

RESEARCH ARTICLE

Tendon elastic strain energy in the human ankle plantar-flexors and its role with increased running speed

Adrian Lai, Anthony G. Schache, Yi-Chung Lin and Marcus G. Pandy*

ABSTRACT

The human ankle plantar-flexors, the soleus and gastrocnemius, utilize tendon elastic strain energy to reduce muscle fiber work and optimize contractile conditions during running. However, studies to date have considered only slow to moderate running speeds up to 5 m s^{-1} . Little is known about how the human ankle plantar-flexors utilize tendon elastic strain energy as running speed is advanced towards maximum sprinting. We used data obtained from gait experiments in conjunction with musculoskeletal modeling and optimization techniques to calculate muscle–tendon unit (MTU) work, tendon elastic strain energy and muscle fiber work for the ankle plantar-flexors as participants ran at five discrete steady-state speeds ranging from jogging ($\sim 2 \text{ m s}^{-1}$) to sprinting ($\geq 8 \text{ m s}^{-1}$). As running speed progressed from jogging to sprinting, the contribution of tendon elastic strain energy to the positive work generated by the MTU increased from 53% to 74% for the soleus and from 62% to 75% for the gastrocnemius. This increase was facilitated by greater muscle activation and the relatively isometric behavior of the soleus and gastrocnemius muscle fibers. Both of these characteristics enhanced tendon stretch and recoil, which contributed to the bulk of the change in MTU length. Our results suggest that as steady-state running speed is advanced towards maximum sprinting, the human ankle plantar-flexors continue to prioritize the storage and recovery of tendon elastic strain energy over muscle fiber work.

KEY WORDS: Achilles tendon strain, Muscle fiber, Muscle force, Human gait, Sprinting, Efficiency, Musculoskeletal modeling

INTRODUCTION

The human ankle plantar-flexors, the soleus and gastrocnemius, have an important biomechanical role during running. Experimental data are available demonstrating that these muscles together produce forces of up to 12 times body weight (BW) during running (Komi, 1990). Moreover, musculoskeletal modeling studies have demonstrated that, during running, the ankle plantar-flexors generate the largest forces of all the major lower-limb muscle groups (Dorn et al., 2012). As running speed advances towards maximum sprinting, the soleus and gastrocnemius must also generate force in an increasingly shorter period of time (Weyand et al., 2000; Weyand et al., 2010). The ankle plantar-flexors are therefore required to contract more forcefully and rapidly with faster running speeds.

The muscle–tendon units (MTUs) of the ankle plantar-flexors likely function in a highly complex and tightly integrated manner to generate the force and energy needed to power running (Roberts et al., 1997; Roberts, 2002; Lichtwark et al., 2007). When compared

with the other major human lower-limb muscles, the gastrocnemius and soleus have unique designs in that both have short muscle fibers connected to the heel via a long and compliant Achilles tendon. The function of the tendon can influence that of the muscle fibers in such a way that muscle fiber behavior is decoupled from the overall behavior of the MTU, thereby optimizing muscle fiber contractile conditions and minimizing mechanical energy expenditure (Roberts and Azizi, 2011). For instance, *in vivo* ultrasonography studies of the ankle plantar-flexors have demonstrated that tendon stretch can optimize the regions in which muscle fibers operate on their force–length–velocity relationship during walking and slow speeds of running (Fukunaga et al., 2001; Ishikawa et al., 2005; Lichtwark et al., 2007; Farris and Sawicki, 2012). Furthermore, musculoskeletal modeling studies investigating the function of the ankle plantar-flexors during walking and running have calculated the contributions of muscle fiber work and tendon elastic strain energy to the mechanical energetics of the MTU (Hof et al., 2002; Sasaki and Neptune, 2006). These studies have demonstrated the ability of tendons to store strain energy and contribute to the mechanical work done by the ankle plantar-flexors during running. Cadaveric studies have also shown that the substantial capacity of the Achilles tendon to store elastic strain energy can reduce muscle fiber work and metabolic energy expenditure (Alexander and Bennet-Clark, 1977; Alexander, 1987; Ker et al., 1987). Importantly, however, all of the aforementioned studies have been limited to running speeds no greater than 5 m s^{-1} . We were therefore interested in understanding how the contribution of tendon elastic strain energy to the mechanical work done by the MTU varies across the complete spectrum of human running speeds. Specifically, what happens as running speed is advanced towards maximum sprinting?

It has been postulated that the utilization of tendon elastic strain energy is enhanced with increased running speed (Cavagna, 2009), which is consistent with findings that have highlighted the discrepancy in mechanical work done and metabolic energy expenditure during locomotion (Cavagna et al., 1964; Cavagna et al., 1977; Cavagna and Kaneko, 1977; Heglund et al., 1982). Specifically, the efficiency of generating positive work is greater than would be predicted from muscle shortening alone, with this disparity increasing steadily with running speed. Such observations suggest that tendons contribute proportionally more positive work as running speed increases, thus allowing the muscle fibers to operate more efficiently than would be the case if tendon elastic strain energy were not utilized (Alexander, 1988; Alexander, 2002; Roberts, 2002; Biewener, 2003). Several animal studies have demonstrated that the magnitude of elastic strain energy recovery increases with locomotion speed, for example, in running turkeys (Roberts et al., 1997) and galloping horses (Biewener, 1998b; Harrison et al., 2010). Furthermore, a study investigating the lateral gastrocnemius and plantaris muscles of wallabies at various steady-state speeds found that as speed increased, the relative contribution of tendon elastic strain energy to the positive mechanical work done

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List of symbols and abbreviations

BW	body weight
d.f.	degrees of freedom
EMG	electromyography
F – L	force–length
$F_{o,M}$	maximum isometric force
F – V	force–velocity
GRF	ground reaction force
$l_{o,M}$	optimal fiber length
$l_{s,T}$	tendon slack length
MTU	muscle–tendon unit
V_M	muscle shortening velocity
V_T	tendon shortening velocity
V_{max}	maximum shortening velocity
w	muscle width
α	pennation angle

by the MTU also increased, accounting for 92–97% of the positive work done by the MTU at faster hopping speeds (Biewener and Baudinette, 1995; Biewener et al., 1998). However, the influence of running speed on the storage and recovery of tendon elastic strain energy in the human ankle plantar-flexors requires further investigation.

In the present study, experimental gait data were used in conjunction with three-dimensional musculoskeletal modeling to investigate the mechanical interaction between muscle and tendon components of the human ankle plantar-flexors as running speed increased from jogging to sprinting. The specific aim was to calculate the contributions of tendon elastic strain energy and muscle fiber work to the positive mechanical work done by the MTU for the soleus and gastrocnemius during stance as a function of running speed. We hypothesized that ankle plantar-flexor muscle performance is enhanced at faster running speeds primarily because tendon elastic strain energy contributes a greater proportion of MTU positive work during the stance phase of the stride cycle.

RESULTS

Model-based muscle fiber length changes and mean muscle activations were consistent with data obtained from ultrasound measurements reported in the literature and experimentally recorded mean electromyography (EMG) data, respectively (Figs 1 and 2; see also supplementary material Fig. S1). For gastrocnemius, both model-based and ultrasound-measured muscle fiber length changes underwent a stretch–shortening cycle during the stance phase for walking at both moderate (1.5 m s^{−1}) and fast speeds (2.1 m s^{−1}), a behavior that was noticeably absent for running (2.1 and 3.5 m s^{−1}). A progressive increase was observed in the magnitude of the mean EMG signal measured for the soleus and the two sub-regions of the gastrocnemius (medial gastrocnemius and lateral gastrocnemius) with each increment in running speed. Mean model-based muscle activations displayed similar relative increases in activation with faster running.

We observed differences in MTU, muscle fiber and tendon lengths and velocities with increased running speed for the soleus and gastrocnemius. In both muscles, muscle fiber length change was decoupled from MTU length change, irrespective of running speed (Figs 3 and 4). For example, during mid-stance for sprinting, the MTU lengthened and then shortened, whereas little change occurred in muscle fiber length. Muscle fiber length change remained small relative to MTU length change for both muscles across all running speed increments, especially during the period of high force development where the change in muscle fiber length became smaller with faster running (Fig. 5). Specifically, as running speed advanced from 2.1 to ≥ 8 m s^{−1}, peak muscle fiber length change decreased from 5.1% and 4.4% of the optimal fiber length ($l_{o,M}$) to 1.7% and 2.1% for the soleus and gastrocnemius, respectively, during the time when the force developed by each muscle exceeded 80% of its peak force (Fig. 5). In addition, the length of the muscle fiber when peak force occurred became increasingly shorter with faster running for both the soleus [range: $0.82 \pm 0.06 l_{o,M}$ (jogging at 2.1 m s^{−1}) to $0.64 \pm 0.07 l_{o,M}$ (sprinting at ≥ 8 m s^{−1})] and gastrocnemius [range: $0.71 \pm 0.04 l_{o,M}$ (jogging at 2.1 m s^{−1}) to $0.58 \pm 0.05 l_{o,M}$ (sprinting at ≥ 8 m s^{−1})] (Fig. 6).

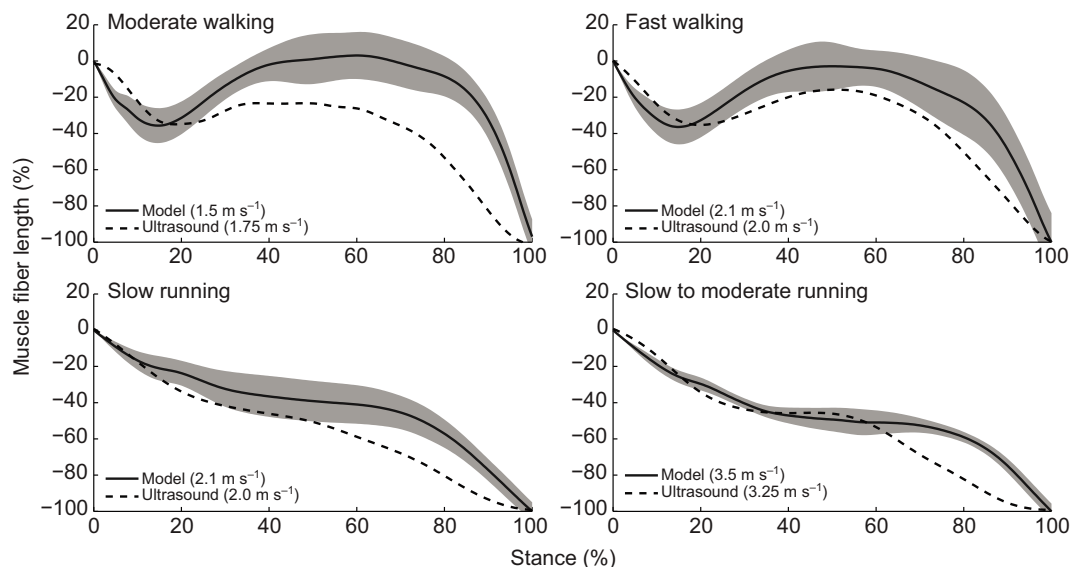


Fig. 1. Comparison of *in vivo* measured and model-based gastrocnemius muscle fiber lengths for walking and slow speeds of running. *In vivo* measurements from ultrasound of gastrocnemius muscle fiber lengths were reported elsewhere (Farris and Sawicki, 2012). Note that the data reported by Farris and Sawicki for running correspond to rear-foot strikers. In order to compare the data, muscle fiber lengths were converted to the same units of measurement (i.e. expressed as a percentage of the total change in muscle fiber length that occurred from foot strike to toe-off). For consistency, the model results shown correspond to participants that exhibited a rear-foot strike pattern during running ($N=3$).

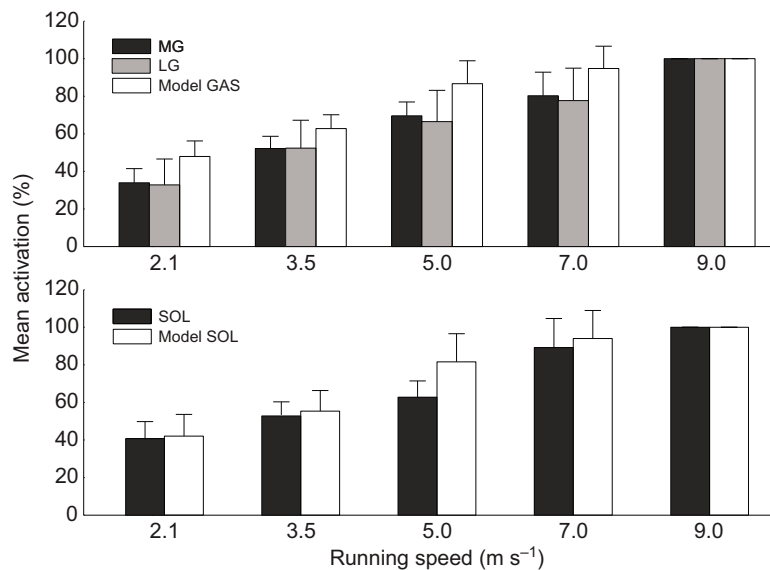


Fig. 2. Experimentally recorded electromyography (EMG) data compared with predicted (model-based) muscle activation for each running speed. Top: mean EMG signal measured for the medial gastrocnemius (MG) and lateral gastrocnemius (LG) compared against mean model-based gastrocnemius (GAS) muscle activation. Bottom: mean EMG signal measured from the soleus (SOL) compared against mean model-based soleus activation. Experimental and model-based data were normalized by the mean EMG signal measured and the mean model-based activation calculated for sprinting, respectively. The error bars represent ± 1 s.d. Note that because of the normalization process, the maximum sprinting condition, by definition, does not have a ± 1 s.d. error bar.

MTU shortening velocity also increased with running speed for both muscles (Figs 3 and 4). When running progressed from 2.1 to ≥ 8 m s⁻¹, MTU shortening velocity at the time of peak positive power generation for the soleus and gastrocnemius increased by 0.22 ± 0.06 m s⁻¹ ($92.2 \pm 23.1\%$) and 0.20 ± 0.04 m s⁻¹ ($92.8 \pm 20.4\%$), respectively. Tendon recoil velocity was responsible for the majority of the MTU shortening velocity for both muscles at all running speeds. For example, when jogging at 2.1 m s⁻¹, the contribution of tendon recoil velocity to MTU shortening velocity was $67.6 \pm 13.4\%$ for the soleus and $78.5 \pm 16.1\%$ for the gastrocnemius. As running speed progressed to sprinting at ≥ 8 m s⁻¹, the contribution of tendon recoil velocity increased to $78.8 \pm 16.7\%$ for the soleus, whereas it remained of a similar magnitude ($79.5 \pm 11.3\%$) for the gastrocnemius. Muscle fiber shortening velocity at the time of peak force development remained relatively consistent in magnitude with faster running; it decreased by only 0.04 ± 0.04 maximum shortening velocity (V_{\max}) and $0.02 \pm 0.05 V_{\max}$ for the soleus and gastrocnemius, respectively, as running speed progressed from 2.1 to ≥ 8 m s⁻¹ (Fig. 6).

Increased running speed influenced muscle fiber work and tendon elastic strain energy as well as their respective contributions to the positive work done by the MTU for the soleus and gastrocnemius (Fig. 7). There was a uniform increase in muscle fiber work and tendon elastic strain energy for both muscles as running speed increased from 2.1 to 5.0 m s⁻¹ (Fig. 7, top). Beyond 5.0 m s⁻¹, positive work done by the two components decreased for both muscles in accordance with the decrease in positive work done by the MTU. Across all running speeds, the majority of the positive muscle fiber work done during the stance phase occurred when the MTU was generating power (Fig. 7). Specifically, between 70.4–87.3% and 57.1–64.6% of the positive muscle fiber work done during the stance phase occurred when the MTU generated positive power for the soleus and gastrocnemius, respectively. Muscle force and positive work were substantially greater for the soleus than for the gastrocnemius, irrespective of running speed (Fig. 5 and Fig. 7, top). For example, when jogging at 2.1 m s⁻¹, muscle force and positive work generated by the soleus were at least threefold larger than that calculated for gastrocnemius, and this difference became

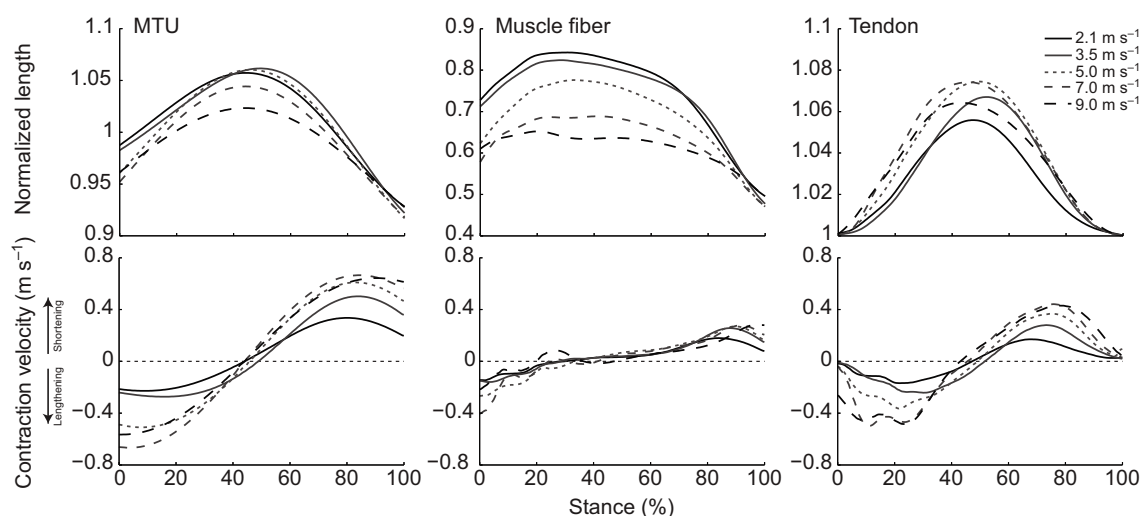


Fig. 3. Normalized mean muscle–tendon unit (MTU), muscle fiber and tendon lengths and shortening velocities for the soleus across five different running speeds. MTU, muscle fiber and tendon length changes were normalized by the resting MTU length, optimal fiber length and tendon slack length, respectively.

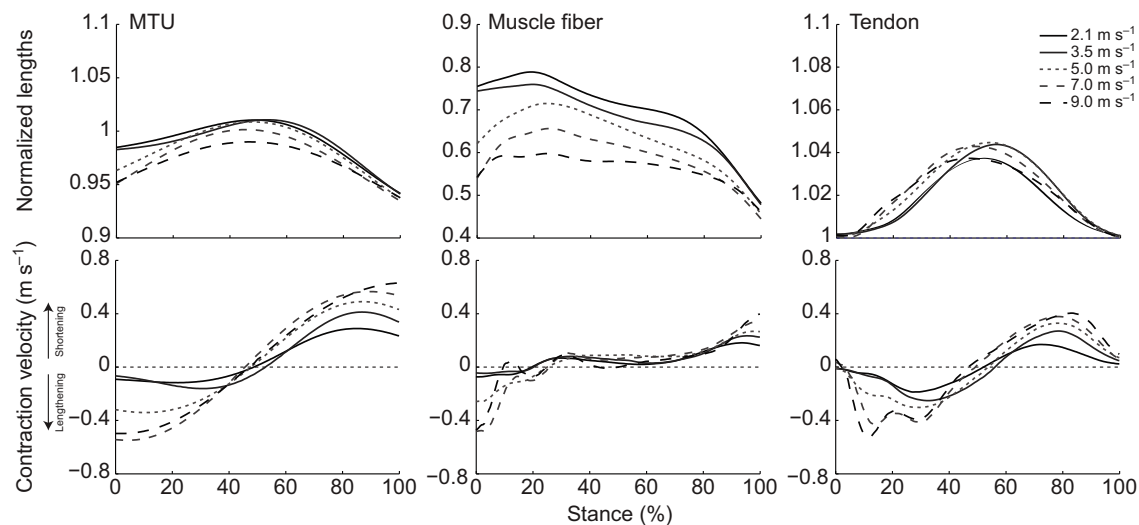


Fig. 4. Normalized mean MTU, muscle fiber and tendon lengths and shortening velocities for the gastrocnemius across five different running speeds. MTU, muscle fiber and tendon length changes were normalized by the resting MTU length, optimal fiber length and tendon slack length, respectively.

fourfold when sprinting at $\geq 8 \text{ m s}^{-1}$. Tendon elastic strain energy provided a greater contribution to MTU positive work than muscle fiber work for both muscles at all running speeds (Fig. 7, bottom). Furthermore, the contribution of tendon elastic strain energy increased with faster running. When comparing jogging at 2.1 m s^{-1} with sprinting at $\geq 8 \text{ m s}^{-1}$, the contribution of tendon elastic strain energy significantly increased from $53.1 \pm 10.6\%$ to $74.2 \pm 13.6\%$ for the soleus ($P < 0.001$). The increase in elastic strain energy for soleus occurred steadily with each running speed increment. Elastic strain energy for the gastrocnemius also increased from $61.9 \pm 11.9\%$ at 2.1 m s^{-1} to $75.3 \pm 11.9\%$ at $\geq 8 \text{ m s}^{-1}$, but this change was not significant ($P = 0.069$).

DISCUSSION

The human ankle plantar-flexor muscles perform a critical function during running. They are the dominant contributors to the acceleration of the body's center of mass during the second half of stance at all running speeds (Dorn et al., 2012; Hamner and Delp, 2013). It has been postulated that these muscles favor utilizing tendon elastic strain energy over muscle fiber work (Biewener, 1998a; Lichtwark et al., 2007), and that tendon elastic strain energy is enhanced when running speed advances towards maximum sprinting (Cavagna and Kaneko, 1977; Cavagna, 2009). Therefore, we hypothesized that with increased running speed, tendon elastic strain energy would contribute a greater proportion of the positive work done by the MTU for the ankle plantar-flexors, thereby enhancing the performance of the muscle fibers by allowing them

to operate in a more isometric manner than would otherwise occur without the presence of an elastic tendon. The model calculations support this proposition. For both the soleus and gastrocnemius, the relative contribution of tendon elastic strain energy to the positive work done by the MTU was greater than that of muscle fiber work and this contribution increased with running speed. For the soleus, the relative contribution of the tendon increased uniformly from 53% to 74% with faster running, whereas for the gastrocnemius, it remained relatively constant at around 65% across most running speeds before increasing to 75% when sprinting (Fig. 7).

The musculoskeletal modeling approach used in the present study was limited in three respects. First, static optimization theory was applied to calculate lower-limb muscle forces, whereby activation dynamics was neglected. It is acknowledged that neglecting activation dynamics can influence predicted muscle performance and coordination strategies, especially during high-speed cyclic contractions (Neptune and Kautz, 2001). Nevertheless, previous studies have shown that the omission of activation dynamics may only cause differences in the magnitude of the estimated muscle force during running (Pandy and Andriacchi, 2010; Lin et al., 2012), which we do not believe would substantially affect our main findings regarding the relative behavior of the muscle fibers and tendon in response to an increase in running speed. Second, the same cost function was used to calculate muscle forces across all running speeds. A minimum muscle activation criterion, as applied in this study, has been used previously to investigate muscle function during running (Glitsch and Baumann, 1997; Pandy and

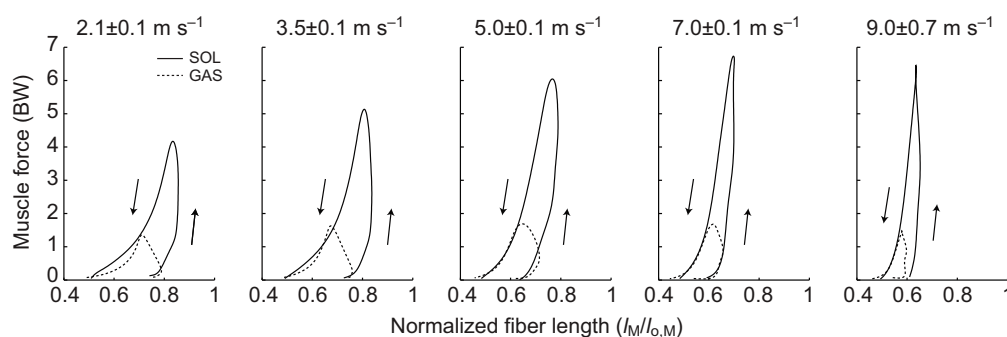


Fig. 5. Work loops for the soleus and gastrocnemius muscles across five different running speeds. Muscle force and muscle fiber length (l_M) were normalized by body weight (BW) and optimal fiber length ($l_{0,M}$), respectively.

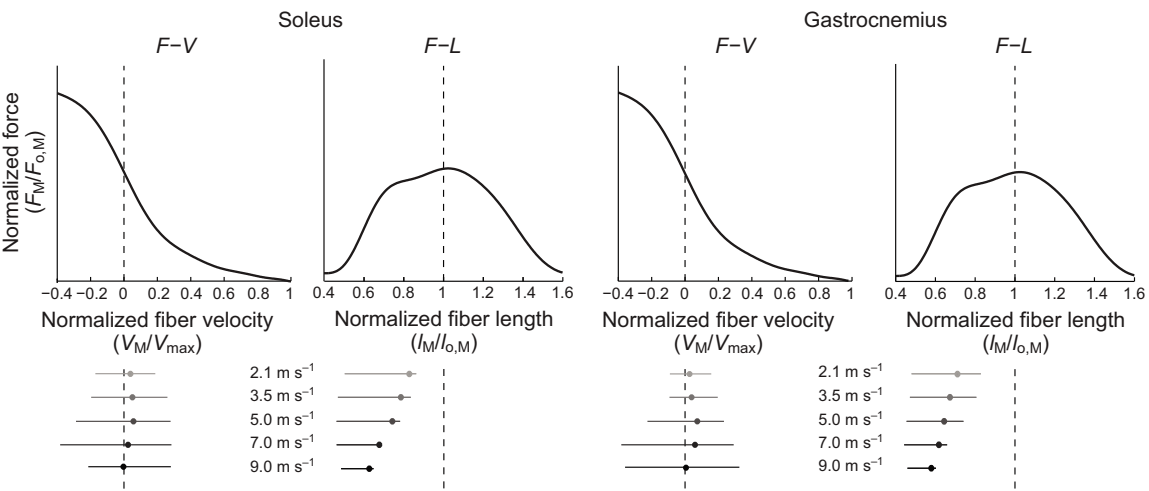


Fig. 6. Operating regions for the soleus (left) and gastrocnemius (right) muscles on the force–velocity (F – V) and force–length (F – L) curves across five different running speeds. The circles below the F – V and F – L curves represent the muscle fiber velocity and length, respectively, at which peak muscle force occurred for the corresponding running speed. The horizontal lines represent the muscle fiber operating ranges on the F – V and F – L curves during stance for the corresponding running speed. Muscle force (F_M), muscle fiber velocity (V_M) and muscle fiber length (l_M) were normalized by the peak isometric force ($F_{0,M}$), maximum shortening velocity (V_{max}) and optimal fiber length ($l_{0,M}$), respectively. The vertical dashed lines represent isometric fiber velocity and the optimal fiber length on the F – V and F – L curves, respectively.

Andriacchi, 2010; Miller et al., 2011; Dorn et al., 2012). Although other criteria, such as maximizing muscular power generation (Cavagna et al., 1971; Ward-Smith, 1985), may potentially be more applicable for time-dependent locomotion tasks like maximum sprinting, they are unlikely to apply at submaximal running speeds. Third, the predicted muscle fiber behavior for the soleus and gastrocnemius is likely sensitive to the tendon mechanical properties and muscle–tendon architecture assumed in the model. Arnold et al. (Arnold et al., 2013) found that estimates of muscle fiber behavior with a less compliant tendon do not agree well with *in vivo* measurements at corresponding locomotion speeds. Yet,

tendon stiffness for the human ankle plantar-flexors has been reported to vary between 145 and 390 N mm^{−1} (Lichtwark and Wilson, 2005; Muraoka et al., 2005). To examine the influence of tendon stiffness on our results, a sensitivity analysis was performed on one participant with the nominal value of tendon stiffness varied by ±20% (i.e. 160–240 N mm^{−1}). As expected, the absolute magnitudes of muscle fiber work and tendon elastic strain energy were altered; however, the relative contribution of each component to the positive work done by the MTU remained similar. It is also noted that the ankle plantar-flexors in this study were represented as two separate MTUs, each having their own tendon, rather than a

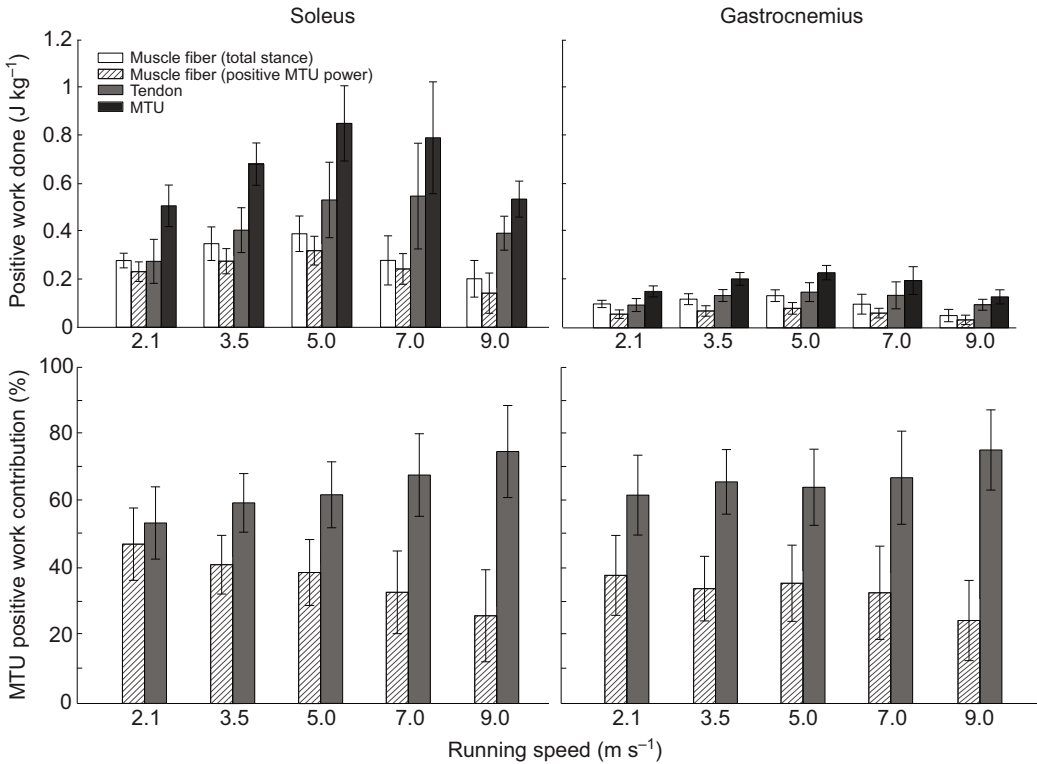


Fig. 7. Muscle fiber, tendon and MTU work done as a function of running speed. Absolute positive work done by the muscle fiber [total positive work done throughout the entire stance phase (open column) and work done when the MTU was generating positive power (hatched column)], tendon and MTU (top), and the relative contributions of the muscle fibers and tendon to the positive MTU work done (bottom) for the soleus (left) and gastrocnemius (right) muscles across five different running speeds. Absolute positive work done was normalized by body mass.

common Achilles tendon. The consequence of this configuration on muscle fiber and tendon behavior as well as muscle energetics remains an area of future research. Nevertheless, the results of this study were able to replicate measured *in vivo* muscle fiber behavior over a range of walking and running speeds (Fig. 1). Despite the aforementioned limitations, we are confident that our model estimates of mechanical work for the ankle plantar-flexors are physiologically reasonable.

The results from the present study are comparable with those of previous studies that have estimated the relative contribution of tendon elastic strain energy to the positive work done by the MTU for the ankle plantar-flexors during running. Hof et al. (Hof et al., 2002) used an inverse-dynamics-based model to calculate the positive work done by the MTU and muscle fibers for the soleus and gastrocnemius across a range of running speeds ($2.7\text{--}5.4\text{ m s}^{-1}$). They found that the tendon contributed 59% and 77% of MTU positive work for the soleus and gastrocnemius, respectively, for running at 3.1 m s^{-1} . These data are similar to those of the present study, where the tendon contributed 59% and 66% for the soleus and gastrocnemius, respectively, at a comparable running speed (3.5 m s^{-1}). The relative contributions for the gastrocnemius obtained in the present study are also consistent with those reported by Farris and Sawicki (Farris and Sawicki, 2012), who quantified the work done by the muscle fibers versus tendon during slow running ($2.0\text{--}3.25\text{ m s}^{-1}$). They used ultrasonography to measure muscle fiber length changes and a simple inverse dynamics-based model to calculate muscle force. Tendon elastic strain energy was found to contribute 57% of the MTU positive work for the gastrocnemius for running at 2.0 m s^{-1} , which is consistent with the 62% contribution of tendon elastic strain energy calculated in the present study for an equivalent running speed (2.1 m s^{-1}). Small discrepancies between the results of this study and those of Hof et al. (Hof et al., 2002) and Farris and Sawicki (Farris and Sawicki, 2012) may be attributable to differences in modeling approaches. Unlike the present study, Hof et al. (Hof et al., 2002) and Farris and Sawicki (Farris and Sawicki, 2012) considered only the ankle joint moment when calculating ankle plantar-flexor muscle force. Omission of the knee joint would affect the calculated gastrocnemius force, as the force-producing constraint imposed on the gastrocnemius by the knee joint was not included in these studies (Frayssé et al., 2009). In addition, the simple inverse-dynamics-based approach used by Hof et al. (Hof et al., 2002) and Farris and Sawicki (Farris and Sawicki, 2012) did not take into consideration the intrinsic muscle properties in predicting muscle forces. Despite the methodological differences amongst studies, the common finding is that tendon elastic strain energy contributes a greater proportion of the MTU propulsive work developed by the ankle plantar-flexors compared with muscle fiber work during running.

Our estimates of tendon elastic strain energy are also consistent with those obtained from previous experimental studies investigating ankle plantar-flexor mechanical energetics during running. Alexander and Bennet-Clark (Alexander and Bennet-Clark, 1977) and Ker et al. (Ker et al., 1987) estimated that the Achilles tendon stored 35 J of elastic strain energy when running at 4.5 m s^{-1} . Furthermore, Sasaki and Neptune (Sasaki and Neptune, 2006) and Hof et al. (Hof et al., 2002) estimated 28 and 45.3 J of stored tendon elastic strain energy in the ankle plantar-flexors during jogging (2.4 m s^{-1}) and running ($3.63\text{--}5.39\text{ m s}^{-1}$), respectively. These results are in good agreement with those from the present study, where the values of tendon elastic strain energy utilized by the ankle plantar-flexors were calculated to be 27.4, 39.7 and 50.7 J when running at 2.1, 3.5 and 5.0 m s^{-1} , respectively (Fig. 7, top).

To the best of our knowledge, the present study is the first to quantify muscle fiber and tendon lengths and velocities for the ankle plantar-flexors during stance across the full spectrum of human running speeds (i.e. jogging through to sprinting). The results support previous assertions that tendon elastic strain energy is enhanced when running speed advances towards sprinting (Cavagna and Kaneko, 1977; Cavagna, 2009). This phenomenon may be a result of the muscle fibers in the ankle plantar-flexors remaining relatively isometric as running speed increases, a behavior that generates larger muscle forces and facilitates greater storage and recovery of tendon elastic strain energy. The results from the present study demonstrated that muscle fiber shortening velocity for the soleus and gastrocnemius remained low throughout the period of high force development, irrespective of running speed (Fig. 6). Previous studies investigating the behavior of the lateral gastrocnemius in the turkey and the wallaby found similar near-isometric muscle fiber contractions, irrespective of locomotion speed (Taylor, 1994; Roberts et al., 1997; Biewener et al., 1998; Gabaldón et al., 2008). Muscle fiber length change for the human ankle plantar-flexors has also been observed to be small during running in experimental studies involving dynamic ultrasound recordings (Lichtwark et al., 2007; Farris and Sawicki, 2012; Rubenson et al., 2012; Cronin and Finni, 2013) as well as in a recent musculoskeletal modeling study (Arnold et al., 2013). The small muscle fiber length change noted in these studies (and in the present study) implies that the soleus and gastrocnemius muscle fibers operate under favorable contractile conditions on their force–velocity ($F\text{--}V$) relationship, allowing the development of larger muscle forces than would otherwise be possible. These larger muscle forces increase the stretch and recoil of the tendon, thereby facilitating greater storage and recovery of tendon elastic strain energy. We found that tendon elastic strain energy provided a greater relative contribution to the positive work done by the MTU for the soleus and gastrocnemius than positive muscle fiber work, and this relative contribution increased with faster running (Fig. 5). This result is consistent with previous studies that have suggested muscle fibers in distal limb muscles, such as the ankle plantar-flexors, act like isometric struts to facilitate greater storage and recovery of tendon elastic strain energy at fast locomotion speeds (Biewener and Roberts, 2000; Dickinson et al., 2000).

Minimization of muscle fiber length change by greater utilization of tendon stretch and recoil may be attributable to the capacity of tendons to recoil at high velocities. Tendons can achieve much higher recoil velocities than the rate at which muscle fibers can shorten (Ker, 1981; Alexander, 2002). As a result, tendon recoil may be favored over muscle fiber shortening to generate the rapid MTU shortening velocities that are needed during faster running. For instance, when jogging at 2.1 m s^{-1} , 68% and 79% of the MTU shortening was contributed by tendon recoil for the soleus and gastrocnemius, respectively. As running speed progressed to sprinting at $\geq 8\text{ m s}^{-1}$, the contribution of tendon recoil increased to 79% for the soleus, while it remained unchanged for the gastrocnemius (Figs 3 and 4). These results are consistent with those of Lichtwark and Wilson (Lichtwark and Wilson, 2006), who found tendon recoil for the gastrocnemius contributed around 70–75% of MTU shortening velocity at a running speed of 2.8 m s^{-1} . By contributing to the bulk of the length change in the MTU, a compliant tendon effectively reduces the shortening velocity of the muscle fibers, allowing a more favorable $F\text{--}V$ condition to be maintained during propulsion (Bobbett et al., 1986; Proske and Morgan, 1987; Kubo et al., 2000). Hence, the results from the present study suggest that the elastic recoil of the tendon in the ankle

plantar-flexors has an important role in allowing faster running speeds to be achieved. This premise is entirely consistent with the reduction in maximum sprinting speed that has been predicted to occur if the force–extension properties of the Achilles tendon are neglected (Miller et al., 2012).

Another possible way that sprinting athletes optimize the F – V relationship of their ankle plantar-flexors concerns muscle fiber size. Several studies have found that sprinters have longer gastrocnemius muscle fibers compared with recreational and distance runners (Abe et al., 2000; Kumagai et al., 2000; Lee and Piazza, 2009). Longer muscle fibers will possess a larger number of in-series sarcomeres. Consequently, for a given muscle fiber shortening velocity, the shortening velocity of each sarcomere can be expected to be less for a longer muscle fiber compared with a shorter one. This allows each sarcomere in a longer muscle fiber to generate more force for a given muscle fiber shortening velocity. Therefore, longer muscle fibers together with the utilization of tendon stretch and recoil may explain how the ankle plantar-flexor muscle fibers of sprinting athletes are able to operate more effectively with respect to the F – V relationship.

Tendons may be able to store greater amounts of elastic strain energy through muscle fiber shortening prior to the propulsion phase. Previous studies have demonstrated that during dynamic activities, muscle fibers usually begin to shorten while the tendon is being stretched prior to the propulsion phase (Roberts, 2002; Roberts and Scales, 2002; Roberts and Azizi, 2011). This shortening generates positive work, which is stored directly in the tendon as elastic strain energy, thereby enhancing the amount of tendon elastic strain energy recovered during propulsion. Our results are consistent with this premise as we observed a 15–40% difference between the positive muscle fiber work done during the entire stance phase and the positive muscle fiber work done when the MTUs for the soleus and gastrocnemius were generating positive power (Fig. 7, top – open and hatched columns). Hence, it is likely that some of the elastic strain energy stored in the tendon originated as positive muscle fiber work. This power amplification mechanism suggests that the ankle plantar-flexors attempt to maximize the storage of tendon elastic strain energy during running.

The greater storage and recovery of tendon elastic strain energy appears to occur at the expense of the muscle fibers on their force–length (F – L) relationship. With faster running, the ankle plantar-flexor muscle fibers functioned under increasingly unfavorable contractile conditions, as illustrated by the operating regions of these muscles on their F – L curves. Specifically, the muscle fiber operating regions for the soleus and gastrocnemius shifted down the ascending limb of the F – L curve when running speed increased (Fig. 6). It is likely that the observed increase in EMG activity with faster running (Fig. 2) reflected a greater volume of active muscle recruited in an effort to counter these increasingly unfavorable contractile conditions. Operating on the ascending limb of the F – L curve may be a strategy employed by the ankle plantar-flexors to lessen the likelihood of muscle damage caused by active eccentric contractions (Lieber and Fridén, 1993; Proske and Morgan, 2001). Regardless, shorter muscle fiber lengths allowed for greater tendon stretch and recoil with faster running, thus facilitating the increased contribution of tendon elastic strain energy to the positive work done by the MTU.

Conclusions

The present study quantified the mechanical interactions between muscle and tendon in the human ankle plantar-flexors as running speed advanced from jogging to sprinting. We found tendon elastic strain energy to provide a greater relative contribution than muscle

fiber work to the positive work done by the MTU with increasing running speed. The increased utilization of tendon elastic strain energy with faster running was facilitated by larger activation levels and a relatively isometric muscle fiber behavior. Storage and recovery of tendon elastic strain energy in the human ankle plantar-flexors enhances muscle performance and is likely integral to achieving maximum sprinting speeds.

MATERIALS AND METHODS

Participants

Nine experienced runners (five males, four females; mean \pm 1 s.d. age 27.7 \pm 8.0 years, body mass 73.1 \pm 8.6 kg, height 176 \pm 7 cm) gave informed consent to participate in the study. None of the participants had an injury that was likely to affect their ability to run. Ethical approval for the study was obtained from the Human Research Ethics Committees at the University of Melbourne and the Australian Institute of Sport.

Gait experiments

All data were collected while participants ran on a straight 110 m indoor synthetic track located in the Biomechanics Laboratory at the Australian Institute of Sport. The calibrated data capture volume was situated ~60 m along the track, which provided a sufficient distance to accelerate to the desired speed, maintain a steady-state speed during data capture, and then safely decelerate to rest. Participants were asked to complete the following discrete running speeds: jogging at 2.1 m s⁻¹; slow running at 3.5 m s⁻¹; medium-paced running at 5 m s⁻¹; fast running at 7 m s⁻¹; and sprinting at 8 m s⁻¹ or greater. Participants were permitted to self-select their foot strike pattern. To obtain the average steady-state speed for each trial, timing gates (Speedlight Telemetry Timing, Swift Performance Equipment, Walcol, QLD, Australia) were placed at the start and end of the data capture volume. Trials were repeated for a given running speed until a single trial was obtained where the measured speed was within \pm 5% of the target speed. Sufficient rest was given to participants between trials to prevent fatigue. Of the nine participants, one female was unable to complete the sprinting condition, while another female was unable to complete both the fast running and sprinting conditions.

Three-dimensional kinematic data were collected using a 22-camera, video-based, motion capture system (VICON, Oxford Metrics Ltd, Oxford, UK) sampling at a frequency of 250 Hz. Small reflective markers (14 mm in diameter) were placed at specific locations on the upper and lower limbs as described previously (Dorn et al., 2012). Standard running sandals (Nike Strapranner IV, Nike, Beaverton, OR, USA) were worn by all participants to allow as many markers as possible to be attached directly to the skin on the foot.

Ground reaction force (GRF) data were collected from eight force plates (Kistler Instrument Corp., Amherst, NY, USA) sampling at a frequency of 1500 Hz. The force plates were positioned directly adjacent to each other and embedded within the synthetic track. To prevent force plate targeting, a layer of rubber material (matching the synthetic track) covered the surface of the plates. A fourth-order, low-pass Butterworth filter with a cut-off frequency of 60 Hz was used to smooth the GRF data.

Muscle activation was recorded using a telemetered system (Noraxon Telemyo 2400T G2, Noraxon USA Inc., Scottsdale, AZ, USA) sampling at a frequency of 1500 Hz. Ag/AgCl surface electrodes were attached to the skin in accordance with SENIAM (surface electromyography for the non-invasive assessment of muscles) recommendations (Hermens et al., 2000). A test leg was randomly selected and EMG data were measured from three muscles: medial gastrocnemius, lateral gastrocnemius and soleus. To generate a linear envelope, EMG data were rectified and then low- and high-pass filtered using fourth-order Butterworth filters with cut-off frequencies of 8 and 20 Hz, respectively. The magnitude of muscle activation was expressed by quantifying the mean of the linear envelope for each muscle over the entire stance phase. The experimentally recorded EMG data were used to investigate changes in ankle plantar-flexor muscle activation with faster running. We also collected these data to generate an independent measure that could be used to verify our musculoskeletal model outputs (see details below).

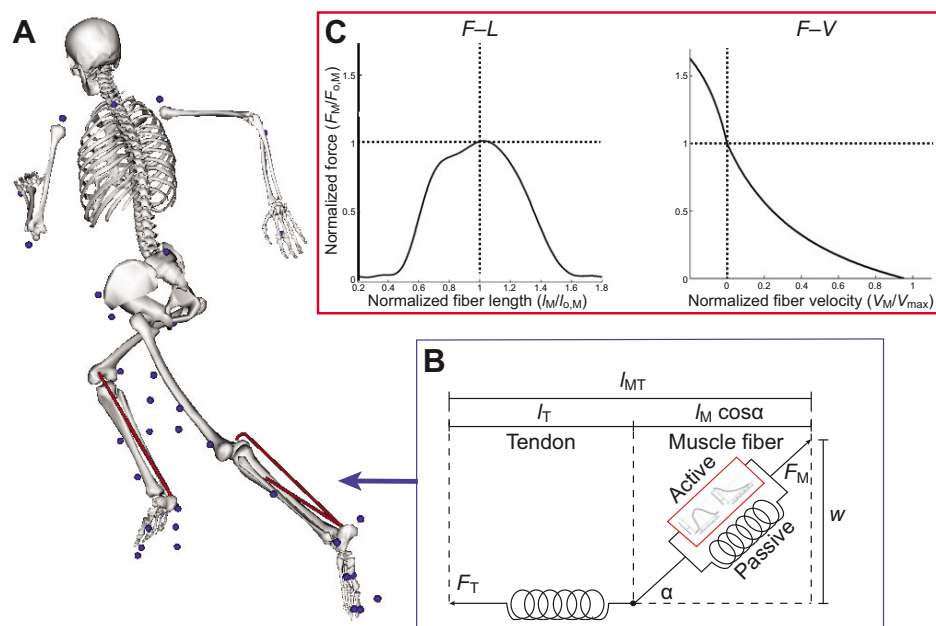


Fig. 8. The musculoskeletal model used in the study. (A) The body was represented as a 10-segment, 21 degree-of-freedom (d.f.) articulated linkage actuated by 54 MTUs. (B) Each MTU was modeled as a Hill-type muscle attached to a compliant tendon. MTU length (l_{MT}), defined as the distance between the origin and insertion points, and muscle pennation angle (α) were used to compute muscle fiber and tendon lengths (l_M , l_T), muscle fiber and tendon shortening velocities (V_M , V_T) and muscle and tendon forces (F_M , F_T). Muscle width (w) was defined as the perpendicular distance between the origin and insertion points. (C) Active muscle force development was constrained by the muscle's force-length-velocity relationship, which is governed by three parameters: peak isometric muscle force ($F_{o,M}$), optimal muscle fiber length ($l_{o,M}$) and muscle maximum shortening velocity ($V_{max}=20\ l_{o,M}\ s^{-1}$). The tendon was represented as a non-linear elastic material whose mechanical behavior was governed by its stiffness and slack length.

Musculoskeletal model

The model skeleton was represented as a 10-segment, 21-degree-of-freedom (d.f.) mechanical linkage (Anderson and Pandey, 1999) (Fig. 8A). The hip was modeled as a ball-and-socket joint (3 d.f.), the knee as a hinge joint (1 d.f.) and the ankle-subtalar complex as a universal joint (2 d.f.). The head, arms and torso were modeled as a single rigid body, which articulated with the pelvis via a ball-and-socket joint (3 d.f.). The pelvis was free to translate and rotate in space with 6 d.f. The model was actuated by 54 MTUs. The nominal muscle properties [peak isometric force ($F_{o,M}$), optimal fiber length ($l_{o,M}$), pennation angle (α) and tendon slack length ($l_{s,T}$), attachment sites and three-dimensional paths of the MTUs were based on data reported elsewhere (Anderson and Pandey, 1999). Maximum shortening velocity (V_{max}) was assumed to be $20\ l_{o,M}\ s^{-1}$ (Dorn et al., 2012). Each MTU was modeled as a Hill-type muscle with passive and in-parallel active muscle fibers attached in series to a compliant tendon (Fig. 8B). The architecture of the MTU was defined by the lengths of the muscle fibers and tendon, and the pennation angle of the muscle, defined as the angle of insertion of the muscle fibers relative to the long axis of the tendon. The perpendicular distance between the origin and insertion points (i.e. muscle width) was assumed to be constant. Because the muscle contracts at a constant volume (Matsubara and Elliott, 1972; Otten, 1988; Zajac, 1989), the assumption of constant muscle width meant that the pennation angle increased during muscle contraction.

The ankle plantar-flexor muscles, the soleus and gastrocnemius, were modeled as two separate MTU actuators with two independent tendons representing the Achilles tendon. The combined stiffness of the two tendons was assumed to be $200\ N\ mm^{-1}$, which is within the range of values ($145\text{--}390\ N\ mm^{-1}$) reported in previous experimental studies (Rosager et al., 2002; Hansen et al., 2003; Lichtwark and Wilson, 2005; Muraoka et al., 2005). A similar value of Achilles tendon compliance was used recently (see Arnold et al., 2013) in simulations of walking and running. Tendon stiffness was calculated as the product of the tendon elastic modulus and cross-sectional area divided by tendon slack length (Zajac, 1989). Tendon elastic modulus was assumed to be $1.2\ GPa$ for all MTUs (Zajac, 1989), and tendon cross-sectional area was assumed to be proportional to the corresponding peak isometric muscle force (Muraoka et al., 2005). Achilles tendon stiffness was partitioned between the soleus and gastrocnemius MTUs using the ratio of peak isometric force to tendon slack length (Zajac, 1989).

Data processing

Scaling and inverse kinematics

Segment lengths, segment inertial properties, MTU attachment sites, optimal muscle fiber lengths and tendon slack lengths in the model were scaled to each participant's height and mass. At each instant of the stride cycle, a set

of joint angles was computed by performing an inverse kinematics analysis that minimized the sum of the squares of the differences between the positions of virtual markers defined in the model and reflective markers mounted on the participant (Lu and O'Connor, 1999).

Calculation of muscle forces and activation

Lower-limb muscle forces were determined by applying inverse dynamics in conjunction with a static optimization approach (Anderson and Pandey, 2001). The measured GRFs and joint motion were used to compute the net joint torques developed about the back, hip, knee and ankle joints (Winter, 2009). Static optimization was then used to decompose the net joint torques into a set of muscle forces at each discrete time point, such that the sum of all the muscle activations squared was minimized in accordance with the force-length-velocity properties of the muscle (Kaufman et al., 1991; Anderson and Pandey, 2001). The muscle forces predicted by static optimization were also constrained to produce the net joint moments calculated from inverse dynamics with muscle activations bounded between zero (no active muscle force) and one (maximum active muscle force).

Muscle fiber and tendon mechanical work

We calculated the power developed by the MTU, muscle fiber and tendon by multiplying MTU, muscle fiber and tendon force, respectively, by their corresponding contraction velocity at each instant during the stance phase of the stride cycle. Mechanical work done by the MTU, muscle fiber and tendon was found by integrating the corresponding power curves over the entire stance phase (Fig. 9). Positive work done by the MTU represented the portion of stance where the MTU generated positive power (Anderson and Pandey, 1993). Positive muscle fiber work represented the generation of mechanical energy by the muscle fibers during the stance phase, which was calculated in two ways: (a) total positive muscle fiber work done throughout the entire stance phase; and (b) positive muscle fiber work done after the MTU began generating positive power. Positive tendon work represented the utilization of elastic strain energy that was stored earlier in the stance phase.

We were specifically interested in calculating the relative contributions of positive muscle fiber work and tendon elastic strain energy to the positive work done by the MTU (propulsion energy). These contributions were found using Eqn 1:

$$\%MTU\ contribution = \frac{W}{W_{MTU}} \times 100, \quad (1)$$

where W is the area underneath the W_{MTU} curve attributable to the positive work done by the muscle fiber or tendon and W_{MTU} is the positive work done by the MTU.

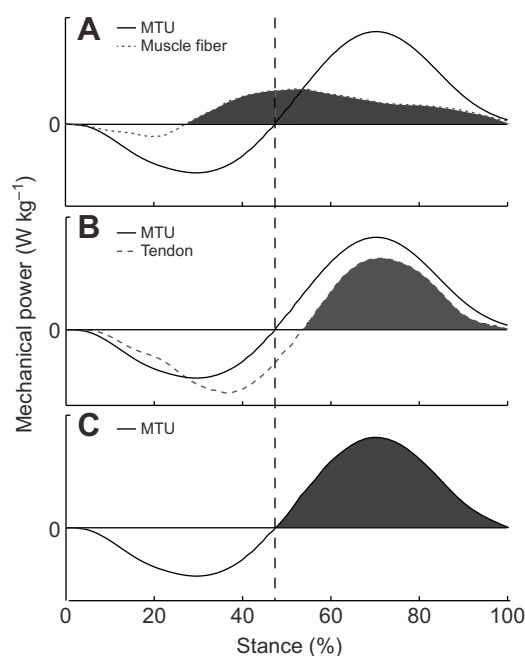


Fig. 9. Exemplar calculations of muscle fiber, tendon and MTU work done. Hypothetical example illustrating the calculations performed to determine the positive work done by the muscle fiber (A, dark shaded region), tendon elastic strain energy (B, dark shaded region) and the positive work done by the MTU (C, dark shaded region). Data shown are for running at 5 m s^{-1} . Mechanical power was normalized by body mass. The vertical dashed line identifies the time at which the MTU begins generating positive power. Note that the illustration for positive work done by the muscle fiber (A, dark shaded region) depicts the total positive work done throughout the entire stance phase.

Data analysis

All data collected for a single stance phase per locomotion condition per participant were time normalized, and group mean ± 1 s.d. values were calculated. MTU, muscle fiber and tendon lengths were normalized by the resting MTU length, optimal fiber length ($l_{0,M}$) and tendon slack length ($l_{s,T}$), respectively. Mechanical power and work done were normalized by body mass. For each muscle, EMG data were normalized by expressing the magnitude of the mean of the linear envelope for each locomotion speed as a percentage of that calculated for the sprinting condition.

To verify the musculoskeletal model outputs, we evaluated model-derived data with available experimental data. Mean experimentally recorded EMG data were compared with mean model-based muscle activations, expressed as a percentage of the muscle activations calculated for maximum sprinting. For three participants that exhibited a rear-foot strike pattern during running, we collected additional walking data in order to directly compare our model-derived muscle fiber lengths with available *in vivo* walking and running data recorded in a previous experimental study where participants ran with a rear-foot strike pattern (Farris and Sawicki, 2012).

A one-way repeated measures ANOVA was used to test the significance of the contributions of tendon elastic strain energy on the positive work done by the MTU with increased running speed. A *P*-value of 0.05 was set as the criterion for statistical significance.

Competing interests

The authors declare no competing financial interests.

Author contributions

A.L., A.G.S. and M.G.P. formulated the study; A.G.S. conducted the experiments; A.L. and Y.-C.L. analyzed the data; A.L., A.G.S., Y.-C.L. and M.G.P. prepared and edited the manuscript.

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Supplementary material

Supplementary material available online at <http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.100826/-/DC1>

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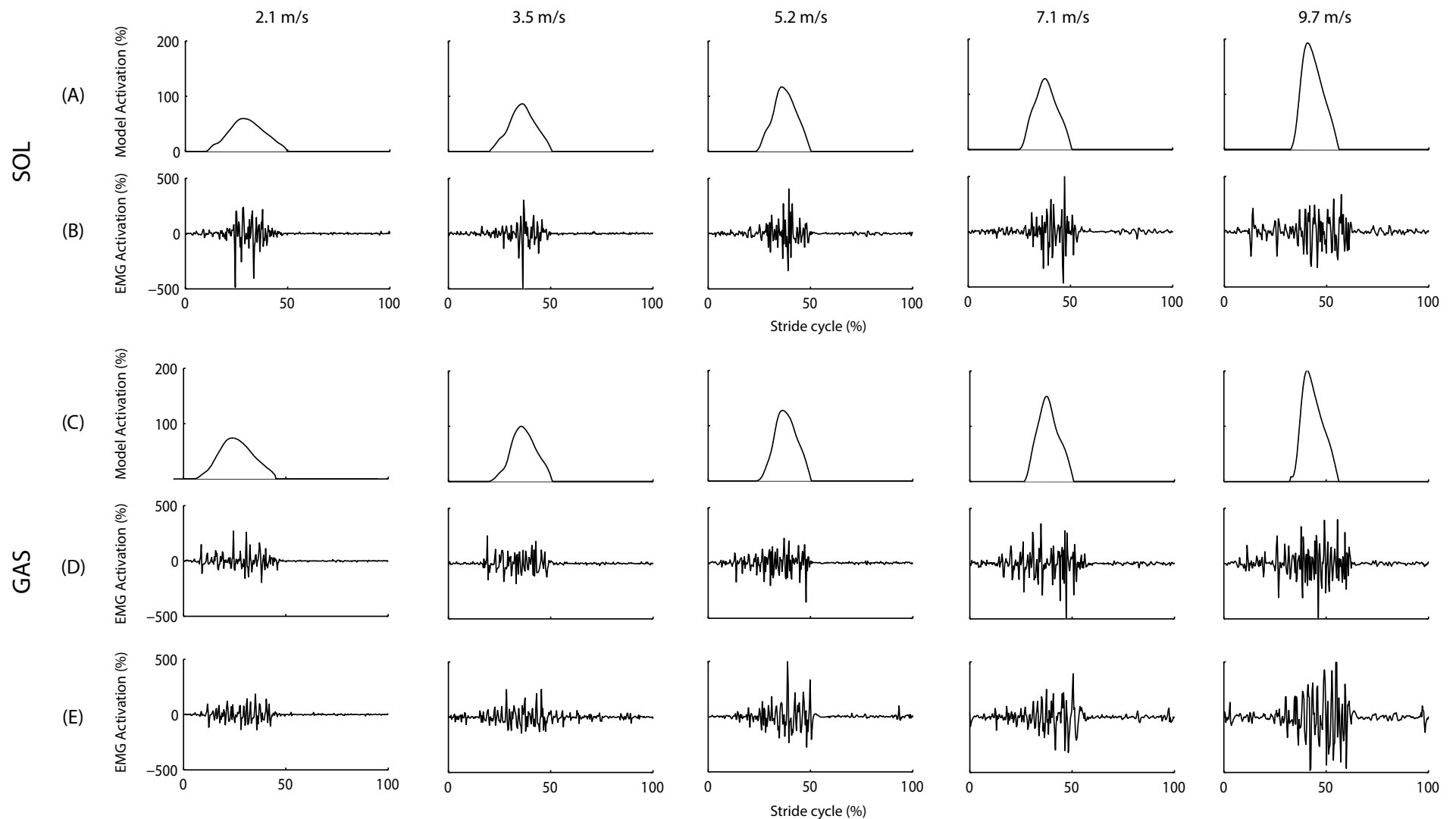


Fig. S1. Model-based activations and raw EMG activations for one representative subject across five running speeds. (A) soleus model-based activations, (B) soleus high-pass filtered EMG activations, (C) gastrocnemius model-based activations, (D) MG high pass filtered EMG activations and (E) LG high pass filtered EMG activations. Time was normalized to stride cycle beginning and ending at contralateral toe-off. Model-based activations and EMG activations were normalised by the mean model-based activation and mean EMG activation calculated for the maximum sprinting condition, respectively. Note that the running speeds indicated are for one representative subject, and hence, may slightly differ to the group mean ± 1 s.d. running speed.