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Human ankle plantar flexor muscle–tendon mechanics and energetics during maximum acceleration sprinting

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Tendon elastic strain energy is the dominant contributor to muscle–tendon work during steady-state running. Does this behaviour also occur for sprint accelerations? We used experimental data and computational modelling to quantify muscle fascicle work and tendon elastic strain energy for the human ankle plantar flexors (specifically soleus and medial gastrocnemius) for multiple foot contacts of a maximal sprint as well as for running at a steady-state speed. Positive work done by the soleus and medial gastrocnemius muscle fascicles decreased incrementally throughout the maximal sprint and both muscles performed more work for the first foot contact of the maximal sprint (FC1) compared with steady-state running at 5 m s^{-1} (SS5). However, the differences in tendon strain energy for both muscles were negligible throughout the maximal sprint and when comparing FC1 to SS5. Consequently, the contribution of muscle fascicle work to stored tendon elastic strain energy was greater for FC1 compared with subsequent foot contacts of the maximal sprint and compared with SS5. We conclude that tendon elastic strain energy in the ankle plantar flexors is just as vital at the start of a maximal sprint as it is at the end, and as it is for running at a constant speed.

1. Introduction

The human ankle plantar flexors, consisting primarily of the soleus (SO), medial gastrocnemius (MG) and lateral gastrocnemius muscles, play an indispensable role in running. Musculoskeletal modelling studies suggest that the ankle plantar flexors provide the largest contribution of all the major lower-limb muscles to the upward and forward accelerations of the body's centre of mass (COM) during the stance phase of running [1–3]. The ankle plantar flexors comprise short, highly pennated muscle fascicles connected to a long, elastic Achilles tendon, a configuration that allows tendon elasticity to significantly influence muscle fascicle behaviour (lengths and velocities) and energetics [4–6]. For instance, when running at a steady-state speed, these muscles store and recover a substantial amount of tendon elastic strain energy, which contributes to the required muscle–tendon unit (MTU) positive work and often exceeds the work done by the muscle fascicles [7–10]. Moreover, the muscle fascicles in the ankle plantar flexors maintain a relatively low shortening velocity compared with that of the MTU allowing them to operate in more favourable regions of the force–velocity (F-V) and force–length (F-L) relationships [10,11].

The mechanical energetic demands placed on human lower limb MTUs are fundamentally different between the steady-state and acceleration phases of running. When running at a steady-state speed, the lower limb muscles act in a spring-like manner absorbing and recovering the mechanical energy of the body [12–14]. The kinetic and potential energy of the body that is lost during the first half of stance is largely stored as elastic strain energy in compliant tissues

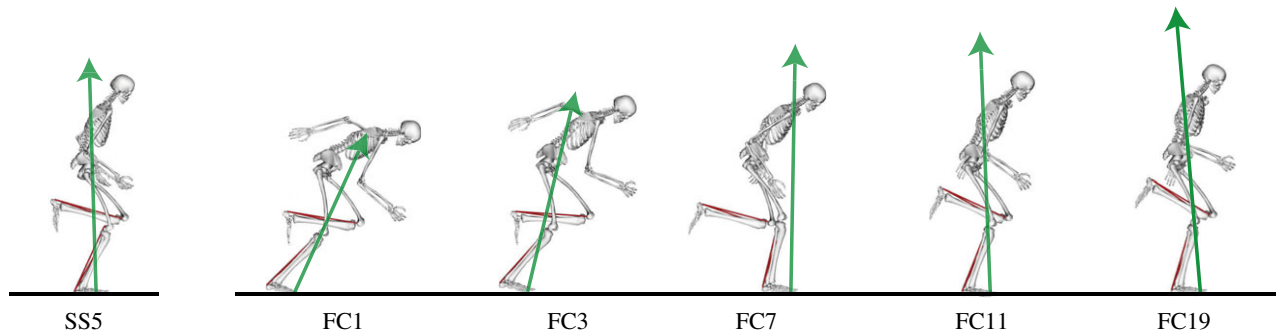


Figure 1. Sagittal-plane images of a representative participant during mid-stance for running at a steady-state speed of 5 m s^{-1} (SS5) and for five selected foot contacts of the maximal sprint (FC1, FC3, FC7, FC11 and FC19). Mid-stance was defined as the time when peak resultant ground reaction force (GRF) was generated by the participant. The arrows represent the magnitude and direction of the resultant GRF vector. Note that for this representative participant, the right leg was the dominant leg. (Online version in colour.)

like the Achilles tendon [15,16]. The stored elastic strain energy is then recovered during the second half of stance contributing to the propulsion energy generated by the MTU. This utilization of elastic strain energy reduces the positive work done by the muscle fascicles and allows them to behave like near-isometric struts developing force at favourable regions of the F-V and F-L relationships [9,17,18]. Conversely, at the start of a maximal sprint, the lower limb MTUs must operate in a motor-like manner to generate net positive mechanical energy output [19–21]. The net positive mechanical energy can be achieved by minimizing the negative work done during early stance or by increasing the positive work done during late stance. Because tendons cannot perform net positive work, it is reasonable to presume that the work done by the muscle fascicles will be greater during a maximal sprint compared with running at a steady-state speed [22]. Furthermore, previous studies investigating ballistic movements such as jumping have suggested that the fascicles of distal limb muscles shorten during the loading phase, while the MTU is lengthening, which thereby allows tendon elastic strain energy to be stored even for movements associated with the minimal loss in mechanical energy of the body [18,23,24]. We were therefore interested in confirming whether the human ankle plantar flexor muscle fascicles exhibit a similar strategy at the start of a maximal sprint.

In this study, experimental gait data were used in conjunction with computational modelling to compare muscle fascicle and tendon energetics of the human ankle plantar flexors between multiple foot contacts in a maximal sprint as well as for running at a steady-state speed. Specifically, for both running conditions, we compared the work done by the MTU and the muscle fascicles as well as the storage and recovery of tendon elastic strain energy for the SO and MG during the stance phase of the stride cycle. We hypothesized that positive work done by the ankle plantar flexor muscle fascicles would be greater and stored tendon elastic strain energy would be less for the first foot contact of the maximal sprint compared to (i) subsequent foot contacts during a maximal sprint and (ii) a representative foot contact during running at a steady-state speed.

2. Material and methods

2.1. Participants

Eight participants (five males and three females; age, 23.8 ± 5.2 years; height, 177.1 ± 7.9 cm; body mass, 70.4 ± 8.1 kg) gave

their informed consent to participate in the study. All participants were national level 100–400 m sprinters. On the day of testing, no participants were suffering from any pre-existing musculoskeletal injury that might affect their ability to perform a maximal sprint.

2.2. Experimental data collection

Testing took place in the Biomechanics Laboratory, Australian Institute of Sport, Canberra. Participants wore standard sprinting footwear and were required to complete a series of running tasks on a straight 110 m indoor synthetic track. A 22 camera, video-based, motion analysis system (VICON, Oxford Metrics Ltd, Oxford, UK) sampling at 250 Hz was used to record three-dimensional kinematic data. The calibrated capture volume was approximately 8 m in length. Retro-reflective markers (14 mm diameter) were placed at predefined locations on the upper and lower limbs (see Lai *et al.* [9,10] for full details). A fourth-order, low-pass Butterworth filter with a cut-off frequency of 15 Hz was used to filter the marker trajectories. Ground reaction forces (GRF) were collected from eight force plates (Kistler Instrument Corporation, Amherst, NY, USA) with a sampling frequency of 1500 Hz. The force plates were embedded in the synthetic track and mounted flush with each other, spanning a total length of 7.2 m. To prevent force plate targeting, the force plates were covered with a layer of synthetic track. GRF data were filtered using a fourth-order, low-pass Butterworth filter with a cut-off frequency of 15 Hz. The same cut-off frequency was used to filter the GRF data and marker trajectories in order to prevent experimental impact artefacts [25].

Prior to commencing data collection, participants completed their standard pre-event warm-up. Running at a steady-state speed was the first task to be tested. Participants were required to run at a speed of 5 m s^{-1} through the capture volume. This speed was chosen based on our previous study, which found that relative to other steady-state speeds, the ankle plantar flexors generated the greatest amount of work at 5 m s^{-1} . Hence, this speed best typified the ‘bouncing’ gait pattern ascribed to running at a steady-state speed [9]. To measure running speed, timing gates were placed at the start and end of the capture volume. Trials were repeated until a single trial was obtained where the measured speed was within $\pm 10\%$ of the desired speed. Next, we collected data for the maximal sprint (figure 1). Participants were required to accelerate as quickly as possible from a static start until the end of the capture volume before safely decelerating to rest. To obtain data for the first and third foot contacts, the participant was positioned within the capture volume in a three-point crouched configuration without starting blocks. The participant’s dominant leg was the back leg. The start position was adjusted to ensure that the first foot contact of the participant’s dominant leg occurred in the middle of the first force plate. The

right leg was the dominant leg for six participants, while the left leg was the dominant leg for two participants. To obtain data for the 7th, 11th and 19th foot contacts, the start position was shifted approximately 6 m, 12 m and 40 m, respectively, away from the first force plate. Participants were provided with sufficient rest between trials to minimize fatigue and ensure that they were able to achieve a maximal effort during each trial. Data for running at a steady-state speed and for all five selected foot contacts of the maximal sprint (i.e. the 1st, 3rd, 7th, 11th and 19th foot contacts) were collected for seven participants; however, the 11th foot contact of the maximal sprint was not collected for one participant. Henceforth, running at a steady-state speed of 5 m s^{-1} will be referred to as SS5 and the 1st, 3rd, 7th, 11th and 19th foot contacts of the maximal sprint will be referred to as FC1, FC3, FC7, FC11 and FC19, respectively.

2.3. Musculoskeletal model

The skeleton was represented as a generic 12 segment, 31 degree-of-freedom (d.f.) mechanical linkage system, similar to that described by Hamner *et al.* [26]. The pelvis had 6 d.f. and was free to translate and rotate in space; the hip was modelled as a 3 d.f. ball-and-socket joint, the knee as a single degree of freedom hinge joint, and the ankle-subtalar complex as a 2 d.f. universal joint that comprised two non-intersecting hinge joints. The model was actuated by 92 MTUs. The nominal properties of each MTU were taken from cadaveric measurements of muscle architecture [27,28]. Maximum shortening velocity was assumed to be 15 optimal muscle fascicle lengths per second ($l_o^m \text{ s}^{-1}$) consistent with previous modelling studies investigating running [29,30]. Each MTU was modelled as a single-element, Hill-type muscle with passive and active muscle fascicles connected in series with a compliant tendon [31].

The ankle plantar flexors (SO and MG) were modelled as two separate MTUs, each with independent tendons representing the Achilles tendon. Tendon compliance of the SO and MG MTU was set to 10% strain at maximum isometric force production consistent with previous modelling studies investigating running [9,29]. During the computational simulations, tendon strain was within the range of values (5–9%) measured from ultrasound imaging of the SO and MG during locomotion [10,32,33], thereby supporting our decision to increase tendon strain for the ankle plantar flexors from 3.3% to 10% at maximum isometric force production. Tendon strain for all other MTU actuators was kept constant at 3.3% at maximum isometric force production [31].

2.4. Computational simulations

All simulations were performed using OpenSim, an open-source modelling software program [34]. Prior to the dynamic simulations, a generic musculoskeletal model was scaled to the participant's anthropometry measurements. An inverse kinematics analysis was used to calculate a set of joint angles for each time instant, whereby the sum of the squares of the differences between the experimentally recorded markers and the corresponding virtual markers defined in the model was minimized [35].

Muscle force and activation were computed using an inverse dynamics analysis in conjunction with a computed muscle control (CMC) algorithm [36]. Net joint torques generated about the back, hip, knee and ankle joints were computed using a standard inverse dynamics approach [37]. CMC was used to predict a set of muscle excitation patterns that drove the model forward in time using numerical integration (time window = 0.02 s) so that the generalized coordinates and velocities of the model tracked the experimentally measured, dynamically consistent, joint kinematics [36,38]. The muscle excitations were bounded between zero (no active muscle force) and one (maximum active muscle force) with activation and deactivation time constants of

10 ms and 30 ms, respectively [31]. Muscle force and activation were calculated in accordance with the force–length–velocity properties of muscle and tendon [31].

2.5. Mechanical power and work

We calculated MTU, muscle fascicle and tendon powers by multiplying each component's force by its corresponding contraction velocity at each time instant throughout the stance phase. The negative and positive mechanical work done by the three components were obtained by integrating the corresponding power curves over the time period of the stance phase when each component was absorbing and generating power, respectively.

Stored tendon elastic strain energy during early stance originated from positive muscle fascicle work or isometric muscle activity (no work) and negative MTU work. To calculate the source of the stored tendon elastic strain energy during early stance, the percentage contributions of positive muscle fascicle work and negative MTU work to the amount of stored tendon elastic strain energy were calculated from

$$\% \text{stored tendon elastic strain energy} = \frac{W}{W_{\text{ten}}} \times 100,$$

where W is the amount of stored tendon elastic strain energy attributable to the positive work done by the muscle fascicles or the negative work done by the MTU, and W_{ten} is the amount of stored tendon elastic strain energy (see the electronic supplementary material, figure S1).

Mean velocity and net COM mechanical energy for each participant were calculated using the displacement of the COM of the participant and the resultant ground reaction force vector. The position of the COM of the participant was located approximately at the centre of the pelvis and was adjusted during the scaling procedure. Instantaneous COM displacement in the vertical, horizontal and medio-lateral directions for each time instant was obtained from the inverse kinematics analysis. Instantaneous COM velocity was calculated by differentiating the instantaneous COM displacement with respect to time. Mean velocity was calculated as the averaged instantaneous COM velocity in the horizontal direction over the duration of the stance phase. Net COM mechanical energy was calculated by integrating the product of the instantaneous COM velocity and the resultant ground reaction force vector over the duration of the stance phase [39].

2.6. Data analysis

Data were collected for a single stance phase per running condition per participant and were time normalized and used to calculate group mean \pm s.d. values. MTU, muscle fascicle and tendon lengths were normalized, respectively, to resting MTU length (l_s^{MTU}) obtained at the participant's neutral standing position, optimal muscle fascicle length (l_o^m) and tendon slack length. Mechanical power and work were normalized by the participant's body mass.

To test whether the model-based predictions were physiologically reasonable, we compared the model-based muscle fascicle lengths for the ankle plantar flexors against previously reported ultrasound measurements. For one representative participant, we collected additional data for running at a steady-state speed of 3.5 m s^{-1} in order to directly compare model-based fascicle lengths to ultrasound-measured fascicle lengths for the SO and MG [10,40,41].

In addition, electromyographic (EMG) data for the SO and MG were measured from one representative participant for FC1, FC19 and SS5 to verify the model-based predictions of SO and MG activation. EMG data were recorded using a telemetered system (Noraxon, Telemetry 2400 T G2, Noraxon USA Inc.,

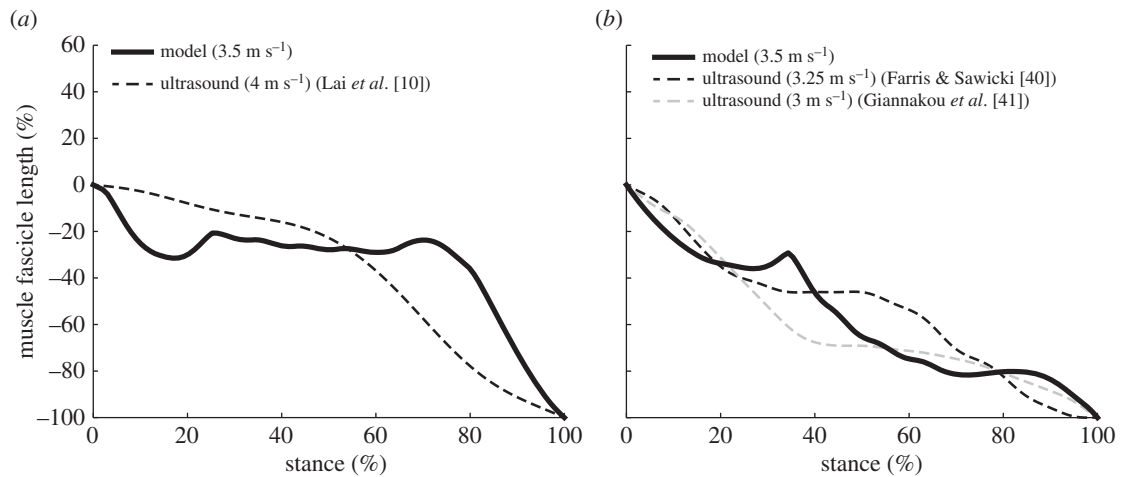


Figure 2. Comparison of *in vivo* measured and model-predicted muscle fascicle lengths for the (a) SO and (b) MG from one representative participant throughout stance for running at a steady-state speed of 3.5 m s^{-1} . Muscle fascicle lengths are expressed as a percentage of the total muscle fascicle length change that occurred from foot strike to toe-off. Data for *in vivo* measured (ultrasound-based) muscle fascicle lengths for the SO and MG were obtained from the literature [10,40,41]. Note that available ultrasound-based data have been collected from participants predominantly exhibiting a rear-foot strike pattern. Note that muscle fascicle behaviour for sprinting, where participants exhibit a fore-foot strike pattern, is likely to differ somewhat from that observed for running with a rear-foot strike pattern.

Scottsdale, AZ, USA) sampling at a frequency of 1500 Hz. The EMG data were high-pass filtered using a fourth-order Butterworth filter with a cut-off frequency of 20 Hz, full-wave rectified and then finally low-pass filtered using a fourth-order Butterworth filter with cut-off frequency of 8 Hz. The cut-off frequencies for the high- and low-pass filters were chosen in order to obtain a linear envelope that optimally represented the EMG burst profile without being influenced by experimental artefacts. The magnitude of the measured and predicted muscle activations were normalized to peak muscle activation for FC1, which was the running condition for which muscle activations in the SO and MG were highest.

A range of key variables specific to the ankle plantar flexors (SO and MG) were extracted for statistical analysis: MTU and muscle fascicle normalized lengths at foot strike; peak tendon strain; MTU, muscle fascicle and tendon work done; and the percentage contributions of positive muscle fascicle work and negative MTU work to the stored tendon elastic strain energy. Data were assessed using the Shapiro–Wilk test for normality, and all key variables of interest were found to be normally distributed ($p > 0.05$). To generate a complete dataset for purposes of statistical analyses, missing data for one participant for FC11 were imputed using a mean substitution from the data of the other participants. One-way repeated-measures ANOVA tests were used to test whether foot contact during the maximal sprint (i.e. FC1, FC3, FC7, FC11 and FC19) had a significant effect on the key variables of interest. When a significant main effect was obtained, post hoc paired *t*-tests were used to determine which foot contacts were significantly different from each other. Paired *t*-tests were also used to determine whether significant differences existed between FC1 and SS5. Given the number of comparisons, a conservative level of significance was set from the outset at $p < 0.01$ for all tests.

3. Results

Model-predicted muscle fascicle lengths and muscle activations for the SO and MG were compared against previously reported ultrasound measurements of muscle fascicle lengths and measured EMG data (figures 2 and 3).

In vivo measured and model-predicted fascicle lengths for the SO when running at a steady-state speed of 3.5 m s^{-1} tended to exhibit minimal length change during early and mid-stance before rapidly shortening during late stance, whereas for the MG, *in vivo* measured and model-predicted muscle fascicle lengths shortened throughout the entire stance phase (figure 2). EMG-measured and model-predicted muscle activations for the SO and MG displayed reasonable overall agreement for SS5, FC1 and FC19 (figure 3). Specifically, for the SO, EMG-measured and model-predicted activations gradually increased throughout stance for SS5, FC1 and FC19. For the MG, EMG-measured and model-predicted activations were comparable during mid and late stance, whereas during early stance, model-predicted activations underestimated EMG measurements, especially for FC1 and FC19.

3.1. Maximal sprint (FC1, FC3, FC7, FC11 and FC19)

Throughout the maximal sprint, net COM mechanical energy progressively decreased, whereas mean velocity progressively increased (figure 4). When comparing FC19 with FC1, net COM mechanical energy decreased by $3.1 \pm 0.5 \text{ J kg}^{-1}$, whereas mean velocity increased by $4.9 \pm 0.6 \text{ m s}^{-1}$.

Overall, the SO MTU and muscle fascicles became progressively shorter in length at foot strike as sprinting speed increased ($p < 0.001$, both cases, table 1). During the early stage of the maximal sprint (i.e. FC1, FC3 and FC7), SO muscle fascicles exhibited predominantly isometric and shortening behaviour throughout stance (figure 5). During the latter stage of the maximal sprint (i.e. FC11 and FC19), SO muscle fascicles began to display a stretch-shortening cycle. By contrast, no significant main effects for foot contact occurred for MG MTU and muscle fascicle lengths and velocities (figure 5 and table 1).

Throughout the maximal sprint, muscle fascicle and MTU power generation profiles for the SO and MG transitioned from predominantly generating power to absorbing and generating equal amounts of power (figure 6). Significant main

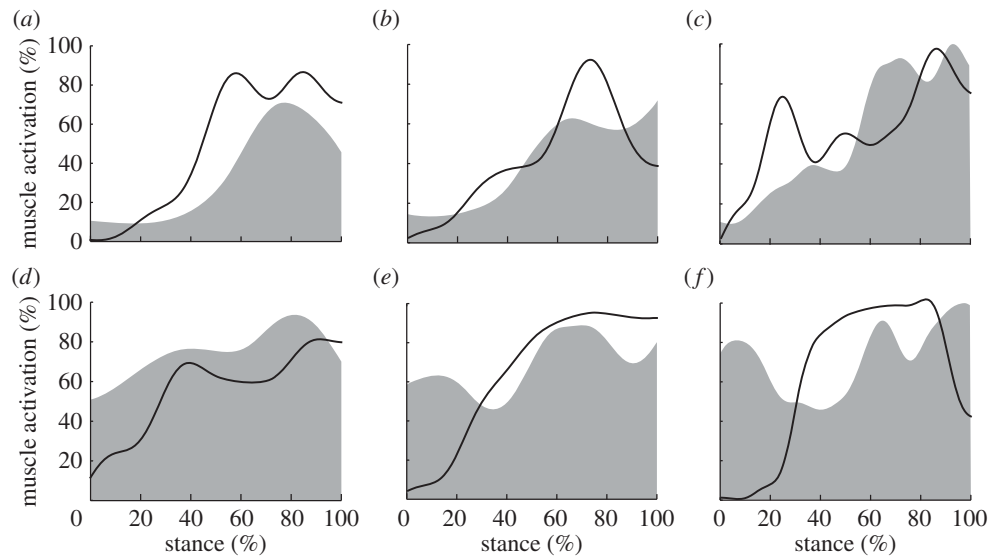


Figure 3. Comparison of measured EMG activity (shaded regions) and model-predicted activations (solid lines) for the SO (*a–c*) and MG (*d–f*) from one representative participant for running at a steady-state speed of 5 m s^{-1} (SS5, (*a,d*)) and for the first foot contact (FC1, (*b,e*)) and 19th foot contact (FC19, (*c,f*)) of the maximal sprint. EMG activity and model-predicted muscle activations were normalized to the peak EMG activity measured and peak model-predicted muscle activation calculated for FC1, respectively. EMG activity and model-predicted activations were highest for FC1, and therefore, this condition was chosen for normalization purposes.

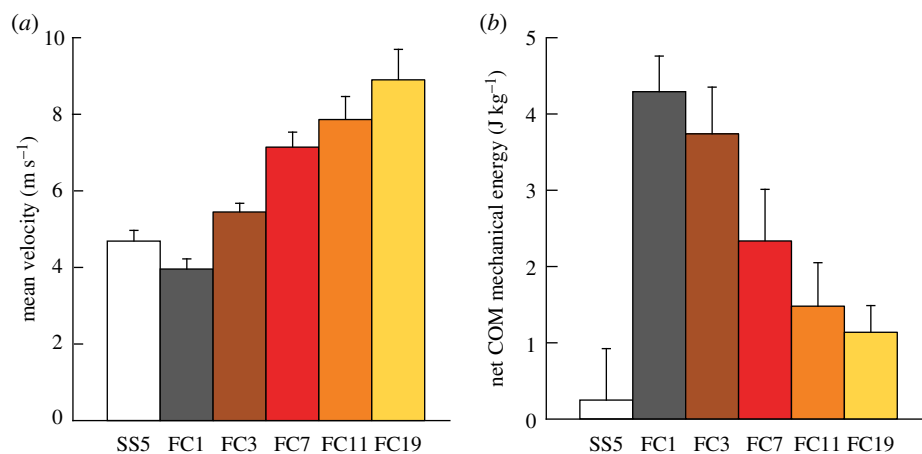


Figure 4. (*a*) Mean velocity and (*b*) net COM mechanical energy throughout stance for running at a steady-state speed of 5 m s^{-1} (SS5) and for the five selected foot contacts of the maximal sprint (FC1, FC3, FC7, FC11 and FC19). Mean velocity was calculated by averaging the differentiated instantaneous COM displacement in the horizontal direction over the duration of stance phase. Net COM mechanical energy was calculated by integrating the product of the instantaneous COM velocity and the resultant ground reaction force vector over the duration of stance phase. (Online version in colour.)

effects for foot contact were evident for the positive work done by the MG muscle fascicles ($p = 0.005$) and the amount of tendon elastic strain energy stored in the MG ($p = 0.002$) (table 1). By contrast, although the amount of positive muscle fascicle work done by the SO decreased throughout the maximal sprint, a significant main effect for foot contact was not observed ($p = 0.028$). Furthermore, the amount of stored tendon elastic strain energy in the SO did not differ significantly either ($p = 0.571$). With respect to the proportion of the stored tendon elastic strain energy originating from positive muscle fascicle work, a significant main effect for foot contact was found for both the SO and MG ($p = 0.001$, both cases). When comparing FC19 to FC1, the contribution of muscle fascicle work to tendon elastic strain energy decreased by $26.9 \pm 15.6\%$ and $24.4 \pm 18.2\%$ for the SO and MG, respectively (table 1).

3.2. Start of the maximal sprint (FC1) versus running at steady-state speed of 5 m s^{-1} (SS5)

Net COM mechanical energy was $4.1 \pm 1.1 \text{ J kg}^{-1}$ less for SS5 compared with that for FC1 (figure 4).

The SO MTU and muscle fascicles were significantly longer at foot strike for FC1 compared with that for SS5 ($p < 0.001$, both cases; table 1). For FC1, the SO muscle fascicles shortened throughout the stance phase, whereas the SO MTU lengthened slightly during the first half of stance before shortening thereafter (figure 5). This behaviour differed during SS5, where both the SO MTU and muscle fascicles underwent a stretch-shortening cycle during stance. By contrast, the MG MTU and muscle fascicle lengths and velocities displayed similar profiles and magnitudes for FC1 and SS5 (figure 5). Peak tendon strain was

Table 1. MTU, muscle fascicle and tendon lengths, velocities and work done throughout stance for running at a steady-state speed of 5 m s⁻¹ (SSS) and for the five selected foot contacts of the maximal sprint (FC1, FC3, FC7, FC11 and FC19). Results are given as mean (s.d.).

variable	soleus						medial gastrocnemius					
	SSS (n = 8)	FC1 (n = 8)	FC3 (n = 8)	FC7 (n = 8)	FC11 (n = 7)	FC19 (n = 8)	SSS (n = 8)	FC1 (n = 8)	FC3 (n = 8)	FC7 (n = 8)	FC11 (n = 7)	FC19 (n = 8)
normalized length at foot strike	0.98(0.06)	1.03(0.05) ^{7,11,19}	1.02(0.05) ^{7,11,19}	1.0(0.05) ^{1,3}	0.99(0.05) ^{1,3}	0.98(0.05) ^{1,3,7}	0.98(0.05)	0.97(0.04)	0.97(0.04)	0.97(0.04)	0.97(0.04)	0.97(0.04)
tendon strain (%)	0.84(0.14)	1.08(0.07) ^{7,11,19}	1.03(0.05) ^{7,11,19}	0.94(0.05) ^{1,3}	0.87(0.09) ^{1,3}	0.83(0.07) ^{1,3,7}	0.85(0.15)	0.79(0.09)	0.82(0.06)	0.76(0.08)	0.73(0.06)	0.76(0.06)
absolute positive work (J kg ⁻¹)	5.56(0.56)	5.72(0.89)	5.49(0.88)	6.02(0.8)	5.82(0.65)	5.72(1.05)	5.62(0.54)	5.72(0.64)	5.27(0.62)	5.29(0.65)	4.59(0.77) ⁷	5.15(0.54) ¹
absolute negative work (J kg ⁻¹)	0.6(0.14)	0.74(0.21)	0.66(0.28)	0.67(0.12)	0.68(0.13)	0.67(0.15)	0.38(0.14)	0.43(0.09)	0.44(0.1)	0.36(0.1)	0.33(0.07)	0.37(0.08)
absolute negative work (J kg ⁻¹)	0.24(0.12)	0.48(0.2)	0.33(0.22)	0.25(0.16)	0.26(0.15)	0.23(0.07)	0.19(0.12)	0.31(0.1)	0.33(0.1)	0.2(0.05)	0.24(0.07)	0.24(0.08)
absolute negative work (J kg ⁻¹)	0.45(0.09)	0.49(0.16)	0.45(0.19)	0.55(0.17)	0.5(0.12)	0.49(0.24)	0.32(0.05)	0.32(0.1)	0.27(0.09)	0.26(0.07)	0.18(0.07) ^{1,7}	0.22(0.07) ¹
absolute negative work (J kg ⁻¹)	0.56(0.11)	0.32(0.11)	0.39(0.12)	0.25(0.16) ¹⁹	0.26(0.15) ¹⁹	0.68(0.32) ^{7,11}	0.32(0.08)	0.2(0.07)	0.15(0.06)	0.25(0.08)	0.16(0.08)	0.21(0.09)
absolute negative work (J kg ⁻¹)	0.19(0.1)	0.05(0.05)	0.05(0.06)	0.15(0.2)	0.21(0.2)	0.25(0.15)	0.12(0.1)	0.07(0.05)	0.02(0.01)	0.08(0.09)	0.07(0.06)	0.05(0.03)
contributions to tendon elastic strain energy (%)	0.45(0.09)	0.48(0.15)	0.45(0.19)	0.55(0.18)	0.51(0.12)	0.48(0.23)	0.32(0.06)	0.33(0.09)	0.28(0.09)	0.26(0.09)	0.17(0.07) ¹	0.24(0.06) ¹
contributions to tendon elastic strain energy (%)	85.7(9.8)	65.3(22.6) ¹⁹	82.1(12.2)	86(12.5)	92.5(6.2)	92.3(12.9) ¹	76.8(11.5)	47.8(14)	48(17.7)	84.4(11.3) ^{1,3}	61.2(26.7)	72(20) ^{1,3}
contributions to tendon elastic strain energy (%)	14.3(9.7)	34.7(22.5) ¹⁹	18.2(12)	13.5(11.9)	8(7.2)	7.9(12.5) ¹	23(11.6)	52.3(14)	51.9(17.8)	15.2(11.1) ^{1,3}	38.7(27)	27.9(20) ^{1,3}

^aVariables that exhibited significant differences between SSS and FC1.

^bVariables that exhibited a significant main effect for foot contact for the maximal sprint.

Numerical superscripts ^{1,3,7,11,19} indicate results of the *post hoc* paired t-tests for variables that exhibited a significant main effect between foot contacts. Note that for all tests, a significance level was set *a priori* at *p* < 0.01.

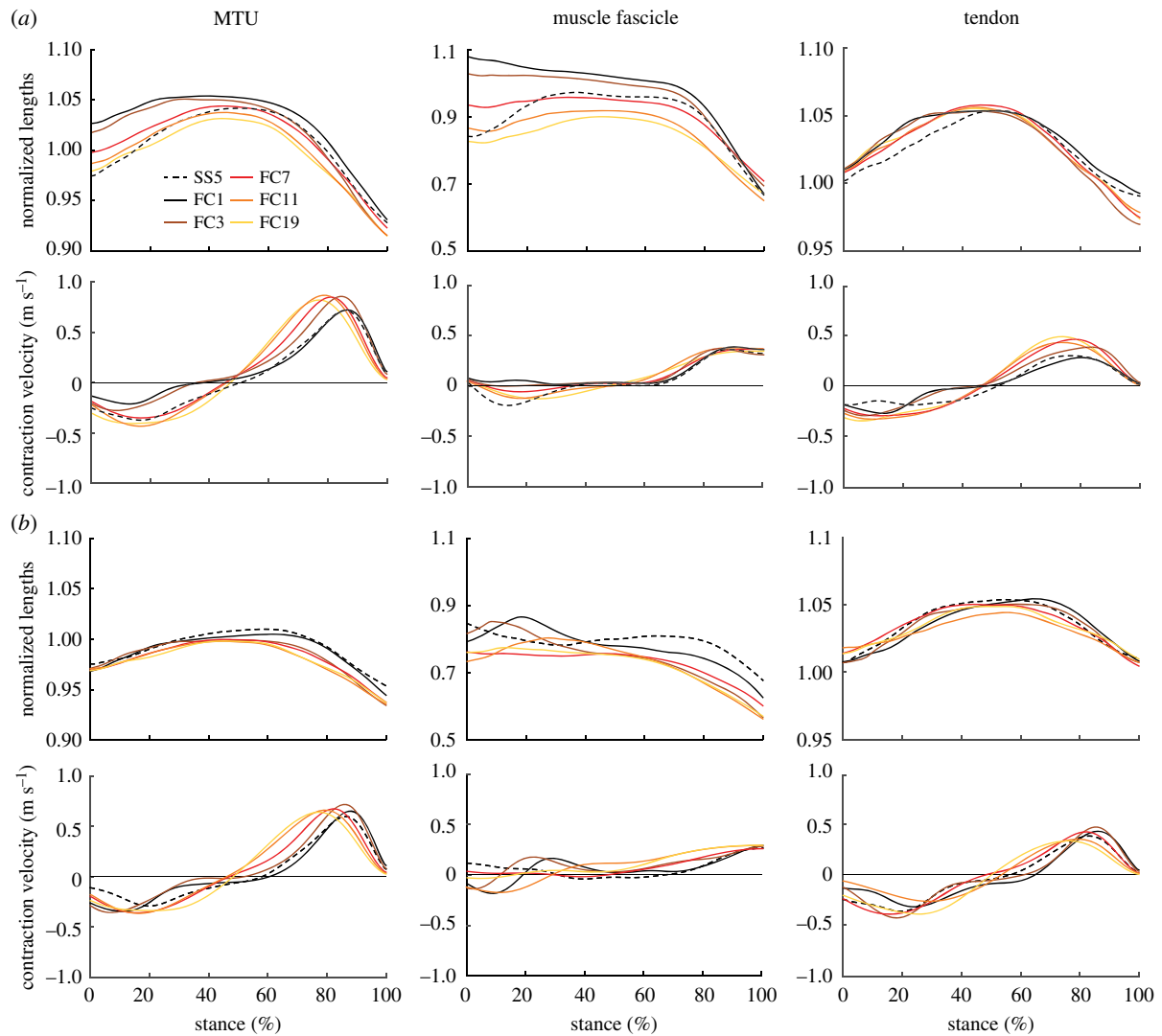


Figure 5. Normalized MTU, muscle fascicle and tendon lengths and velocities for the SO (a) and MG (b) throughout stance for running at a steady-state speed of 5 m s^{-1} (SSS) and for the five selected foot contacts of the maximal sprint (FC1, FC3, FC7, FC11 and FC19). MTU, muscle fascicle and tendon lengths were normalized by the resting MTU length, optimal muscle fascicle length and tendon slack length, respectively. Negative and positive velocities represented lengthening and shortening, respectively. (Online version in colour.)

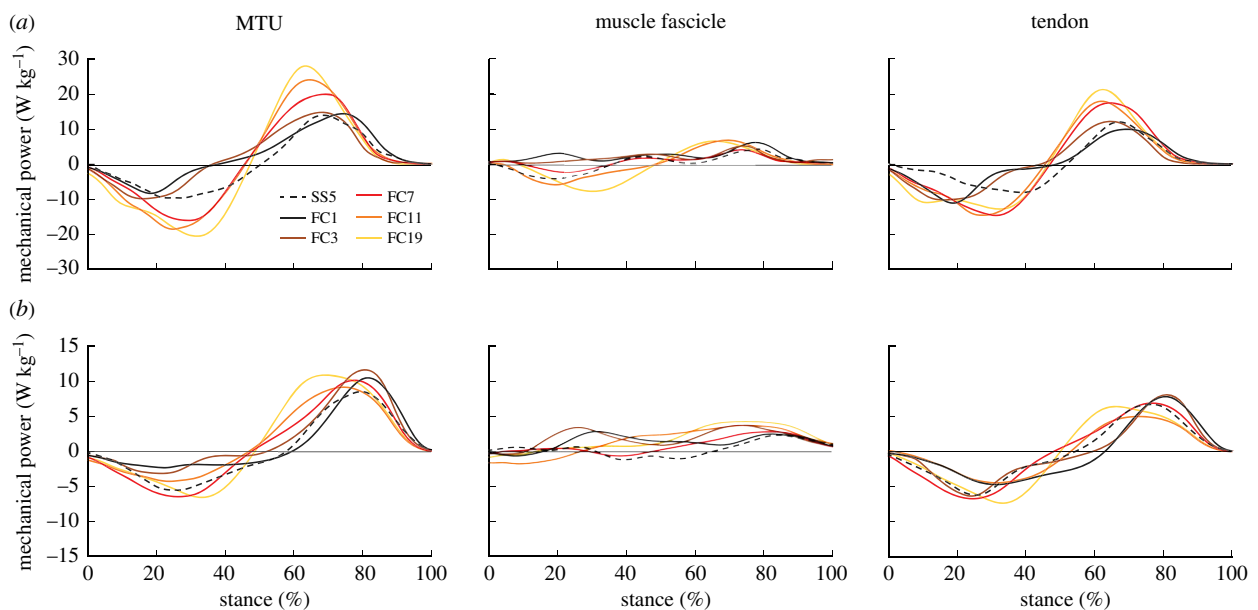


Figure 6. MTU, muscle fascicle and tendon powers for the SO (a) and MG (b) throughout stance for running at a steady-state speed of 5 m s^{-1} (SSS) and for the five selected foot contacts of the maximal sprint (FC1, FC3, FC7, FC11 and FC19). MTU, muscle fascicle and tendon powers were normalized to body mass. (Online version in colour.)

not significantly different between FC1 and SS5 for the SO ($p = 0.52$) and MG ($p = 0.79$).

Positive work done by the SO and MG muscle fascicles was greater for FC1 compared with SS5, though statistical significance was exhibited for the SO ($p = 0.003$) and not the MG ($p = 0.07$) (table 1). By contrast, the amount of stored tendon elastic strain energy for the SO and MG was not significantly different for FC1 compared with SS5 ($p = 0.44$ and $p = 0.81$, respectively). The proportion of the stored tendon elastic strain energy originating from positive muscle fascicle work was significantly greater for FC1 compared with SS5 for both SO and MG ($p < 0.001$, both cases; table 1).

4. Discussion

The human ankle plantar flexors are indispensable for producing force, power and work during running [1,2,42]. This muscle group represents an ideal model for examining the influence of tendon elasticity on muscle fascicle mechanics and energetics, because the ankle plantar flexors possess short, pennated muscle fascicles connected to a long, elastic Achilles tendon [23]. In this study, we investigated how alterations in the net mechanical energy demands on the body during running influence ankle plantar flexor mechanics and energetics. To do so, we compared the first foot contact of a maximal sprint to (i) subsequent foot contacts during a maximal sprint and (ii) a representative foot contact during running at a steady-state speed of 5 m s^{-1} . For both comparisons, we hypothesized that positive work done by the ankle plantar flexor muscle fascicles would be greater and stored tendon elastic strain energy would be less for the first foot contact compared with subsequent foot contacts of a maximal sprint and compared with running at a steady-state speed of 5 m s^{-1} .

The findings of this study partially support our hypothesis regarding muscle fascicle work. Positive muscle fascicle work done by the SO and MG decreased incrementally throughout the maximal sprint and both were found to be greater for FC1 compared with SS5. Nevertheless, a significant difference in positive muscle fascicle work for the selected foot contacts throughout the maximal sprint only occurred for the MG, and a significant difference in positive muscle fascicle work between FC1 and SS5 only occurred for the SO. We reject our hypothesis regarding the amount of tendon elastic strain energy stored in the SO and MG, which varied by only $0.12 \pm 0.05 \text{ J kg}^{-1}$ and $0.08 \pm 0.03 \text{ J kg}^{-1}$, respectively, throughout the maximal sprint, and by only $0.044 \pm 0.12 \text{ J kg}^{-1}$ and $0.005 \pm 0.14 \text{ J kg}^{-1}$, respectively, for FC1 compared with SS5. These results suggest that storage of tendon elastic strain energy in the ankle plantar flexors is just as vital at the start of a maximal sprint as it is at the end, and as it is for running at a steady-state speed. At the start of a maximal sprint, tendon elastic strain energy functions to enhance MTU propulsion work output, whereas at the end of a maximal sprint and when running at a steady-state speed, it functions to reduce muscle fascicle energy expenditure. The key distinction is the way in which the ankle plantar flexors utilize positive muscle fascicle work and negative MTU work to store elastic strain energy in the tendon during early stance.

The results of this study are generally consistent with previous modelling and experimental studies that have investigated muscle fascicle and tendon energetics in the ankle plantar flexors during running and other ballistic movements. Our previous modelling study investigating ankle plantar

flexor energetics for running at a range of steady-state speeds found that the SO and gastrocnemius complex stored 36 J and 11 J of tendon elastic strain energy, respectively, at $5.0 \pm 0.1 \text{ m s}^{-1}$, and stored 22 J and 7 J of elastic strain energy, respectively, at $9.0 \pm 0.7 \text{ m s}^{-1}$ [9]. Other experimental studies have found that the Achilles tendon stored 35 J of elastic strain energy for running at a steady-state speed of 4.5 m s^{-1} [15] and 45 J of elastic energy for running at a steady-state speed of 5.39 m s^{-1} [8]. These results are consistent with calculations obtained in the current study, where the tendon in the SO and MG stored 32 J and 22 J , respectively, for SS5, and 35 J and 15 J , respectively, for FC19. Our predicted magnitudes of tendon elastic strain energy for FC1 of 35 J and 22 J for the SO and MG, respectively, are also consistent with previous values reported for jumping. For example, Fukashiro *et al.* [43] measured *in vivo* Achilles tendon force and estimated that the Achilles tendon stored 34 J and 27 J of energy during squat and counter-movement jumps, respectively. The minor discrepancies are likely to be due to the use of contrasting muscle models or differing ankle plantar flexor configurations when comparing modelling and experimental studies.

Why do the ankle plantar flexors exploit tendon elasticity during ballistic actions like maximal sprint accelerations? A previous inverse dynamics study investigating accelerating turkeys suggested that the storage of elastic strain energy in the tendons of the lower limb muscles may be an unavoidable by-product of the ground forces generated by the connected muscle fascicles during an acceleration [22,44]. It is also possible that the storage and subsequent recovery of elastic strain energy when accelerating is necessary to enhance the power generated by the MTU during propulsion. For example, Roberts & Scales [22] estimated that the peak power output in the MTU of the lower limb muscles exceeded the power output capacity of the muscle fascicles alone. Similar deductions have been made about the hind-limb musculature of frogs during maximal jumping, where the peak power output of the MTU exceeded the total muscle fascicle capacity by more than seven times [45,46]. In a similar manner, we calculated the power output capacity of the SO and MG muscle fascicles to test whether tendon recoil power was needed to supplement muscle fascicle power in order to generate the MTU propulsion power required for running at a steady-state speed and for the maximal sprint. Peak muscle fascicle powers for the SO and MG were calculated by fully activating the muscle fascicles and computing peak power on the power-velocity curve. Peak muscle fascicle power was 15 W kg^{-1} and 6.6 W kg^{-1} for the SO and MG, respectively. These values are slightly lower than the peak instantaneous MTU propulsion powers of 15.6 W kg^{-1} and 9.2 W kg^{-1} for the SO and MG, respectively, during SS5 (figure 6). For the maximal sprint, peak instantaneous MTU propulsion power for the SO and MG varied between 15.1 W kg^{-1} and 11.2 W kg^{-1} , respectively, for FC1, and 28.8 W kg^{-1} and 12.8 W kg^{-1} , respectively, for FC19. Thus, muscle fascicle power alone would not be sufficient to generate the required MTU propulsion power for either running condition, but especially for FC19 of the maximal sprint where muscle fascicle power can only theoretically account for half of the required MTU propulsion power. Hence, irrespective of the running condition, it appears that the recoil of a stretched tendon must exist in order for the MTU of the ankle plantar flexors to generate sufficient propulsive power and energy.

Greater SO and MG muscular work for FC1 compared with subsequent foot contacts of the maximal sprint and compared

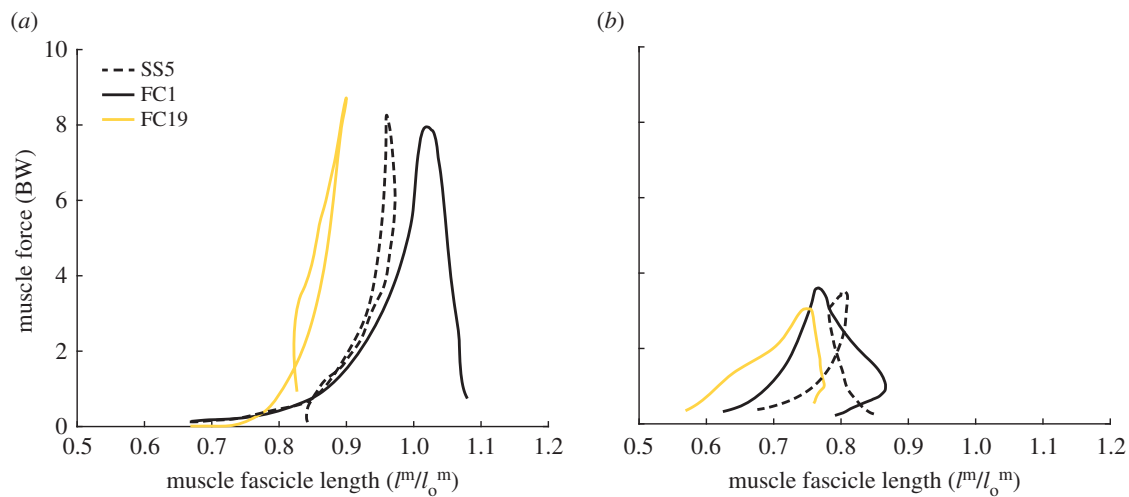


Figure 7. Muscle fascicle work loops for the SO (a) and MG (b) throughout stance for running at a steady-state speed of 5 m s^{-1} (SS5) and for two selected foot contacts of the maximal sprint (FC1, FC19). Muscle force and muscle fascicle lengths were normalized by body weight and optimal fascicle length, respectively. (Online version in colour.)

with SS5 is consistent with the net increase in the positive COM mechanical energy. Running at a steady-state speed (SS5) is characterized by efficient recycling of mechanical energy resulting in negligible net COM mechanical energy, whereas net-positive mechanical energy output was maximized at the start of the maximal sprint (FC1). The consistency between muscular work in the SO and MG and the net COM mechanical energy demonstrates that muscle fascicles in the ankle plantar flexors do have the capacity to vary their function from low-power, isometric struts (e.g. FC19 and SS5) to high-power, motor-like actuators (e.g. FC1) [17,18]. Such a change in function is illustrated by the work loops for the SO and to a lesser extent for the MG, where force was developed in conjunction with a greater excursion in muscle fascicle length for FC1 compared with both FC19 and SS5 (figure 7). The relationship between the shift in positive muscle fascicle work done and the change in the COM mechanical energy demand is consistent with the findings of previous experimental studies investigating accelerating turkeys [44] and incline running in humans [47] and other animals [7,48–50].

Although the start of a maximal sprint places contrasting COM mechanical energy demands relative to running at a steady-state speed, similar amounts of tendon strain and stored elastic strain energy were exhibited by SO and MG for FC1 compared with SS5 (figure 5 and table 1). The storage of tendon elastic strain energy at the start of a maximal acceleration (e.g. FC1 and FC3) was achieved, because the muscle fascicles were able to generate positive work during early stance even though there was minimal length change in the SO and MG MTUs. This positive muscle fascicle work was redistributed as stored tendon elastic strain energy rather than delivered to the skeleton for joint motion [18,22]. The contribution of muscle fascicle work therefore amplifies the stored tendon elastic strain energy derived from the negative MTU work during early stance for FC1 and FC3 which, when recovered as the tendon recoils rapidly during propulsion, enhances the MTU power and work output. Similar power amplification mechanisms have been observed in experimental and modelling studies investigating jumping in humans [51–53] and other animals [45,54,55]. Our results concur with previous suggestions that tendon elasticity plays a vital functional role in managing the changes in the mechanical energy demands

placed on the lower-limb muscles without limiting the ability of the muscle fascicles to also develop net COM mechanical energy during ballistic movements [18,56].

We found that the SO muscle fascicles operated on different regions of the F-L relationship at the start of the maximal sprint compared with the end and compared with running at a steady-state speed. SO muscle fascicle length at foot strike and at the time of peak force development transitioned from longer lengths for FC1 to shorter lengths for subsequent foot contacts during the sprint acceleration. Longer SO muscle fascicle lengths at foot strike for FC1 positioned the muscle fascicles initially on the descending region of the F-L curve. This position on the F-L curve may be advantageous in that the SO muscle fascicles are able to shorten throughout stance without reaching the unfavourable ascending region of the F-L curve. Consistent with this premise, we found muscle fascicle lengths at the time of peak force development to be close to optimum ($1.09 \pm 0.06 l_o^m$). The importance of the longer ankle plantar flexor muscle fascicle length at foot strike in maintaining optimal F-L conditions during stance for sprint accelerations has also been emphasized by Mero *et al.* [57]. Conversely, SO muscle fascicles for SS5 were significantly shorter at foot strike compared with that for FC1, but they were still able to operate close to the optimal muscle fascicle length at the time of peak force development ($0.98 \pm 0.07 l_o^m$), because they initially lengthened during early stance.

Some of the differences observed in SO and MG mechanics and energetics for both running conditions may be a consequence of the knee joint influencing the function of the MG. The MG is a bi-articular muscle, spanning both the knee and ankle joints, while the SO is mono-articular, spanning only the ankle joint. Thus, differences in knee joint kinematics between the maximal sprint and SS5 will propagate to differences in mechanics between the MG and SO. For instance, the knee exhibited a large flexion angle at foot strike and extended throughout stance for FC1, which shortened MG MTU and muscle fascicle lengths (see the electronic supplementary material, figure S2). When progressing from FC1 to FC19, the knee flexion angle reduced at foot strike and transitioned to a flexion–extension cycle, similar to what occurred for SS5. Consequently, MG muscle fascicles operated on relatively consistent regions of the F-L relationship at foot strike and at

the time of peak force development for both running conditions. Hence, the significant differences in SO mechanics and energetics observed between running conditions investigated in this study were not evident for MG.

There were limitations of the computational modelling approach implemented to predict muscle fascicle and tendon mechanics and energetics in the human ankle plantar flexors. Firstly, a static cost function was used to resolve the muscle redundancy problem, which may not be the most appropriate objective function for dynamic movements such as maximal sprint accelerations. Furthermore, the computational model assumed a constant muscle belly width ignoring factors like muscle gearing [58,59] that may cause discrepancies in the predicted muscle forces and activations. However, our model-based predictions of SO (and to an extent MG) muscle activations for SS5, FC1 and FC19 and muscle fascicle lengths for running at a steady-state speed of 3.5 m s^{-1} were able to replicate the temporal behaviour of recorded EMG data and previously reported muscle fascicle lengths measured *in vivo* (figures 3 and 4). Therefore, we have confidence that our model produced physiologically reasonable predictions.

Secondly, previous modelling studies have demonstrated that model-based muscle fascicle behaviour and energetics during running are highly sensitive to the tendon properties in the MTU [9,29]. To evaluate the sensitivity of our findings to the tendon properties assumed in the model, we varied tendon compliance of the SO and MG by $\pm 20\%$ for one representative participant for FC1, FC19 and SS5. As expected, the magnitudes of the work done by the MTU, muscle fascicle and tendon varied with tendon compliance. However, the main findings of the study that muscle fascicle work was greater for FC1 compared with subsequent foot contacts of the maximal sprint and compared with SS5, and that the amount of stored tendon elastic strain energy was comparable between the running conditions, remained unaffected.

Thirdly, previous studies have found that sprinters have shorter plantar flexor moment arms compared with non-sprinters assisting in enhancing force generation [60]. In this study, we used moment arms reported from cadaver studies. Consequently, SO and MG force prediction may have been underestimated. However, we do not believe this limitation affected the main findings of our study because comparisons were made within participants across running conditions. Nevertheless, in the future, more physiologically accurate force predictions may be obtained with the inclusion of subject-specific moment arm data.

Fourthly, our modelling approach underestimated the level of MG muscle activation during early stance. This underestimation was most probably due to the cost function used in the computational simulations (i.e. minimizing the sum of the muscle activations). Previous EMG studies of the ankle plantar flexors during running have reported that the MG pre-activates prior to foot strike [61–63]. These studies have

suggested that such activity functions to increase muscle and joint stiffness in preparation for and to resist impact forces at foot contact [64,65]. Furthermore, this function may be more vital for bi-articular muscles like the MG, which are involved in the fine regulation and distribution of net joint torques over spanned joints [66]. However, MG forces during early stance for all running conditions were relatively low compared with mid-to-late stance. Additionally, we obtained good agreement between model-predicted and EMG-measured SO muscle activations, which on average, produced twice the amount of force developed by the MG. Hence, the discrepancy between model-predicted and EMG-measured activations for the MG during early stance had only a minor influence on the magnitudes of the work done by the MG, and thus would not have altered the main findings of our study.

Finally, the ankle plantar flexors were modelled as two separate MTUs with individual tendons rather than a common Achilles tendon. The influence of this design on muscle fascicle and tendon energetics remains an area of future research. We note here, however, that recent *in vivo* studies on non-uniform Achilles tendon deformation have observed that tendon fascicles arising from the SO and gastrocnemius may function as independent structures during walking [67,68].

5. Conclusion

We quantified the mechanics and energetics of the muscle fascicles and tendon of the human ankle plantar flexors throughout a maximal sprint as well as for running at a steady-state speed. These running conditions impose contrasting mechanical energetic demands on the body, where net COM mechanical energy varies from negligible in steady-state running to markedly positive in a maximal sprint. We found that the SO and MG muscle fascicles generated incrementally less positive work throughout the maximal sprint. Furthermore, both muscles generated greater positive work for FC1 compared with SS5. Conversely, the amount of stored tendon elastic strain energy in the SO and MG remained of a similar magnitude throughout the maximal sprint and exhibited minimal difference between FC1 and SS5. Consequently, the contribution of muscle fascicle work to stored tendon elastic strain energy was greater for FC1 compared with the subsequent foot contacts of the maximal sprint and compared with SS5. Thus, elastic mechanisms appear to play an important role in enhancing power output at the start of a maximal sprint in addition to reducing muscle fascicle energy expenditure when running at a steady-state speed.

Ethics. The institutional human research ethics committee approved the study.

Competing interests. We declare we have no competing interests.

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