. Therefore, participants had to walk in the centre of the treadmill such that their current stance limb passed to the rear belt prior to the other limb making contact with the front belt. This positioning requirement also served to help participants maintain a constant fore–aft position on the treadmill, which was a requirement for the ACC condition. The ACC condition used a recently published approach for emulating the mechanics of real overground acceleration, on a treadmill (Farris, 2016). The method is described and evaluated elsewhere (Farris, 2016), but briefly, an extended length of elastic cord was attached to the back of a chest harness worn by the participants and tensioned with a winch until a force equal to the product of their body mass and the acceleration of the treadmill belt was measured by a load cell in-series with the cord. This horizontal resistive force was intended to compensate for the absence of inertial effects when walking on an accelerating treadmill belt. Within this set-up, participants walked on the treadmill briefly at slow constant speed (0.8 m s⁻¹), before the belt was accelerated at 0.76 m s⁻² until they started to run. This acceleration protocol was repeated 10 times for each position of the ultrasound transducer (see ‘Measurement of muscle fascicle mechanics and electromyography’, below). The 10 repetitions were necessary because participants typically only took one to two walking strides before transitioning to running, but six to eight strides were required for analysis. To be used for analysis, a stride had to start and finish while the belt was accelerating and involve a sequence of gait events consistent with a walking gait (foot–ground contact, contralateral toe-off, contralateral foot–ground contact, ipsilateral toe-off and ipsilateral foot–ground contact). For the CS condition, the participants walked as the treadmill belts moved at a constant speed of 1.25 m s⁻¹. Four CS trials of ten strides each were collected for each ultrasound transducer position (see ‘Measurement of muscle fascicle mechanics and electromyography’, below). Similar to the ACC data, six to eight full strides of CS walking data were analysed.

Kinematic and kinetic data

An eight-camera motion capture system (Oqus, Qualisys, Göteborg, Sweden) was used to record the three-dimensional positions of reflective markers attached to the pelvis and lower limbs. All marker position data were filtered with a bidirectional second-order low-pass Butterworth digital filter using a cut-off frequency of 10 Hz and were implemented with the rigid body model of Arnold et al. (2010) in standard scaling, inverse kinematic and inverse dynamic analyses in OpenSim software (Delp et al., 2007).

Thirty-seven reflective markers were attached to the pelvis and lower limbs of each participant. Twenty of these markers were calibration markers and were placed on strategic anatomical

landmarks to define and scale the segments of a seven-segment rigid body model that incorporated the feet, shanks, thighs and pelvis. For the pelvis, markers were placed over the anterior superior iliac spines (left and right), posterior superior iliac spines (left and right) and the sacrum. The thighs had markers placed over the lateral and medial aspects of the knee joint line and these markers were used with the pelvis markers to scale the thigh. Shank calibration markers included the knee markers and markers placed over the lateral and medial malleoli. For the feet, markers were placed on the participant's shoes over the first and fifth metatarsal–phalangeal joints, the calcaneus and the superior aspect of the most distal tip of the toes. The remaining markers were clusters of four markers attached to rigid plates. These rigid plates were strapped to the thigh and shank segments to track the motion of these segments during walking. Calibration markers on the feet and pelvis served as tracking markers for those segments. Marker positions were recorded during a static calibration trial, where each participant maintained a comfortable stance. These data were used to generate a scaled model for each participant using anatomically positioned markers and standard scaling procedures in OpenSim software version 3.0 (Delp et al., 2007). Inverse kinematic and inverse dynamic analyses of walking trials provided ankle and knee joint angles, ankle joint moments, modelled MTU lengths and moment arms for soleus (SO), medial gastrocnemius (MG) and lateral gastrocnemius (LG) muscles. From these data we also calculated the gear ratio of the SO as the ground reaction force (GRF) moment arm divided by the SO moment arm, similar to Carrier et al. (1994). Ankle joint power was computed as the product of ankle joint moments and angular velocities (derivative of angle). Ankle joint power was integrated over a stride to compute net ankle joint work. Net whole-body centre of mass work was calculated as per the methods of Farris and Raiteri (2017), using measured external forces acting on the body.

Measurement of muscle fascicle mechanics and electromyography

Muscle fascicle lengths and pennation angle with the deep aponeurosis for MG, LG and SO of the right leg were measured from dynamic ultrasound imaging (Farris et al., 2013a) performed with a 96-element linear array transducer (LZ 7.5/60/96Z, Teled, Vilnius, Lithuania). For half of the trials in CS and ACC, the transducer was securely bandaged over the belly of the MG to image fascicles of MG only, as per Farris and Sawicki (2012). For the other half of the trials, the transducer was bandaged over the belly of LG, to image fascicles from both LG and SO, similar to Farris et al. (2016). A systematic review has shown good validity and reliability of using two-dimensional ultrasound images to measure muscle fascicle length and pennation (Kwah et al., 2013). Ultrasound images were sampled at 80 Hz and the length of MG, LG and SO fascicles were measured in each image using previously described tracking software and procedures (Cronin et al., 2011; Gillett et al., 2013; Farris and Lichtwark, 2016). Where the automated tracking algorithm did not track fascicle length change well, manual adjustments were made.

To better understand the contribution of fascicle length change to the positive net work required for acceleration, we calculated an estimate of muscle fascicle work for each of the triceps surae (TS) muscles using an approach similar to Farris and Sawicki (2012). Fascicle work was calculated as the integral of fascicle power, which was calculated as the product of fascicle velocity and force. Fascicle velocity was computed by differentiating fascicle length with respect to time. Computing fascicle force first involved calculating

Achilles tendon force as the net ankle joint moment divided by the instantaneous moment arm of the TS from the musculoskeletal model. Individual TS muscle contributions to this force were then calculated as the Achilles tendon force multiplied by the relative physiological cross-sectional area of each muscle from Fukunaga et al. (1996). To convert muscle force contributions into fascicle forces, individual muscle forces were multiplied by the cosine of pennation angle. Net fascicle work was determined over the transition phase (see 'Data reduction and statistics' section below) and the subsequent plantar flexion phase by integrating power over these phases separately.

Surface electromyography (EMG) was used to measure muscle activations of MG, LG and SOL for the right leg. A bipolar electrode configuration with an inter-electrode distance of 20 mm was used and electrodes were placed just distal to the mid-belly of the respective muscles and aligned along the direction of the underlying muscle fascicles. Raw EMG signals were sampled at 2000 Hz synchronously with motion capture data and processed with a custom MATLAB (The Mathworks Inc., Natick, MA, USA) algorithm. Raw signals had the DC offset removed and were then band-pass filtered (20–300 Hz) and smoothed with a root mean squared (RMS) calculation over consecutive rolling windows of 100 ms. Smoothed signals were separately integrated with respect to time over the stance phase.

Data reduction and statistics

Data were divided into individual strides (right foot–ground contact to right foot–ground contact) based on ground reaction force data. As previously described (Farris, 2016) for the ACC condition, only strides where the total net mechanical work output was within 10% of the expected net work output (calculated knowing body mass and acceleration) were included for further analysis. Fascicle and MTU length changes were computed separately during MTU lengthening and subsequent MTU shortening, along with the ratio of fascicle:MTU length change during these two periods. Total fascicle shortening from maximum fascicle length to the end of shortening was also calculated. To test if the fascicles and MTUs of MG, LG and SO could be treated as a homogenous group with regard to these metrics, we compared if the slopes of linear regression analyses (acceleration and muscle as factors) performed on the data from each muscle were significantly different. No statistically significant differences ($P > 0.05$) were found for regression slopes between muscles, so initial statistical tests analysed fascicle and MTU kinematics as one TS group. TS kinematic metrics were compared between CS and ACC using paired *t*-tests ($\alpha = 0.05$).

To address our third hypothesis, we analysed muscle mechanics during the transition phase of ankle mechanics. This period starts at ~30% of the stride cycle, where there is a clear increase in the slope of the ankle joint moment-angle loop, and ends at ~50% of the stride cycle where peak ankle joint moment occurs. Fascicle and MTU length changes in SO were calculated during this phase and tested for differences between CS and ACC using a paired *t*-test ($\alpha = 0.05$). The data point at the onset of the transition phase was visually identified and selected from an interactive plot of ankle angle versus ankle moment for each stride in the analysis. The end of the transition phase was when the peak ankle joint moment occurred. The phase from peak moment to toe-off will be referred to as the plantar flexion phase. For metrics calculated during the transition period and the plantar flexion phase, the effect of ACC on SO mechanics was not the same as for MG and LG. Therefore, the TS could not be treated as a homogenous group for this analysis of the transition phase and SO was examined separately.

RESULTS

The mean treadmill speed during ACC steps across all participants was $1.31 \pm 0.3 \text{ m s}^{-1}$ and therefore similar to the treadmill belt speed during CS. Vertical and horizontal (anterior–posterior) ground reaction forces from the treadmill, and the horizontal force in the elastic cord, are plotted against normalized stride time in Fig. 1A. The relationship between the impulse generated by the cord and the net horizontal impulse generated by the participants can be seen in the scatterplot in Fig. 1B. As would be expected from the criteria for including strides in the analysis, there was clearly a direct negative relationship between these two variables.

The fascicles of the three TS muscles were found to shorten more prior to the onset of MTU shortening and shortened more overall (Fig. 2 and Table 1). However, the lengthening and shortening of the TS MTUs were not significantly different between CS and ACC (Fig. 2D–F and Table 1). The net effect of fascicle and MTU length changes resulted in a significantly higher ratio of fascicle shortening

to MTU length change in ACC prior to and during MTU shortening (Table 1).

For the biarticular gastrocnemii, there was little apparent difference in MTU lengths throughout the gait cycle for ACC and CS (Fig. 2D,E) and this was linked to counteracting effects of increased knee flexion and ankle dorsiflexion during early- to mid-stance (Fig. 3). Despite the overall magnitude of SO MTU lengthening being the same in CS and ACC, there was an obvious distinction in the pattern of how this lengthening occurred between CS and ACC (Fig. 2F). During the transition phase, SO fascicles shortened more in ACC than CS (Table 2), but in the same phase, the SO MTU was almost isometric in ACC, whereas it lengthened by almost 10 mm in CS (Table 2). In addition, ankle joint moments were similar in both conditions during the transition phase (Fig. 4A), while the SO moment arm was less and gear ratio was higher for ACC than for CS (Fig. 4B,C).

All three muscles were calculated to have generated significantly more positive work in ACC than in CS for both the transition phase and during ankle plantar flexion (Table 3). Summing the contributions of all three TS muscles in ACC results in nearly 11 J of positive work during the transition phase and 12.5 J during ankle plantar flexion (Table 3). Net positive work at the ankle joint increased from 2.5 J in CS to 33.6 J in ACC. The net work done on the body centre of mass in ACC steps was $62.2 \pm 10.2 \text{ J}$, but this value is difficult to relate to ankle joint or plantar flexor muscle work as it includes net negative work done by the contralateral limb and at the ipsilateral knee joint.

The RMS EMG signals were generally higher for SO and MG during the stance phase in ACC than CS (Fig. 5A,B) and these higher magnitude signals resulted in a significant increase in the integrated EMG for SO and MG in ACC compared with CS (Fig. 5D). Although LG exhibited a larger burst of EMG in late stance (Fig. 5C), the integrated value for this muscle was not significantly different between CS and ACC (Fig. 5D).

DISCUSSION

As predicted, we found that the human TS fascicles underwent greater active shortening, which was accompanied by greater muscle activations of the MG and SOL, to help accelerate the body during walking. We also found that additional fascicle shortening occurred prior to the onset of ankle plantar flexion and MTU shortening for accelerative walking. Here we will first consider the findings that were common features of MTU interaction among the TS muscles during the CS and ACC trials, before we focus specifically on results regarding our final hypothesis on MTU interaction during the transition phase of the walking stride (where it was evident that only the SO muscle–tendon interactions differed between CS and ACC).

Overall triceps surae mechanics in accelerative walking

For the metrics discussed in this section, the slopes of multiple linear regression analyses (acceleration and muscle as factors) were not different between muscles. Therefore, statistical tests were run on data from all three muscles and the results were considered for the triceps surae as a whole. On average, TS muscle fascicles shortened by 7 mm more during stance in ACC than in CS (Fig. 2A–C and Table 1). Furthermore, based on the integrated EMG data (Fig. 5D), all of the TS muscles were more active during stance in ACC. Therefore, as predicted, ACC involved overall greater active shortening of the TS fascicles than CS and this resulted in significantly greater fascicle work for all three muscles in ACC. Combining positive work estimates for all three muscles during the

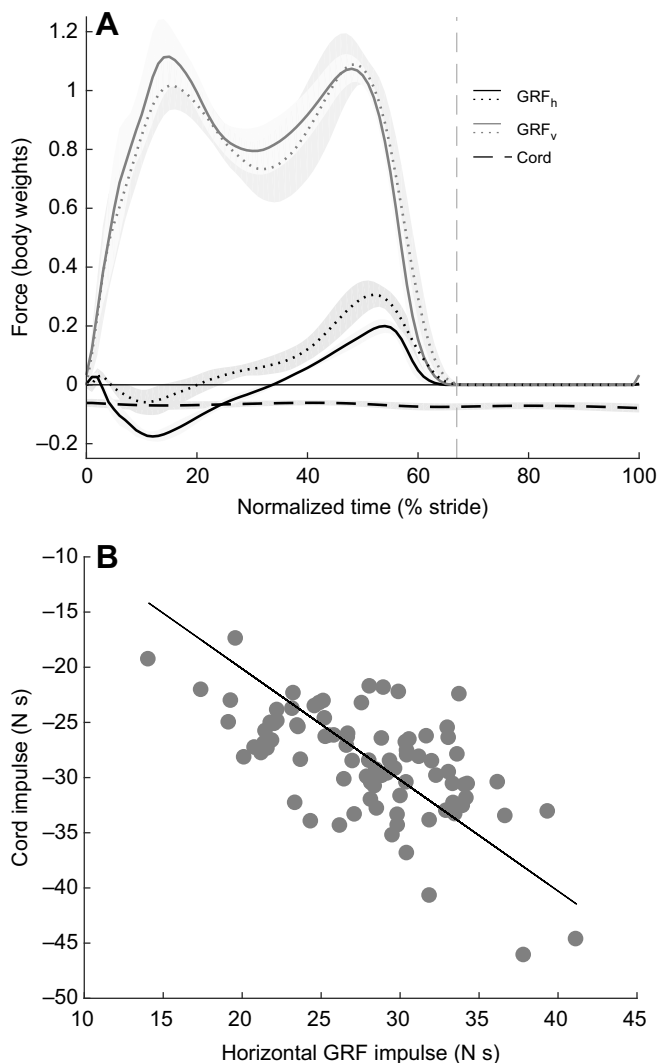


Fig. 1. External forces and the horizontal impulses acting on participants. (A) Group mean \pm s.d. ($N=6$) time series plots of vertical (GRF_v) and horizontal (GRF_h) components of ground reaction forces and the horizontal force applied by the elastic cord (measured by a load cell). (B) Scatterplot of the absolute magnitude of the impulse provided by the elastic cord versus the net horizontal GRF impulse for individual strides of ACC walking for all participants. The plotted line is a least-squares linear fit to the data.

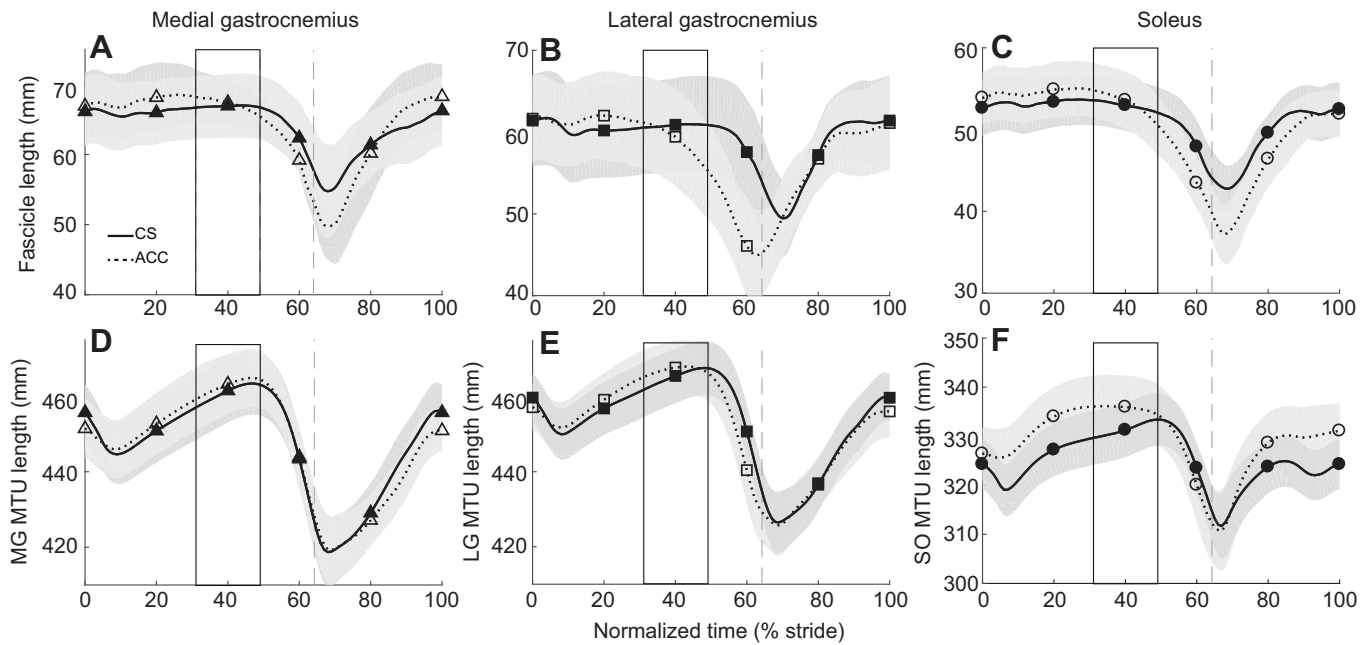


Fig. 2. Comparisons of muscle kinematics during walking at constant speed and acceleration. Group mean \pm s.d. ($N=6$) muscle fascicle (A–C) and muscle–tendon lengths (D–F) for medial gastrocnemius (MG; A, D), lateral gastrocnemius (LG; B, E) and soleus (SO; C, F), plotted from foot–ground contact to ipsilateral foot–ground contact during constant speed (CS; continuous lines, filled shapes) and acceleration (ACC; dotted lines, open shapes). The continuous rectangle indicates the transition phase. The dashed vertical line indicates the end of the stance phase.

transition and plantar flexion phases resulted in the TS fascicles performing over 20 J of work in ACC. This is equivalent to about two-thirds of the additional positive work generated about the ankle in ACC, which in turn accounts for approximately one-third of positive work done about lower limb joints in ACC (Farris and Raiteri, 2017). Fascicle work values are coarse estimates and cannot be directly linked to joint work, but this is certainly evidence that the TS contributed significant amounts of positive work for ACC. However, there is still an appreciable amount of ankle work unaccounted for that was presumably transferred from proximal muscle groups.

An increase in TS work for acceleration is consistent with the results of simulations of TS mechanics during accelerative sprinting, where the active positive work contribution of TS muscles was greater than for constant-speed maximal sprinting (Lai et al., 2016). Broadly speaking, such muscle mechanics are in line with animal studies that

show increased active muscle fascicle shortening to generate net positive joint work with increasing substrate grade (Daley, 2003; Gabaldon, 2004; Yoo et al., 2004; McGuigan et al., 2009). However, our result for accelerative walking differs from results for human MG fascicle length changes during incline walking, which showed no difference from level walking (Lichtwark and Wilson, 2006). This discrepancy may be explained by the relatively low incline used in that study (10% grade).

Although it may seem intuitive that increased ankle joint work comes from greater active shortening of TS muscles, we have already noted that the significant in-series compliance of these muscles decouples fascicle length changes from joint rotation and similarly, fascicle work from joint work. Thus it was interesting that the magnitude of lengthening and shortening of TS MTUs did not change between CS and ACC (Fig. 2D–F and Table 1). Furthermore, the shortening of TS fascicles during lengthening of their respective MTUs increased nearly threefold during ACC versus CS (Table 1). This increase in fascicle shortening with no concurrent change in MTU length change indicates a greater stretch of series elastic tissues during MTU lengthening for ACC compared with CS. This finding supported our second hypothesis that increased active shortening of the TS fascicles in ACC would occur prior to MTU shortening, and thus additional contractile work was transferred later to external work through elastic energy stored in series elastic elements. This is the same mechanism that these muscles have been shown to use to generate net positive work during squat jumping (Anderson and Pandy, 1993; Farris et al., 2016) and in simulations of accelerative sprinting (Lai et al., 2016). Therefore, although human plantar flexor muscles fit the mould of highly compliant distal limb muscles that are useful for spring-like mechanics, there is increasing evidence that their muscle–tendon interactions can be modulated to fulfil a significant work-generating function when net positive work is required.

Table 1. Group mean triceps surae fascicle and muscle–tendon unit length changes and ratios for constant speed and acceleration

	Constant speed	Acceleration
Total fascicle shortening (mm)	-11.9 ± 3	$-19.6 \pm 3^{**}$
MTU lengthening (mm)	17.0 ± 3.2	15.9 ± 5.2
MTU shortening (mm)	-35.8 ± 11.2	-39.2 ± 11.6
Fascicle shortening during MTU lengthening (mm)	-1.4 ± 1.2	$-4.1 \pm 3.5^*$
Ratio of fascicle shortening:MTU lengthening	-0.1 ± 0.2	$-0.26 \pm 0.3^*$
Fascicle shortening during MTU shortening (mm)	-10.5 ± 3.4	$-15.5 \pm 4.5^{**}$
Ratio of fascicle shortening:MTU shortening	0.32 ± 0.13	$0.43 \pm 0.17^*$

Values are means \pm s.d. *Significant difference at $P < 0.05$; **significant difference at $P < 0.01$. MTU, muscle–tendon unit.

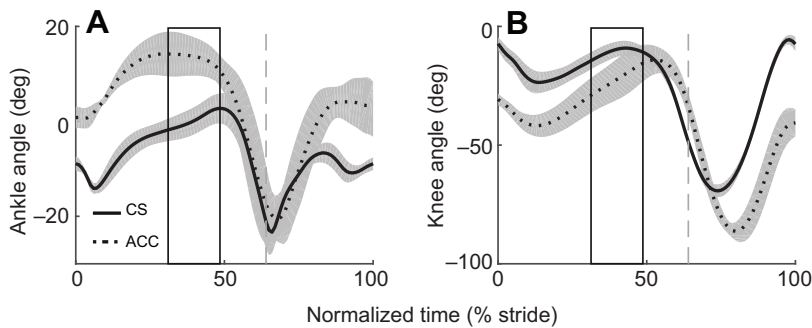


Fig. 3. Comparisons of ankle and knee kinematics during walking at constant speed and acceleration. Group mean \pm s.d. ($N=6$) ankle plantar/dorsiflexion (A) and knee flexion–extension (B) joint angles plotted from foot–ground contact to ipsilateral foot–ground contact during CS (continuous lines) and ACC (dotted lines). For A, 0 deg is a neutral angle, positive angles are into dorsiflexion and negative angles are into plantar flexion. For B, 0 deg represents full knee extension and the negative direction is flexion. The continuous rectangle indicates the transition phase. The dashed vertical line indicates the end of the stance phase.

Soleus MTU interaction

While gross trends in fascicle behaviour were generalizable to the whole TS group, the uniaxial SO exhibited a distinct change in muscle–tendon interaction that helped produce net positive work at the ankle joint. Fig. 2D,E shows that the length change patterns for the biarticular gastrocnemii MTUs were unchanged between CS and ACC. This lack of change was linked to counteracting alterations in ankle and knee kinematics (Fig. 3). In agreement with previous reports (Qiao and Jindrich, 2016; Farris and Raiteri, 2017), the knee began the stance phase more flexed and proceeded to extend more through stance in ACC (Fig. 3B). The ankle began the stance phase more dorsiflexed in ACC and proceeded to dorsiflex early in stance, but stopped dorsiflexing relatively earlier than in CS and remained at a relatively constant joint position until the onset of plantar flexion in late stance (Fig. 3A). These counteracting kinematic alterations at the knee and ankle resulted in similar MTU lengths throughout a stride for MG and LG in ACC and CS (Fig. 2D,E). However, the altered pattern of ankle kinematics was indicative of a difference in SO MTU length change and the SO muscle–tendon interaction employed for ACC.

Of particular interest was a period of the stance phase from approximately 30–50% of the stride cycle (vertical lines in all figures), which has previously been referred to as the ‘transition phase’ (Frigo et al., 1996), ‘late rising phase’ (Crenna and Frigo, 2011) or ‘dual flexion’ (Shamaei et al., 2013). Crenna and Frigo (2011) found a significant correlation between the slope of the moment–angle loop during the transition phase and net work done by the ankle joint during constant-speed walking. Also, our prior work (Farris and Raiteri, 2017) has indicated that the transition phase of the moment–angle loop may be adjusted for accelerative walking, where net positive work is required at the ankle. Thus it appears that the transition phase of the gait cycle requires deeper examination for understanding accelerative walking.

During the transition phase, the ankle joint moment increased to its greatest magnitude (Fig. 4) and in CS, the ankle concurrently dorsiflexed, but in ACC it rotated very little (Fig. 3A). Minimal ankle rotation in ACC seems to be in accordance with the link between ankle joint quasi-stiffness during this period and net joint work found by Crenna and Frigo (2011). The reduced dorsiflexion during the transition phase in ACC was linked to SO having a

relatively constant MTU length during most of this time for ACC, while in CS the SO MTU was lengthening throughout the transition phase (Fig. 2F and Table 2). Also in the transition phase, SO fascicles shortened by 5 mm in ACC, but only 0.7 mm in CS (Table 2). Thus the muscle–tendon interaction of SO in CS was precisely as has been observed previously for the TS (Ishikawa et al., 2005; Lichtwark et al., 2007), with the fascicles acting almost isometrically, while the MTU lengthens and the series elastic tissues are assumed to be stretched, storing energy. However, in ACC, the SO MTU remained relatively isometric while its fascicles shortened, which obligates that the fascicles did positive work on the series elastic tissues that store this work as strain energy. In both cases, the stored elastic energy is later returned as positive work at the ankle joint. The important distinction is that in ACC, storing the energy requires an active shortening contraction of the muscle fascicles during the transition phase (Fig. 2C and Table 2) while concurrently minimal joint work is done (Farris and Raiteri, 2017). However, for CS, storing elastic energy requires a period of negative ankle joint work (Lichtwark et al., 2007; Farris and Sawicki, 2012; Farris and Raiteri, 2017). The considerable negative ankle joint work preceding positive work in CS means that net positive work is minimized (Qiao and Jindrich, 2016; Farris and Raiteri, 2017), whereas the reduced negative ankle joint work in ACC facilitates the necessary net positive joint work (Qiao and Jindrich, 2016; Farris and Raiteri, 2017). Our estimates of fascicle work indicate that SO did approximately 7 J of positive work during the transition phase to contribute to this mechanism. Considering that 33 J of positive work about the ankle joint were observed in ACC, this is a moderate but significant contribution to the positive work required for ACC.

Crenna and Frigo (2011) found that the ankle’s moment–angle loop became more open (i.e. net work increased) with walking speed, and suggested that the shape of the loop and modulation of the loop shape might be achieved through adjustments to the threshold and gain of the calf muscles’ stretch reflex. However, our data show that the increased area within the moment–angle loop occurs in conjunction with SO contractile element shortening, implying that the stretch reflex and its parameters are not important for the control of the quasi-stiffness of the ankle joint during the transition phase of accelerative walking. Furthermore, it was also apparent from the EMG data (Fig. 5) that the shortening contraction of SO in ACC required greater muscle activation compared with CS. Therefore, our data suggest that greater voluntary activation of the SO during mid-stance helps to generate a shortening contraction of the SO fascicles to store energy in SO series elastic elements to ultimately generate net positive work at the ankle joint in accelerative walking strides.

Given the altered muscle–tendon interaction for SO during ACC, it is important to further consider how the changes were accommodated in the context of body mechanics. Interestingly,

Table 2. Group mean soleus fascicle and muscle–tendon unit length changes during the transition phase of the walking stride for constant speed and acceleration

	Constant speed	Acceleration	P-value
Soleus fascicle ΔL (mm)	-0.7 ± 1.4	-5.5 ± 2.5	0.0006
Soleus MTU ΔL (mm)	9.9 ± 2.7	-1.0 ± 3.7	0.002

Values are means \pm s.d. MTU, muscle–tendon unit; ΔL , length change.

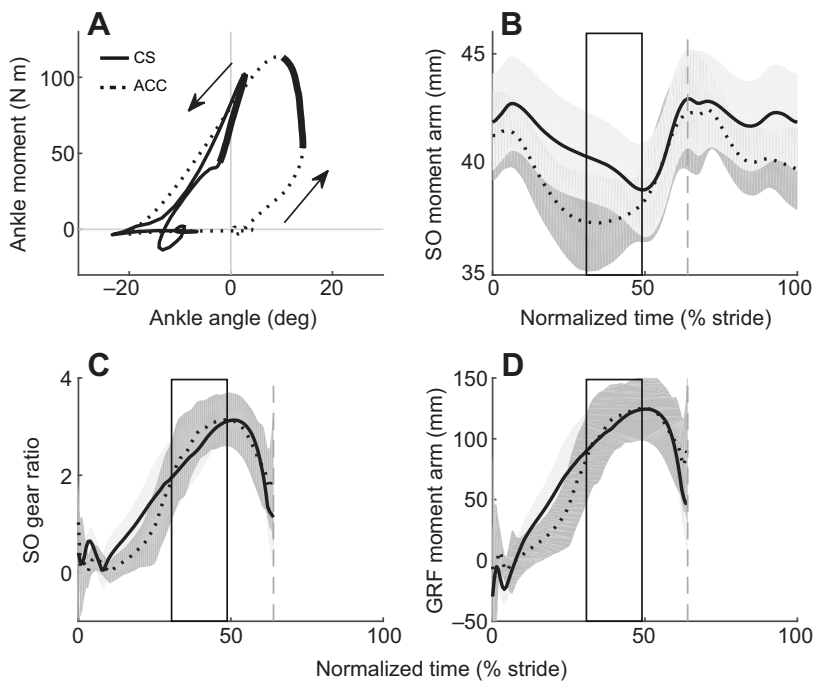


Fig. 4. Comparisons of ankle kinetics, and soleus and ground reaction force moment arms during walking at constant speed and acceleration. Group mean \pm s.d. ($N=6$) ankle joint moment-angle loop (A), soleus (SO) moment arm (B), SO gear ratio (C) and ground reaction force (GRF) moment arm (D). Data are plotted from foot–ground contact to ipsilateral foot–ground contact during CS (continuous lines) and ACC (dotted lines), but with no data for C and D during swing. For A, thick black lines indicate the transition phase and arrows indicate loop direction. For B–D, the continuous rectangle indicates the transition phase. The dashed vertical line indicates the end of the stance phase.

ankle joint moments were unchanged between CS and ACC (Fig. 4A). At first glance the similarity of joint moments was surprising because the greater activation and earlier shortening of SO muscle fascicles in ACC implied a larger, earlier stretch of its series elastic tissues. In turn, greater series elastic stretch implies that Achilles tendon forces rose earlier in ACC and it was expected that the plantar flexor moment would do the same. However, as can be observed in Fig. 4B, the moment arm of SO was less in ACC throughout much of stance (including the transition phase), which explains how the assumed increase in tendon force did not cause any increase in plantar flexor joint moment. Furthermore, there was an interesting trend in the gear ratio of SO, whereby prior to the transition phase it was lower in ACC than CS, but at the onset of the transition it became higher than in CS. A higher gear ratio favours a lower MTU velocity (Carrier et al., 1994) and this seems congruent with the reduced length change of SO also observed during the transition phase (Fig. 2C and Table 2). Therefore, it may be that variable gearing of SO in ACC helped to minimize SO MTU length change during the transition phase and aided the observed changes in muscle–tendon interaction. Carrier et al. (1994) also proposed that ankle power output for accelerative running was aided by maintaining a lower gear ratio during push-off, to keep ankle muscles closer to optimum shortening velocities for power and force generation. During push-off (post-transition) in our data the gear ratio followed a similar trend in both ACC and CS, which by the previous assertion would not favour power production in ACC compared with CS. However, if one considers that most of the positive power at the ankle during push-off in walking is likely from

recoil of elastic tissues that are not bound by the force–velocity relationship, then there is little benefit for power production to be derived from lowering the gear ratio and slowing the MTU during this period.

Limitations

In our interpretation of these data, we have suggested that increased active shortening of muscle fascicles while the MTU is isometric implies greater series elastic element (SEE) stretch and energy storage. This seems a reasonable assumption, but we have not directly measured SEE stretch, and the relationship between fascicle length change and SEE stretch is complicated by pennation angle changes. Muscle gearing may be regionally dependent within a muscle (Shin et al., 2009) and SEE strain is complex as it incorporates biaxial strain of aponeuroses (Azizi and Roberts, 2009; Raiteri et al., 2016) and differential strain patterns throughout the SEE (Farris et al., 2013b). Thus we felt it appropriate to make inferences from measured fascicle mechanics rather than attempt to estimate SEE strain from fascicle and MTU lengths. The inverse approach for calculating tendon and muscle forces has multiple assumptions that limit them to being a coarse estimate. The calculation ignores contributions of antagonistic ankle muscles such as tibialis anterior to the net moment (Sasaki et al., 2009), intramuscular force transmission (Maas and Sandercock, 2010) and assumes that the TS all have similar relative activations throughout the movement. While these assumptions limit confidence in the accuracy of the values of fascicle work, the differences observed between ACC and CS were primarily due to the differences in measured fascicle lengths. Therefore, we believe that our conclusions

Table 3. Group mean fascicle work during the transition phase, and subsequent muscle–tendon unit shortening phase of stance

	Transition phase		MTU shortening phase	
	Constant speed	Acceleration	Constant speed	Acceleration
Soleus fascicle work (J)	1.9 \pm 0.8	7.2 \pm 3.4*	3.5 \pm 1.5	8.7 \pm 1.8*
Medial gastrocnemius fascicle work (J)	0.0 \pm 0.6	3.3 \pm 1.6*	0.8 \pm 0.5	2.5 \pm 1.6*
Lateral gastrocnemius fascicle work (J)	0.0 \pm 0.2	0.5 \pm 0.4*	0.4 \pm 0.2	1.3 \pm 0.6*

*Significant difference at $P<0.05$. Values are means \pm s.d. MTU, muscle–tendon unit.

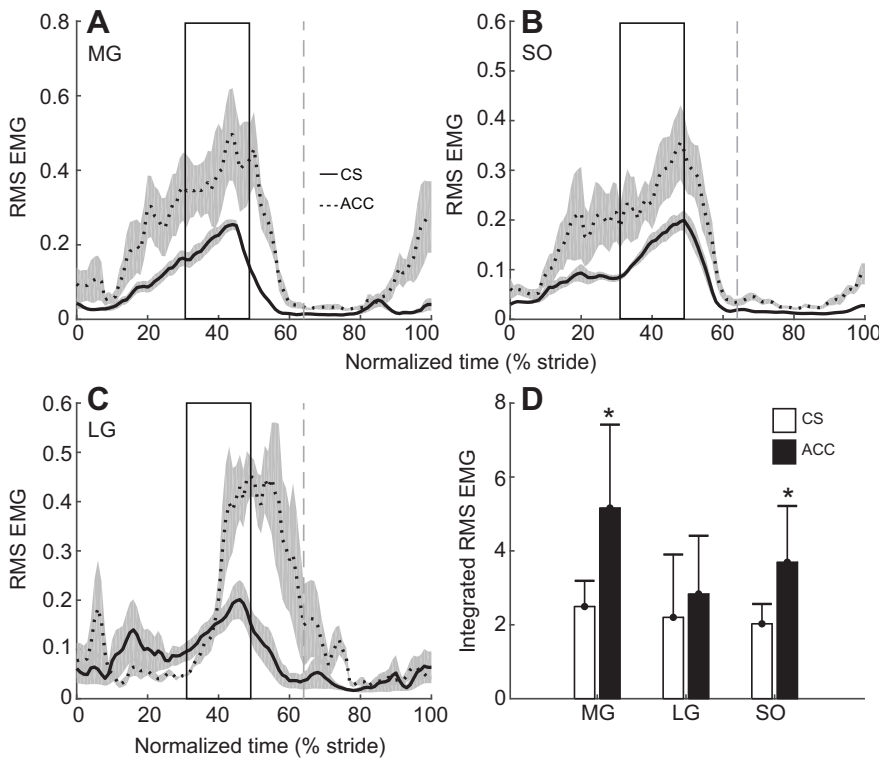


Fig. 5. Summary of electromyographic data from the triceps surae during walking at constant speed and acceleration. Group mean \pm s.d. ($N=6$) root mean square (RMS) amplitude EMG signals plotted from foot–ground contact to ipsilateral foot–ground contact during CS (continuous lines) and ACC (dotted lines) for MG (A), SO (B) and LG (C). The continuous rectangle indicates the transition phase. The dashed vertical line indicates the end of the stance phase. (D) Bar plot of group mean \pm s.d. integrated RMS EMG over the stance phase for each muscle. *Significant ($P < 0.05$) difference between CS and ACC conditions for that muscle, determined by a Student's paired t -test.

are reasonable. Finally, with our data we cannot quantify work that is transferred to the ankle joint from more proximal leg muscles, which we have suggested contributes to the net positive work required for acceleration. This work is probably transferred via the actions of biarticular muscles, such as the two heads of the gastrocnemius.

Conclusions

Storage and return of elastic energy in the compliant elastic elements of distal leg MTUs has long been considered important for the economy of steady-state, constant-speed locomotion in humans. However, the same muscle architecture might be considered sub-optimal for generating net positive work at a joint, and thus distal leg muscles are not always thought to contribute to tasks like acceleration. Here we have shown that compliant MTUs like the human plantar flexors can be utilized to contribute to net positive work in an accelerative walking task and that their architecture does not preclude such a contribution. Thus the function of these muscles and the elastic mechanisms that they use should be strongly considered when determining how net positive work is generated for locomotor tasks that require it. The mechanisms exhibited by such muscles to generate net positive work at the ankle may also vary between uniaxial and biarticular synergists.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: D.J.F.; Methodology: D.J.F.; Software: D.J.F.; Formal analysis: D.J.F., B.J.R.; Investigation: D.J.F., B.J.R.; Data curation: D.J.F., B.J.R.; Writing - original draft: D.J.F.; Writing - review & editing: D.J.F., B.J.R.; Funding acquisition: D.J.F.

Funding

D.J.F. was funded by a post-doctoral fellowship granted by the Australian Sports Commission. This study was also funded by an Early Career Researcher Grant awarded to D.J.F. by The University of Queensland.

References

- Alexander, R. M. N. (1995). Leg design and jumping technique for humans, other vertebrates and insects. *Philos. Trans. R. Soc. B Biol. Sci.* **347**, 235–248.
- Anderson, F. C. and Pandy, M. G. (1993). Storage and utilization of elastic strain-energy during jumping. *J. Biomech.* **26**, 1413–1427.
- Arnold, E. M., Ward, S. R., Lieber, R. L. and Delp, S. L. (2010). A model of the lower limb for analysis of human movement. *Ann. Biomed. Eng.* **38**, 269–279.
- Astley, H. C. and Roberts, T. J. (2012). Evidence for a vertebrate catapult: elastic energy storage in the plantaris. *Biol. Lett.* **8**, 386–389.
- Astley, H. C. and Roberts, T. J. (2014). The mechanics of elastic loading and recoil in anuran jumping. *J. Exp. Biol.* **217**, 4372–4378.
- Azizi, E. and Roberts, T. J. (2009). Biaxial strain and variable stiffness in aponeuroses. *J. Physiol. Lond.* **587**, 4309–4318.
- Bennet-Clark, H. C. (1975). Energetics of jump of locust *Schistocerca gregaria*. *J. Exp. Biol.* **63**, 53–83.
- Biewener, A. and Baudinette, R. (1995). *In vivo* muscle force and elastic energy storage during steady-speed hopping of tammar wallabies (*Macropus eugenii*). *J. Exp. Biol.* **198**, 1829–1841.
- Biewener, A. A. and Roberts, T. J. (2000). Muscle and tendon contributions to force, work, and elastic energy savings: a comparative perspective. *Exerc. Sport Sci. Rev.* **28**, 99–107.
- Bobbert, M. F., Gerritsen, K. G. M., Litjens, M. C. A. and Van Soest, A. J. (1996). Why is countermovement jump height greater than squat jump height? *Med. Sci. Sports Exerc.* **28**, 1402–1412.
- Bobbert, M. F., Huijijng, P. A. and van Ingen Schenau, G. J. (1986). An estimation of power output and work done by the human triceps surae muscle-tendon complex in jumping. *J. Biomech.* **19**, 899–906.
- Bobbert, M. F. and van Ingen Schenau, G. J. (1988). Coordination in vertical jumping. *J. Biomech.* **21**, 249–262.
- Carrier, D. R., Heglund, N. C. and Earls, K. D. (1994). Variable gearing during locomotion in the human musculoskeletal system. *Science* **265**, 651–653.
- Crenna, P. and Frigo, C. (2011). Dynamics of the ankle joint analyzed through moment-angle loops during human walking: gender and age effects. *Hum. Mov. Sci.* **30**, 1185–1198.
- Cronin, N. J., Carty, C. P., Barrett, R. S. and Lichtwark, G. (2011). Automatic tracking of medial gastrocnemius fascicle length during human locomotion. *J. Appl. Physiol.* **111**, 1491–1496.
- Daley, M. A. (2003). Muscle force–length dynamics during level versus incline locomotion: a comparison of *in vivo* performance of two guinea-fowl ankle extensors. *J. Exp. Biol.* **206**, 2941–2958.
- Delp, S. L., Anderson, F. C., Arnold, A. S., Loan, P., Habib, A., John, C. T., Guendelman, E. and Thelen, D. G. (2007). Opensim: Open-source software to

- create and analyze dynamic simulations of movement. *IEEE Trans. Biomed. Eng.* **54**, 1940–1950.
- Farley, C. T. and Morgenroth, D. C.** (1999). Leg stiffness primarily depends on ankle stiffness during human hopping. *J. Biomech.* **32**, 267–273.
- Farris, D. J.** (2016). Emulating constant acceleration locomotion mechanics on a treadmill. *J. Biomech.* **49**, 653–658.
- Farris, D. J. and Lichtwark, G. A.** (2016). Ultratrack: software for semi-automated tracking of muscle fascicles in sequences of b-mode ultrasound images. *Comput. Methods Programs Biomed.* **128**, 111–118.
- Farris, D. J., Lichtwark, G. A., Brown, N. A. T. and Cresswell, A. G.** (2016). The role of human ankle plantar flexor muscle–tendon interaction and architecture in maximal vertical jumping examined *in vivo*. *J. Exp. Biol.* **219**, 528–534.
- Farris, D. J. and Raiteri, B. J.** (2017). Modulation of leg joint function to produce emulated acceleration during walking and running in humans. *R. Soc. Open Sci.* **4**, 160901.
- Farris, D. J., Robertson, B. D. and Sawicki, G. S.** (2013a). Elastic ankle exoskeletons reduce soleus muscle force but not work in human hopping. *J. Appl. Physiol.* **115**, 579–585.
- Farris, D. J. and Sawicki, G. S.** (2012). Human medial gastrocnemius force–velocity behavior shifts with locomotion speed and gait. *Proc. Natl. Acad. Sci.* **109**, 977–982.
- Farris, D. J., Trewartha, G., McGuigan, M. P. and Lichtwark, G. A.** (2013b). Differential strain patterns of the human Achilles tendon determined *in vivo* with freehand three-dimensional ultrasound imaging. *J. Exp. Biol.* **216**, 594–600.
- Frigo, C., Crenna, P. and Jensen, L. M.** (1996). Moment–angle relationship at lower limb joints during human walking at different velocities. *J. Electromyogr. Kinesiol.* **6**, 177–190.
- Fukunaga, T., Roy, R. R., Shellock, F. G., Hodgson, J. A. and Edgerton, V. R.** (1996). Specific tension of human plantar flexors and dorsiflexors. *J. Appl. Physiol.* **80**, 158–165.
- Gabaldon, A. M.** (2004). Mechanical function of two ankle extensors in wild turkeys: shifts from energy production to energy absorption during incline versus decline running. *J. Exp. Biol.* **207**, 2277–2288.
- Gillett, J. G., Barrett, R. S. and Lichtwark, G. A.** (2013). 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.* **16**, 678–687.
- Hansen, A. H., Childress, D. S., Miff, S. C., Gard, S. A. and Mesplay, K. P.** (2004). The human ankle during walking: implications for design of biomimetic ankle prostheses. *J. Biomech.* **37**, 1467–1474.
- Ishikawa, M., Komi, P. V., Grey, M. J., Lepola, V. and Bruggemann, G.** (2005). Muscle–tendon interaction and elastic energy usage in human walking. *J. Appl. Physiol.* **99**, 603–608.
- Kwah, L. K., Pinto, R. Z., Diong, J. and Herbert, R. D.** (2013). Reliability and validity of ultrasound measurements of muscle fascicle length and pennation in humans: a systematic review. *J. Appl. Physiol.* **114**, 761–769.
- Lai, A., Schache, A. G., Brown, N. A. and Pandey, M. G.** (2016). Human ankle plantar flexor muscle–tendon mechanics and energetics during maximum acceleration sprinting. *J. R. Soc. Interface* **13**, pii: 20170261.
- Lichtwark, G. A., Bougoulas, K. and Wilson, A. M.** (2007). Muscle fascicle and series elastic element length changes along the length of the human gastrocnemius during walking and running. *J. Biomech.* **40**, 157–164.
- Lichtwark, G. A. and Wilson, A. M.** (2006). Interactions between the human gastrocnemius muscle and the Achilles tendon during incline, level and decline locomotion. *J. Exp. Biol.* **209**, 4379–4388.
- 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.
- Maas, H. and Sandercock, T. G.** (2010). Force transmission between synergistic skeletal muscles through connective tissue linkages. *J. Biomed. Biotechnol.* **2010**, 575672.
- McGowan, C. P., Baudinette, R. V. and Biewener, A. A.** (2005). Joint work and power associated with acceleration and deceleration in tammar wallabies (*Macropus eugenii*). *J. Exp. Biol.* **208**, 41–53.
- McGowan, C. P., Baudinette, R. V. and Biewener, A. A.** (2007). Modulation of proximal muscle function during level versus incline hopping in tammar wallabies (*Macropus eugenii*). *J. Exp. Biol.* **210**, 1255–1265.
- McGuigan, M. P., Yoo, E., Lee, D. V. and Biewener, A. A.** (2009). Dynamics of goat distal hindlimb muscle–tendon function in response to locomotor grade. *J. Exp. Biol.* **212**, 2092–2104.
- Orendurff, M. S., Bernatz, G. C., Schoen, J. A. and Klute, G. K.** (2008). Kinetic mechanisms to alter walking speed. *Gait Posture* **27**, 603–610.
- Peterson, C. L., Kautz, S. A. and Neptune, R. R.** (2011). Braking and propulsive impulses increase with speed during accelerated and decelerated walking. *Gait Posture* **33**, 562–567.
- Qiao, M. and Jindrich, D. L.** (2016). Leg joint function during walking acceleration and deceleration. *J. Biomech.* **49**, 66–72.
- Raiteri, B. J., Cresswell, A. G. and Lichtwark, G. A.** (2016). Three-dimensional geometrical changes of the human tibialis anterior muscle and its central aponeurosis measured with three-dimensional ultrasound during isometric contractions. *PeerJ* **4**, e2260.
- Roberts, T. J.** (2002). The integrated function of muscles and tendons during locomotion. *Comp. Biochem. Physiol. A* **133**, 1087–1099.
- Roberts, T. J. and Azizi, E.** (2011). Flexible mechanisms: the diverse roles of biological springs in vertebrate movement. *J. Exp. Biol.* **214**, 353–361.
- Roberts, T. J. and Belliveau, R. A.** (2005). Sources of mechanical power for uphill running in humans. *J. Exp. Biol.* **208**, 1963–1970.
- Roberts, T. J., Higginson, B. K., Nelson, F. E. and Gabaldon, A. M.** (2007). Muscle strain is modulated more with running slope than speed in wild turkey knee and hip extensors. *J. Exp. Biol.* **210**, 2510–2517.
- Roberts, T. J. and Scales, J. A.** (2002). Mechanical power output during running accelerations in wild turkeys. *J. Exp. Biol.* **205**, 1485–1494.
- Roberts, T. J. and Scales, J. A.** (2004). Adjusting muscle function to demand: joint work during acceleration in wild turkeys. *J. Exp. Biol.* **207**, 4165–4174.
- Sasaki, K., Neptune, R. R. and Kautz, S. A.** (2009). The relationships between muscle, external, internal and joint mechanical work during normal walking. *J. Exp. Biol.* **212**, 738–744.
- Sawicki, G. S., Lewis, C. L. and Ferris, D. P.** (2009). It pays to have a spring in your step. *Exerc. Sport Sci. Rev.* **37**, 130–138.
- Shamaei, K., Sawicki, G. S. and Dollar, A. M.** (2013). Estimation of quasi-stiffness and propulsive work of the human ankle in the stance phase of walking. *PLoS ONE* **8**, e59935.
- Shin, D. D., Hodgson, J. A., Edgerton, V. R. and Sinha, S.** (2009). *In vivo* intramuscular fascicle–aponeuroses dynamics of the human medial gastrocnemius during plantarflexion and dorsiflexion of the foot. *J. Appl. Physiol.* (1985) **107**, 1276–1284.
- Van Caekenberghe, I., Segers, V., Aerts, P., Willems, P. and De Clercq, D.** (2013a). Joint kinematics and kinetics of overground accelerated running versus running on an accelerated treadmill. *J. R. Soc. Interface* **10**, 20130222.
- Van Caekenberghe, I., Segers, V., Willems, P., Gosseye, T., Aerts, P. and De Clercq, D.** (2013b). Mechanics of overground accelerated running versus running on an accelerated treadmill. *Gait Posture* **38**, 125–131.
- Walter, R. M. and Carrier, D. R.** (2009). Rapid acceleration in dogs: ground forces and body posture dynamics. *J. Exp. Biol.* **212**, 1930–1939.
- Yoo, E. H., McGuigan, M. P. and Biewener, A. A.** (2004). *In vivo* strain and activation patterns of an ankle extensor in pygmy goats (*Capra hircus*) during incline versus level locomotion. *Integr. Comp. Biol.* **44**, 670–670.