

## RESEARCH ARTICLE

# Tibialis anterior tendinous tissue plays a key role in energy absorption during human walking

Jayishni N. Maharaj\*, Andrew G. Cresswell and Glen A. Lichtwark

## ABSTRACT

The elastic tendinous tissues of distal lower limb muscles can improve the economy of walking and running, amplify the power generated by a muscle and absorb energy. This paper explores the behaviour of the tibialis anterior (TA) muscle and its tendinous tissue during gait, as it absorbs energy during contact and controls foot position during swing. Simultaneous measurements of ultrasound, surface electromyography and 3D motion capture with musculoskeletal modelling from 12 healthy participants were recorded as they walked at preferred and fast walking speeds. We quantified the length changes and velocities of the TA muscle–tendon unit (MTU) and its fascicles across the stride at each speed. Fascicle length changes and velocities were relatively consistent across speeds, although the magnitude of fascicle length change differed between the deep and superficial regions. At contact, when the TA is actively generating force, the fascicles remained relatively isometric as the MTU actively lengthened, presumably stretching the TA tendinous tissue and absorbing energy. This potentially protects the muscle fibres from damage during weight acceptance and allows energy to be returned to the system later in the stride. During early swing, the fascicles and MTU both actively shortened to dorsiflex the foot, clearing the toes from the ground; however, at the fast walking velocity, the majority of shortening occurred through tendinous tissue recoil, highlighting its role in accelerating ankle dorsiflexion to power rapid foot clearance in swing.

**KEY WORDS:** Fascicle, Muscle mechanics, Biomechanics, Musculoskeletal modelling, Ultrasound

## INTRODUCTION

Muscles in the distal lower limb utilise connective tissue elasticity (e.g. tendon, aponeurosis) to enhance their performance. Investigations into a variety of anti-gravity muscles across a range of animals, including human gastrocnemius and soleus (Cronin et al., 2013; Lichtwark and Wilson, 2005), tammar wallaby plantaris and gastrocnemius (Biewener et al., 1998), horse superficial digital flexor (Butcher et al., 2009), turkey gastrocnemius (Roberts et al., 1997) and cat gastrocnemius (Griffiths, 1991; Maas et al., 2009), have clearly demonstrated that elastic tendinous tissues undergo much of the active lengthening of the muscle–tendon unit (MTU). Recycling of elastic energy through tendons contributes to both negative and positive work performed on the body's centre of mass (Cavagna and Kaneko, 1977; Heglund et al., 1982), but importantly allows muscles to operate relatively isometrically, which is thought to reduce energy

consumption of the muscle (Lichtwark, 2005; Roberts et al., 1997). There are also instances where elastic energy from tendons is beneficial for power production to rapidly propel limbs forward during swing phase (Farris et al., 2016; Konow et al., 2015; Richards and Sawicki, 2012; Wilson et al., 2003) or to assist in the dissipation of energy (Konow et al., 2012; Werkhausen et al., 2017). In human locomotion, elastic mechanisms are well known to power propulsion through recovery of elastic energy (Ishikawa et al., 2005; Lichtwark and Wilson, 2006); however, they may also have a role in energy absorption during foot contact (Maharaj et al., 2016).

The human tibialis anterior (TA) MTU has an essential role in absorbing energy during human walking (Usherwood et al., 2012; McGowan et al., 2010). The TA absorbs energy across the ankle joint as the foot contacts the ground, generating force while the ankle plantar flexes and stretches the MTU (Usherwood et al., 2012). Architecturally, the TA is similar to other distal lower limb muscles that are known to utilise elastic mechanisms for energy absorption and recycling (e.g. human triceps surae and tibialis posterior). The TA muscle has relatively short muscle fibres (~6.8 cm) compared with its long MTU length (26 cm) (Ward et al., 2009). TA muscle fascicles have also been shown to have limited length change during walking in early stance, while the MTU is presumably lengthening (Chleboun et al., 2007). This suggests that the TA tendinous tissue is likely to be absorbing energy, potentially protecting its muscle fibres from active lengthening and muscle damage. What is uncertain is whether energy absorbed by the tendinous tissue in early stance is later dissipated by the muscle fascicles or recycled during stance. Temporary energy storage in the tendon may protect muscle fascicles against damage from rapid and forceful lengthening, and could also be recycled later in mid-stance to facilitate forward progression of the shank over the foot. The TA also has a key role in controlling foot position and ensuring toe clearance during swing. In particular, the muscle is active at the end of the stance phase and into early swing (Hof et al., 2002), presumably to help power the ankle into a dorsiflexed position through swing (Hof et al., 2002). The interaction of the muscle and tendinous tissues to precisely control toe clearance remains unclear; however, it is possible that there is a contribution of the tendinous tissue to the power required to accelerate the foot into dorsiflexion as the foot leaves the ground.

In the present study, we investigated the dynamic length changes of the TA muscle fascicles relative to the entire MTU during walking at different speeds, so as to better understand the contribution of the TA tendinous tissue to power requirements in walking. The TA is a bi-pennate muscle, and therefore we were particularly interested in whether the mechanical behaviour of the muscle fascicles was uniform across the stride. We explored three hypotheses: (i) TA muscle fascicles act relatively isometrically in both the deep and superficial regions during early stance, while the MTU lengthens and stores energy in the tendinous tissue, an effect that would be amplified with increased speed as a result of the increased energy absorption requirements; (ii) stored energy

The University of Queensland, School of Human Movement and Nutrition Sciences, Centre for Sensorimotor Neuroscience, Brisbane, QLD 4072, Australia.

\*Author for correspondence (jayishni.m@uq.edu.au)

 J.N.M., 0000-0002-4599-8439

Received 23 August 2018; Accepted 30 April 2019

through stretch of the tendinous tissue is later absorbed by the fascicles through active lengthening while the MTU shortens in mid-stance; and (iii) activation of the TA as the plantar flexors power push-off during late stance would allow for storage of energy in its tendinous tissue that could be used to accelerate the foot into dorsiflexion as the foot leaves the ground.

## MATERIALS AND METHODS

Twelve participants (6 men, 6 women) with no musculoskeletal injuries in the previous 2 years gave written consent to partake in the study. The subjects' mean ( $\pm$ s.d.) age, height and body mass were 26 $\pm$ 74 years, 173 $\pm$ 1 cm and 73 $\pm$ 10 kg, respectively. The protocol was approved by the local university ethics committee and conducted according to the Declaration of Helsinki.

### Experimental protocol

Participants walked barefoot on a force instrumented treadmill (AMTI, Watertown, MA, USA) with two fore-aft running belts as kinematic, kinetic, electromyography (EMG) and ultrasound data (described below) were synchronously recorded from the right leg only. Participants selected their preferred walking velocity as the speed of the treadmill was incrementally increased and subsequently decreased, until they identified the same preferred velocity three times. Participants were tested at preferred and fast (40% faster than preferred) walking velocities in a randomised order. They were given 1 min to normalise their gait prior to a 10 s period of data collection. The average preferred and fast velocity for the group were 1.19 and 1.67 m s<sup>-1</sup>.

### Joint kinematics and kinetics

The motion of reflective markers (9 mm) attached to the leg and foot was collected at 200 Hz using an eight camera, 3D motion capture system (Qualysis, Gothenburg, Sweden) at 200 Hz. Ground reaction forces and moments were collected at 4 kHz from the front and rear force plates mounted beneath the two belts of the treadmill. Participants walked such that the leading leg impacted the front belt and the trailing leg pushed off the rear belt to allow separate left- and right-limb contributions to be determined.

Motion and force data were processed using a modified gait model in musculoskeletal modelling software (OpenSim, Modified Gait 2392 model; Delp et al., 2007). The model was scaled to match the dimensions of each participant based on a quiet standing trial and used for all subsequent analyses. Raw marker positions and ground reaction forces were recursive filtered at the same frequency using a zero-lag second-order low-pass Butterworth filter with a cut-off frequency of 25 Hz. This was necessary to remove noise due to treadmill vibration and prevent filtering artefact during inverse dynamic analysis (van den Bogert and De Koning, 1996). OpenSim inverse kinematics and inverse dynamic analyses, implemented through Matlab (MathWorks, R2014b, Natick, MA, USA), were used to calculate joint angle, joint moment and joint power. Ankle power was computed as the product of net ankle moment and ankle angular velocity. Joint moment and power were normalised to body mass (kg).

### Muscle fascicle and MTU measures

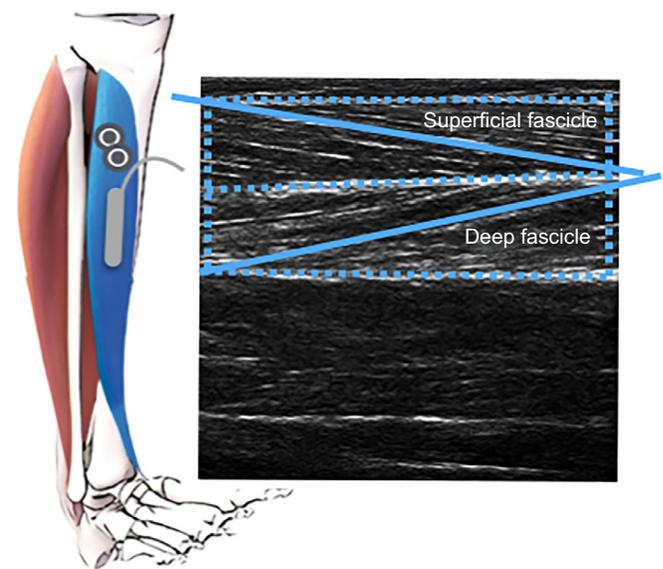
TA MTU length was computed at each point in time using the geometrical model of the muscle included in the rigid body musculoskeletal model (OpenSim). The length was measured from the origin on the tibia to the medial aspect of the forefoot (defined as the calcaneal segment in the model), with appropriate wrapping points around the ankle joint. TA muscle fascicles were imaged using B-mode ultrasound imaging and a flat-shaped 96-element linear multi-frequency probe (LV7.5/60/96, Echoblaster 128, Teleded,

Vilnius, Lithuania) with a central frequency of 6 MHz, a frame rate of 80 Hz and a field of view of 65 mm. Images were collected from the anterolateral aspect of the leg. A semi-automated tracking algorithm (Farris and Lichtwark, 2016) was used to track fascicles of the superficial and deep aponeurosis across three representative stride cycles. Manual adjustments were made where the automatic tracking did not track the fascicle end points well, typically when length changes were large from frame to frame. MTU and fascicle length change were calculated relative to their respective length at 50% of stance. Normalised fascicle length changes used for region comparisons only were calculated relative to their length at 50% of stance, which was assumed to be the time at which minimal forces were applied to the tendinous tissue.

Muscle activity of the TA muscle was assessed using surface EMG. Two bipolar surface electrodes were placed on the muscle belly and parallel to its muscle fibres, proximal to the ultrasound probe (Fig. 1) at a centre-to-centre distance of 2 cm. EMG signals were sampled at 4 kHz and processed with custom-written scripts in Matlab. Following removal of any DC offset, the EMG data were high-pass filtered at 20 Hz. The signal was subsequently rectified, low-pass recursive filtered at 6 Hz using a second-order Butterworth filter and normalised to the maximum amplitude recorded at the preferred walking velocity.

### Data analysis

All raw output data (kinematic, kinetic and fascicle) were filtered at 12 Hz using a bi-directional, second-order low-pass Butterworth filter. Processed kinematic, kinetic, fascicle and EMG data were time normalised to 101 data points by linear interpolation over a single stride (from right heel strike to ipsilateral heel strike). Group means were computed from participant means, which were calculated across three strides. To perform comparisons, we found it convenient to focus on two phases of the gait cycle defined by major regions of positive ankle moments and negative ankle power (see Fig. 2B,C): early stance TA MTU power absorption (approximately



**Fig. 1. The position of the ultrasound transducer on the leg and an example ultrasound image.** The linear transducer was placed on the anterior aspect of the leg such that both the superficial and deep region of the tibialis anterior (TA) muscle could be visualised. Blue dotted lines on the ultrasound image outline the superficial and deep regions of the TA and the solid blue lines represent fascicles within each muscle region.

1–8% of stride) and early swing TA MTU power absorption (61–65% of stride). Outcome variables (peak superficial and deep TA fascicle and MTU length changes and velocities, normalised peak EMG activity, peak dorsiflexion moment and peak ankle power) were calculated during each of these phases. Data were tested for normality using a D'Agostino and Pearson omnibus normality test and analysed using either Student's paired *t*-test or Wilcoxon's test. The significance level was set as  $P \leq 0.05$ . All grouped data are presented as means  $\pm$  s.d.

## RESULTS

### Ankle joint mechanics

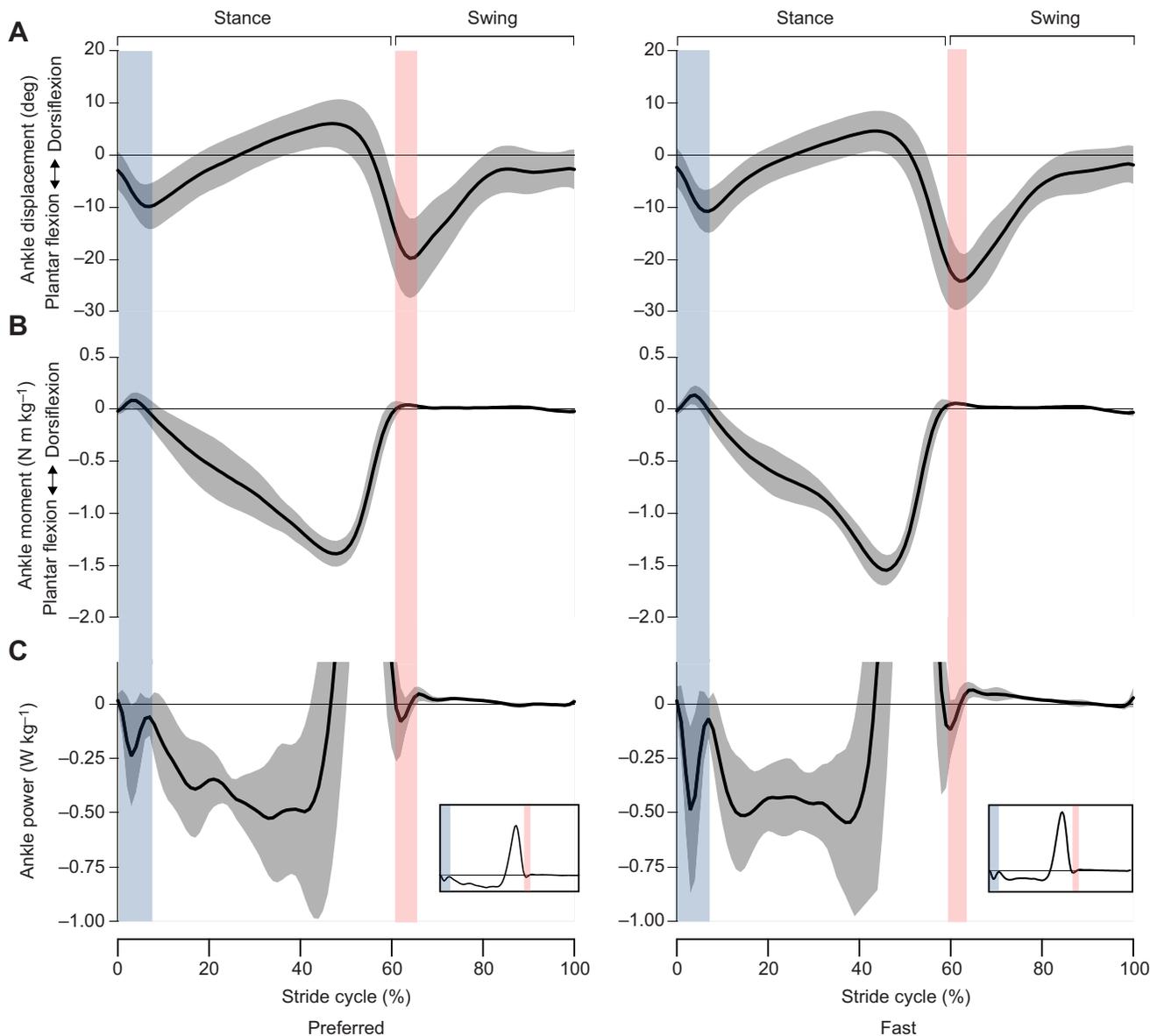
A dorsiflexion moment was evident at the ankle following heel strike at the same time as the ankle plantar flexed (Fig. 2B). This

resulted in a period of power absorption during early stance (indicated by the blue shaded area in Fig. 2) contributed by the dorsiflexors, including the TA. In late stance, a dorsiflexion moment was evident as the ankle continued to plantar flex after propulsion, resulting in a short period of negative power. A period of positive power was then evident as the ankle dorsiflexed during early swing. Therefore, as the foot came off the ground there was a period of energy absorption followed by power generation by the dorsiflexors.

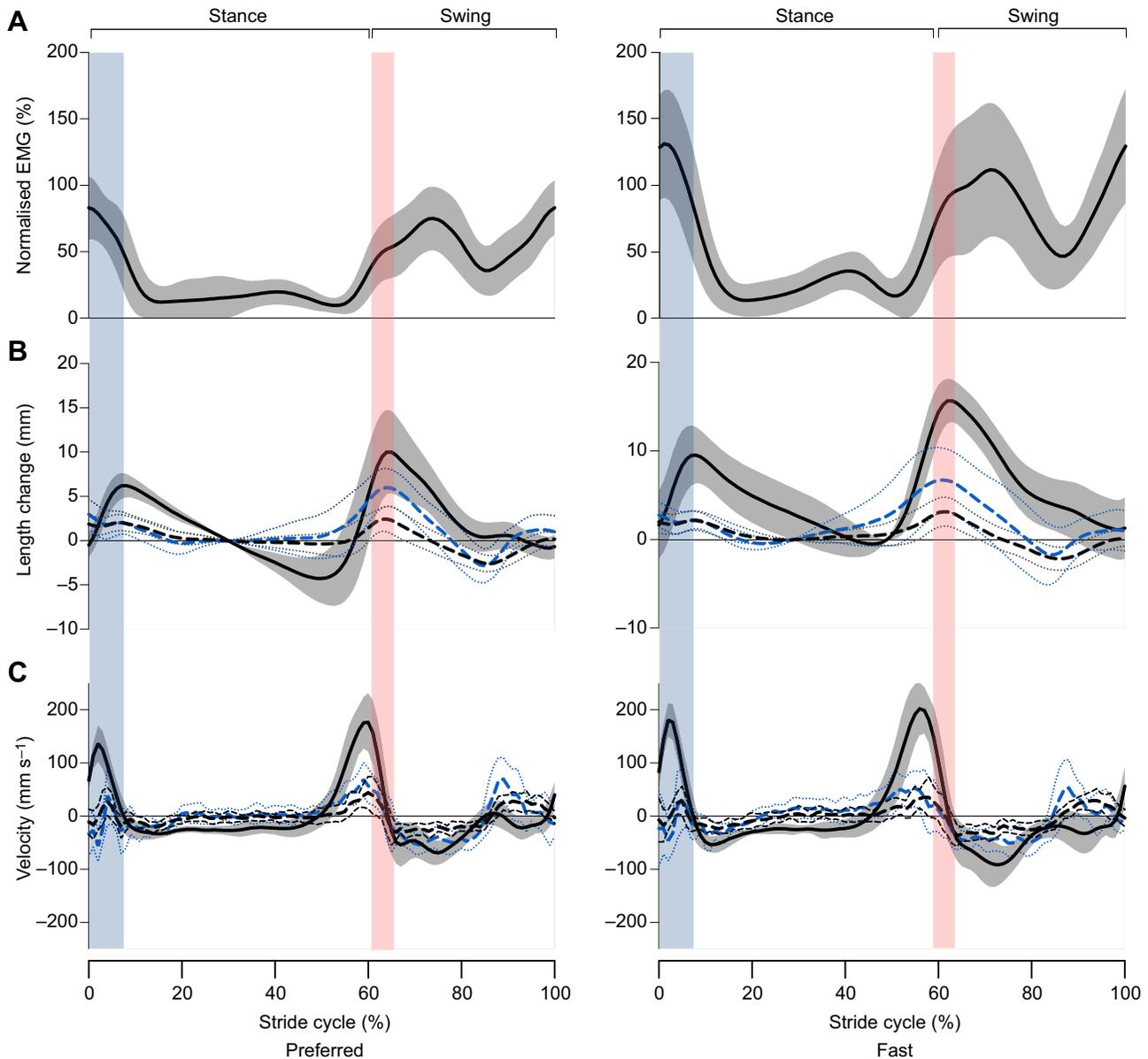
### Muscle fascicle and MTU activity and mechanics

#### TA power absorption during early stance

During the initial power absorption period in early stance at preferred velocity (indicated by the blue shaded area in Figs 2 and 3), the TA



**Fig. 2.** Group mean ( $\pm$ s.d.) time-series data for the ankle during a stride cycle at the preferred (left) and fast (right) walking velocity. (A) Ankle joint displacement. (B) Normalised ankle moment. (C) Normalised ankle power. An increase in walking velocity significantly increased the dorsiflexion moment ( $P \leq 0.01$ ) and negative ankle power ( $P \leq 0.01$ ) during early stance, and the dorsiflexion moment ( $P \leq 0.01$ ) and positive ankle power ( $P \leq 0.01$ ) in late stance. Positive values indicate a dorsiflexed position, increased dorsiflexion moment and positive power, respectively. The ankle power plot focuses on periods of power absorption and generation by the TA only. The inset expands to illustrate total joint power at the ankle. The shaded areas indicate periods of energy absorption in the TA during early stance (blue) and early swing (pink), defined as when power fell below zero as a dorsiflexion moment was generated.



**Fig. 3. Group mean ( $\pm$ s.d.) time-series data for the TA during a stride cycle at the preferred (left) and fast (right) walking velocity. (A) TA muscle activity normalised to maximum amplitude at the preferred walking velocity. (B) TA muscle–tendon unit (MTU, black solid line), TA superficial fascicle (black dashed line) and TA deep fascicle (blue dashed line) length change relative to 50% of stance. (C) Velocities of the same measures as in B. An increase in walking velocity significantly increased TA muscle activity ( $P \leq 0.01$ ) and MTU length change ( $P \leq 0.01$ ) during the negative power period in early stance while fascicle length changes remained relatively invariant, suggesting an increase in energy absorption in the tendinous tissue. During the positive power period in early swing, an increase in walking velocity increased TA electromyography (EMG) amplitude ( $P \leq 0.01$ ) and MTU shortening ( $P \leq 0.01$ ) with minimal differences in fascicle length change behaviour, potentially highlighting a role of TA tendinous tissue recoil in achieving the high dorsiflexion accelerations of the foot for toe clearance. Positive values indicate fascicle and MTU lengthening and lengthening velocity. The shaded areas illustrate periods of energy absorption in the TA during early stance (blue) and early swing (pink).**

reached its peak activation ( $92 \pm 15\%$  of maximum amplitude recorded at the preferred walking velocity) while the fascicles of the superficial and deep regions slightly shortened (mean peak shortening of  $0.4 \pm 0.3$  and  $1.3 \pm 0.5$  mm, respectively) and the MTU lengthened ( $6.5 \pm 1.4$  mm) relative to their length at heel strike (Fig. 3). Fascicles within the two regions shortened at similar times, although significant differences in the magnitude of normalised fascicle length change ( $P \leq 0.001$ ) were evident. Fascicles of the deep region exhibited a greater absolute length change. Subsequently, as TA activation decreased, a small amount of lengthening of the TA

fascicles was evident. The lengthening velocities of the fascicles in the superficial ( $P \leq 0.001$ ) and deep ( $P \leq 0.001$ ) regions were significantly slower than peak MTU stretch velocity (Fig. 3C) during the second half of the power absorption period in early stance. TA activation remained relatively quiescent in mid-stance, while the MTU shortened and fascicles remained at a relatively constant length. It therefore appears that immediately after heel contact, the majority of the lengthening and energy absorption observed in the TA occurs via the tendinous tissue, only a very small amount of which is subsequently dissipated by fascicle stretch.

### TA power absorption during early swing

The TA MTU and its fascicles continued to lengthen in early swing as activation gradually increased, and the TA MTU absorbed power (pink shaded area in Figs 2 and 3). The subsequent lengthening velocities at the preferred velocity were significantly greater for the MTU ( $195.6 \pm 49.2 \text{ mm s}^{-1}$ ) than for the fascicles in the superficial ( $63.2 \pm 18.7 \text{ mm s}^{-1}$ ,  $P \leq 0.001$ ) and deep regions ( $90.2 \pm 24.8 \text{ mm s}^{-1}$ ,  $P \leq 0.001$ ), indicating stretch of the tendinous tissue as the muscle actively generates tension. Following the power absorption period, the fascicles actively shortened with the MTU. Significant differences in the magnitude of normalised fascicle length change ( $P \leq 0.001$ ) were evident between the two regions during this period, such that the fascicles of the deep region exhibited greater peak shortening. At the preferred walking velocity, the shortening velocity of the MTU ( $86.0 \pm 18.7 \text{ mm s}^{-1}$ ) was significantly different to that of the superficial fascicles ( $49.2 \pm 1.0 \text{ mm s}^{-1}$ ,  $P \leq 0.001$ ) but no different to that of fascicles located in the deep region ( $74.2 \pm 12.8 \text{ mm s}^{-1}$ ,  $P = 0.06$ ). At the fast velocity, however, the mean peak MTU shortening velocity ( $111.2 \pm 34.9 \text{ mm s}^{-1}$ ) was significantly greater than the shortening velocity of the superficial ( $50.7 \pm 12.4 \text{ mm s}^{-1}$ ,  $P \leq 0.001$ ) and deep fascicles ( $75.5 \pm 17.2 \text{ mm s}^{-1}$ ,  $P = 0.004$ ). Therefore, it appears that active muscle fascicle shortening and elastic recoil of the tendinous tissue both contribute to dorsiflexion and positive power generation of the ankle during early swing.

### DISCUSSION

The results of this study suggest that, during walking, the MTU of the TA stretches and absorbs mechanical energy during the collision of the foot with the ground. The behaviour of both the deep and superficial TA muscle fascicles during early stance confirms the ability of the muscle to generate force with minimal fascicle length change, enabling the TA tendinous tissue to store increasing amounts of elastic strain energy at faster speeds. In interpreting our data, we make the assumption that the TA tendinous tissue is stretched beyond its slack length during the early energy absorption phase, which is highly likely as the dorsiflexor muscles generate active tension during this time (McGowan et al., 2010). The majority of the energy stored in the tendinous tissue does not appear to be dissipated by the fascicles, as highlighted by the lack of active fascicle lengthening immediately after the initial energy absorption period. Interestingly, in swing, the magnitude of fascicle shortening differed between the two anatomical regions of the TA across speeds such that at the fast walking velocity elastic energy return from the TA tendinous tissue assisted in accelerating the ankle into dorsiflexion so as to successfully clear the toes off the ground.

Contrary to our hypothesis, the TA muscle fascicles did not lengthen in mid-stance; instead, they remained relatively isometric while the MTU shortened, implying recoil of the tendinous tissue and return of absorbed energy. There was, however, a small amount of lengthening of the fascicles in early stance, immediately after the initial stretch of the MTU. However, it is unlikely that the magnitude of fascicle lengthening was sufficient to absorb the majority of the energy stored in the elastic tendinous tissue, particularly as the length change of the fascicles was much smaller than that of the MTU. We interpret this to mean that the TA tendinous tissue returns the elastic energy to the body after the initial energy absorption period, rather than this energy being absorbed by forcibly lengthening the TA fascicles. As the TA muscle activation reduced to zero at approximately 15% of the stride, and given the time course of muscle deactivation, we would expect that any energy stored would be returned by approximately 20% of the

stance phase, after which time there is minimal energy left in the tendon to release and very little length change in the muscle fascicles. Although our interpretations are limited by a lack of TA force estimation, the measurements of Gomes et al. (2017) illustrate that TA forces are minimal by 20% of the stride cycle, which is in agreement with our speculations that energy stored in the tendinous tissue is returned by this point.

While we presume that energy absorbed by the TA tendinous tissue during contact is returned to the body, this does not show up as positive power at the ankle joint. A lack of positive power measured at the ankle does not preclude the TA from a role in recycling energy. A classic example of this is Lombard's Paradox during human cycling, where the knee absorbs power via a flexion moment, but the quadriceps muscles still actively generate power to extend the knee (Kuo, 2002b). It remains unclear where the positive power generated by the TA might be returned; for instance, it may be absorbed by the plantar flexors as they begin to absorb energy during this period. Also, power generated by a muscle is not confined to providing acceleration at a specific joint; it may be returned to generate power at other joints or in different planes. For example, some of this energy may be released to initiate re-supination of the subtalar joint, as the TA has a supination moment arm at the subtalar joint (Klein et al., 1996). Regardless, rapid absorption of energy in the tendinous tissues is likely to help protect the TA muscle fibres from eccentric muscle damage (Konow et al., 2012; Werkhausen et al., 2017). Compliance of the tendinous tissue is also likely to reduce the forces required of the muscle during active lengthening by increasing the time over which forces are applied to decelerate the limb.

A novel finding of this study was the contribution of elastic energy to positive ankle power and acceleration of ankle dorsiflexion in swing. A key role of the TA is to clear the toes off the ground during the swing phase of gait, which was thought to be generated primarily by active muscle fascicle shortening (Chleboun et al., 2007). However, our results demonstrate that once the foot comes off the ground, the TA tendinous tissue can aid the muscle and accelerate the ankle into dorsiflexion. The TA muscle activates as the ankle is generating positive power and the triceps surae muscles are deactivating. During this period, our results indicate that the TA tendinous tissue is likely to be lengthening; the length changes of the fascicles are much smaller than those of the MTU and the fascicles even shorten for a brief period as the MTU is still lengthening. The energy that is potentially stored in the TA tendinous tissue is likely to come from that generated by the plantar flexors and recoil of the Achilles tendon. Once the foot had left the ground, the rate of shortening in the muscle fascicles was typically around 30% (superficial region) to 70% (deep region) of the total MTU shortening speed during fast walking, highlighting a role of TA tendinous tissue recoil in achieving the high dorsiflexion accelerations of the foot in early swing and assisting in toe clearance. Toe clearance is most sensitive to ankle angle (Moosabhoy and Gard, 2006) and inadequate ankle dorsiflexion may risk unintentional ground contact, resulting in trips and falls (Begg and Sparrow, 2009; Kemoun et al., 2002). This complex interaction of seemingly synergistic antagonist muscles suggests that co-activation of muscles may be useful for tuning the stiffness of a joint and increasing the power generated by an individual muscle (Farahat and Herr, 2010), rather than just providing joint stability as traditionally thought.

The amount of energy absorbed and released by the TA tendinous tissues is considerably smaller than that associated with the plantar flexors; however, the role of the TA in energy absorption during foot

contact is still critical for walking performance. While the forces produced by the TA muscle are small, its tendon is sufficiently compliant to lengthen by approximately 20% of the fascicle length (~10–15 mm) during maximum isometric contractions (Maganaris and Baltzopoulos, 1999). The stretch that we are measuring here is therefore approximately 50% of that which would be experienced during a maximum isometric contraction. Usherwood et al. (2012) argues that a heel–sole–toe strategy (where energy is absorbed by the dorsiflexors during contact) is advantageous because the TA is well suited to losing energy so as to redirect the body's centre of mass after collision of the foot with the ground – an energetically optimal method of walking (Kuo, 2002a; Ruina et al., 2005). Our data suggest that rather than just dissipating the energy absorbed during contact, energy absorbed by TA tendinous tissue may be returned in the form of elastic energy.

To the best of our knowledge, the variation in fascicle length changes between the superficial and deep regions of the TA during gait have not previously been reported. Previous studies quantifying fascicle length changes illustrate minimal differences between regions during isometric contractions (Maganaris and Baltzopoulos, 1999; Raiteri et al., 2016) and quiet standing (Day et al., 2013). Here, we show the overall pattern and timing of fascicle length changes between the two regions were similar; however, the normalised fascicle length change magnitude across the gait cycle was notably different, such that the fascicles of the deep region typically exhibited greater length changes. It is unclear which factors drive the differences within the TA; however, disparities in length changes may be an indication of variable activation or stress within the muscle or differences in how the regions interact with the central aponeurosis.

The methods used to study the behaviour of the TA MTU and its muscle fascicle length changes are not without limitations. Capturing TA fascicle length changes using 2D ultrasound imaging is not easy. 2D ultrasound-based measures of muscle fascicle lengths have been shown to be reliable and accurate in static and passive contractions, although testing their validity in dynamic movements is difficult (Kwah et al., 2013). Similarly, accurately modelling the muscle–tendon path of the TA is challenging because of its multi-articular nature. Given the potential limitations of both ultrasound imaging and musculoskeletal modelling, we did not calculate tendinous tissue length changes but rather focused on the general function of TA tendinous tissue, which we are confident is correct.

## Conclusions

In conclusion, the current study has demonstrated the mechanical function of the TA muscle fascicles and MTU during walking. At contact, the contractile component of the muscle functions relatively isometrically as the TA MTU strains, suggesting the majority of the MTU strain occurs in the tendinous tissues, allowing elastic energy absorption during collision of the foot with the ground. This mechanical function of the TA tendinous tissue protects its muscle fibres from active lengthening and potential muscle damage during weight acceptance, and allows energy to be returned to the system. In early swing, the TA tendinous tissue contributes to the power required to accelerate the foot into dorsiflexion through elastic recoil.

## Competing interests

The authors declare no competing or financial interests.

## Author contributions

Conceptualization: J.N.M., A.G.C., G.A.L.; Methodology: J.N.M., A.G.C., G.A.L.; Formal analysis: J.N.M., G.A.L.; Writing - original draft: J.N.M.; Writing - review & editing: J.N.M., A.G.C., G.A.L.; Supervision: G.A.L.

## Funding

J.N.M. is supported by a post-doctoral fellowship funded by the Australian Research Council.

## Data availability

The datasets analysed in the current study are available from the UQ Espace repository: <http://espace.library.uq.edu.au/view/UQ:732135>

## References

- Begg, R. K. and Sparrow, W. A. (2009). Ageing effects on knee and ankle joint angles at key events and phases of the gait cycle. *J. Med. Eng. Technol.* **30**, 382–389. doi:10.1080/03091900500445353
- Biewener, A. A., Konieczynski, D. D. and Baudinette, R. V. (1998). In vivo muscle force-length behavior during steady-speed hopping in tammar wallabies. *J. Exp. Biol.* **201**, 1681–1694.
- Butcher, M. T., Hermanson, J. W., Ducharme, N. G., Mitchell, L. M., Soderholm, L. V. and Bertram, J. E. A. (2009). Contractile behavior of the forelimb digital flexors during steady-state locomotion in horses (*Equus caballus*): An initial test of muscle architectural hypotheses about in vivo function. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **152**, 100–114. doi:10.1016/j.cbpa.2008.09.007
- Cavagna, G. A. and Kaneko, M. (1977). Mechanical work and efficiency in level walking and running. *J. Physiol.* **268**, 467–481. doi:10.1113/jphysiol.1977.sp011866
- Chleboun, G. S., Busic, A. B., Graham, K. K. and Stuckey, H. A. (2007). Fascicle length change of the human tibialis anterior and vastus lateralis during walking. *J. Orthop. Sports Phys. Ther.* **37**, 372–379. doi:10.2519/jospt.2007.2440
- Cronin, N. J., Avela, J., Finni, T. and Peltonen, J. (2013). Differences in contractile behaviour between the soleus and medial gastrocnemius muscles during human walking. *J. Exp. Biol.* **216**, 909–914. doi:10.1242/jeb.078196
- Day, J. T., Lichtwark, G. A. and Cresswell, A. G. (2013). Tibialis anterior muscle fascicle dynamics adequately represent postural sway during standing balance. *PLoS One* **8**, e1000795. doi:10.1371/journal.pone.0100079
- 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. doi:10.1109/TBME.2007.901024
- Farahat, W. A. and Herr, H. M. (2010). Optimal workloop energetics of muscle-actuated systems: an impedance matching view. *PLoS Comput. Biol.* **6**, e1000795. doi:10.1371/journal.pcbi.1000795
- 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. doi:10.1016/j.cmpb.2016.02.016
- 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. doi:10.1242/jeb.126854
- Gomes, A. A., Ackermann, M., Ferreira, J. P., Orselli, M. I. V. and Sacco, I. C. N. (2017). Muscle force distribution of the lower limbs during walking in diabetic individuals with and without polyneuropathy. *J. Neuroeng. Rehabil.* **14**, 111. doi:10.1186/s12984-017-0327-x
- Griffiths, R. I. (1991). Shortening of muscle fibres during stretch of the active cat medial gastrocnemius muscle: the role of tendon compliance. *J. Physiol.* **436**, 219–236. doi:10.1113/jphysiol.1991.sp018547
- Heglund, N. C., Fedak, M. A., Taylor, C. R. and Cavagna, G. A. (1982). Energetics and mechanics of terrestrial locomotion. IV. Total mechanical energy changes as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 57–66.
- Hof, A. L., Elzinga, H., Grimmius, W. and Halbertsma, J. P. K. (2002). Speed dependence of averaged EMG profiles in walking. *Gait Posture* **16**, 78–86. doi:10.1016/S0966-6362(01)00206-5
- Ishikawa, M., Komi, P. V., Grey, M. J., Lepola, V. and Brüggemann, G.-P. (2005). Muscle-tendon interaction and elastic energy usage in human walking. *J. Appl. Physiol.* **99**, 603–608. doi:10.1152/jappphysiol.00189.2005
- Kemoun, G., Thoumie, P., Boisson, D. and Guieu, J. D. (2002). Ankle dorsiflexion delay can predict falls in the elderly. *J. Rehabil. Med.* **34**, 278–283. doi:10.1080/165019702760390374
- Klein, P., Mattys, S. and Rooze, M. (1996). Moment arm length variations of selected muscles acting on talocrural and subtalar joints during movement: an in vitro study. *J. Biomech.* **29**, 21–30. doi:10.1016/0021-9290(95)00025-9
- Konow, N., Azizi, E. and Roberts, T. J. (2012). Muscle power attenuation by tendon during energy dissipation. *Proc. Biol. Sci.* **279**, 1108–1113. doi:10.1098/rspb.2011.1435
- Konow, N., Cheney, J. A., Roberts, T. J., Waldman, J. R. S. and Swartz, S. M. (2015). Spring or string: does tendon elastic action influence wing muscle mechanics in bat flight? *Proc. Biol. Sci.* **282**, 20151832. doi:10.1098/rspb.2015.1832
- Kuo, A. D. (2002a). Energetics of actively powered locomotion using the simplest walking model. *J. Biomech. Eng.* **124**, 113–120. doi:10.1115/1.1427703
- Kuo, A. D. (2002b). *Classics in Movement Science*. Human Kinetics Publishers.
- 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. doi:10.1152/jappphysiol.01430.2011
- Lichtwark, G. A.** (2005). A modified Hill muscle model that predicts muscle power output and efficiency during sinusoidal length changes. *J. Exp. Biol.* **208**, 2831-2843. doi:10.1242/jeb.01709
- Lichtwark, G. A. and Wilson, A. M.** (2005). In vivo mechanical properties of the human Achilles tendon during one-legged hopping. *J. Exp. Biol.* **208**, 4715-4725. doi:10.1242/jeb.01950
- 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. doi:10.1242/jeb.02434
- Maas, H., Gregor, R. J. and Hodson-Tole, E. F.** (2009). Distinct muscle fascicle length changes in feline medial gastrocnemius and soleus muscles during slope walking. *J. Appl. Biomech.* **106**, 1169-1180. doi:10.1152/jappphysiol.01306.2007
- Maganaris, C. N. and Baltzopoulos, V.** (1999). Predictability of in vivo changes in pennation angle of human tibialis anterior muscle from rest to maximum isometric dorsiflexion. *Eur. J. Appl. Physiol. Occup. Physiol.* **79**, 294-297. doi:10.1007/s004210050510
- Maharaj, J. N., Cresswell, A. G. and Lichtwark, G. A.** (2016). The mechanical function of the tibialis posterior muscle and its tendon during locomotion. *J. Biomech.* **49**, 3238-3243. doi:10.1016/j.jbiomech.2016.08.006
- McGowan, C. P., Neptune, R. R., Clark, D. J. and Kautz, S. A.** (2010). Modular control of human walking: Adaptations to altered mechanical demands. *J. Biomech.* **43**, 412-419. doi:10.1016/j.jbiomech.2009.10.009
- Moosabhoy, M. A. and Gard, S. A.** (2006). Methodology for determining the sensitivity of swing leg toe clearance and leg length to swing leg joint angles during gait. *Gait Posture* **24**, 493-501. doi:10.1016/j.gaitpost.2005.12.004
- 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. doi:10.7717/peerj.2260
- Richards, C. T. and Sawicki, G. S.** (2012). Elastic recoil can either amplify or attenuate muscle-tendon power, depending on inertial vs. fluid dynamic loading. *J. Theor. Biol.* **313**, 68-78. doi:10.1016/j.jtbi.2012.07.033
- Roberts, T. J., Marsh, R. L., Weyand, P. G. and Taylor, C. R.** (1997). Muscular force in running turkeys: the economy of minimizing work. *Science* **275**, 1113-1115. doi:10.1126/science.275.5303.1113
- Ruina, A., Bertram, J. E. A. and Srinivasan, M.** (2005). A collisional model of the energetic cost of support work qualitatively explains leg sequencing in walking and galloping, pseudo-elastic leg behavior in running and the walk-to-run transition. *J. Theor. Biol.* **237**, 170-192. doi:10.1016/j.jtbi.2005.04.004
- Usherwood, J. R., Channon, A. J., Myatt, J. P., Rankin, J. W. and Hubel, T. Y.** (2012). The human foot and heel-sole-toe walking strategy: a mechanism enabling an inverted pendular gait with low isometric muscle force? *J. R. Soc. Interface* **9**, 2396-2402. doi:10.1098/rsif.2012.0179
- van den Bogert, A. J. and De Koning, J. J.** (1996). On optimal filtering for inverse dynamics analysis. Proceedings of the IXth Biennial Conference of the Canadian Society for Biomechanics, Vancouver, 1996, pp. 214-215.
- Ward, S. R., Eng, C. M., Smallwood, L. H. and Lieber, R. L.** (2009). Are current measurements of lower extremity muscle architecture accurate? *Clin. Orthop. Relat. Res.* **467**, 1074-1082. doi:10.1007/s11999-008-0594-8
- Werkhausen, A., Albracht, K., Cronin, N. J., Meier, R., Bojsen-Møller, J. and Seynnes, O. R.** (2017). Modulation of muscle-tendon interaction in the human triceps surae during an energy dissipation task. *J. Exp. Biol.* **220**, 4141-4149. doi:10.1242/jeb.164111
- Wilson, A. M., Watson, J. C. and Lichtwark, G. A.** (2003). Biomechanics: a catapult action for rapid limb protraction. *Nature* **421**, 35-36. doi:10.1038/421035a