

Interactions between the human gastrocnemius muscle and the Achilles tendon during incline, level and decline locomotion

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Summary

Muscles are required to perform or absorb mechanical work under different conditions. However the ability of a muscle to do this depends on the interaction between its contractile components and its elastic components. In the present study we have used ultrasound to examine the length changes of the gastrocnemius medialis muscle fascicle along with those of the elastic Achilles tendon during locomotion under different incline conditions. Six male participants walked (at 5 km h⁻¹) on a treadmill at grades of -10%, 0% and 10% and ran (at 10 km h⁻¹) at grades of 0% and 10%, whilst simultaneous ultrasound, electromyography and kinematics were recorded. In both walking and running, force was developed isometrically; however, increases in incline increased the muscle fascicle length at which force was developed. Force was developed at shorter muscle lengths for running when compared to

walking. Substantial levels of Achilles tendon strain were recorded in both walking and running conditions, which allowed the muscle fascicles to act at speeds more favourable for power production. In all conditions, positive work was performed by the muscle. The measurements suggest that there is very little change in the function of the muscle fascicles at different slopes or speeds, despite changes in the required external work. This may be a consequence of the role of this biarticular muscle or of the load sharing between the other muscles of the triceps surae.

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Introduction

The mechanics and energetics of both walking and running have been well documented in the past. In both gait types, elastic energy is thought to be stored within the elastic tissues of the muscle–tendon units that support the body and propel it upwards during the stance phase (Alexander, 1988; Ker et al., 1987; Fukunaga et al., 2001). To achieve versatility, however, the amount of energy stored in the elastic tissues must be modulated by muscular contraction. Here we investigate how the muscle fascicles of the gastrocnemius medialis (GM) interact with the elastic Achilles tendon (AT) to achieve this versatility under different locomotion conditions.

Although there are energetically optimal speeds for each type of terrestrial gait, animals need to perform these gaits under a wide range of conditions. These include differing speeds, accelerations and terrains. Each of these different conditions requires altered forces and moments at each joint to maintain steady locomotion (Roberts and Scales, 2004; Roberts and Belliveau, 2005). Therefore the muscles responsible for

producing these forces are required to have a versatile mechanical function. Muscles must have the ability to either produce or absorb work at different periods of the stride depending on the conditions of locomotion. For instance, it has been demonstrated that during downhill running, the turkey gastrocnemius muscle absorbs work and, conversely, is required to generate power during uphill running (Gabaldon et al., 2004). Similarly, these muscles must produce more work in proportion to acceleration on level ground (Roberts and Scales, 2004).

The ability of a muscle to perform or absorb mechanical work is highly dependent on interactions between the muscle's contractile component and the elastic structures that it attaches to. Compliant tendons and aponeurosis enable fascicle length changes to be uncoupled from that of the whole muscle–tendon unit (MTU) length (Griffiths, 1991; Fukunaga et al., 2000). Numerous investigations on different terrestrial species have demonstrated that during locomotion, the ankle extensor muscles act nearly isometrically (constant length) or

concentrically (shorten) whilst the whole MTU lengthens (Griffiths, 1991; Ishikawa et al., 2005; Fukunaga et al., 2001; Hof et al., 2002; Lichtwark and Wilson, 2005d). This acts to stretch the relatively compliant tendon of this muscle group during the stance phase. Because tendon is an elastic material, energy is stored in the tendon whilst it is stretched and this energy is returned late in the stance phase when the tendon (and subsequently the entire MTU) shortens rapidly. This is elegantly demonstrated in a recent publication by Ishikawa and colleagues (Ishikawa et al., 2005), who simultaneously recorded length changes of the human MG and soleus muscles along with direct measures of AT force to demonstrate the catapult action of these muscles acting on the tendon.

Utilisation of elastic strain energy within the series elastic element has been suggested to make muscles more efficient, particularly during cyclical movements like locomotion (Roberts, 2002; Lichtwark and Wilson, 2005b). Tendon stretch and recoil reduces the mechanical work required from muscle fascicles, and also allows muscle fascicles to operate at speeds more favourable for work production and efficiency. By performing near isometric contractions during the stance phase of gait when the MTU is stretching, a muscle reduces both the mechanical work required and the excess heat involved in shortening a muscle (Ettema, 2001; Lichtwark and Wilson, 2005a). In addition, high MTU speeds can be achieved in excess of the maximum fascicle velocities. The high speeds of recoil of tendon and other series elastic structures prevents the muscle from operating at unfavourable high velocities during the take-off phase of the stride.

To better understand the mechanics and energetics of human muscle contraction it is important to distinguish the roles of the contractile components and also the elastic components. Here we have combined ultrasound imaging and motion analysis techniques to assess the length changes of the GM fascicles, the entire series elastic element and the AT during locomotion under different incline conditions and with different gaits (walking and running). These techniques allow us to assess the contribution of this muscle to force production during gait. By varying the grade of incline and the speed of locomotion (and the gait) we have varied the net external mechanical work produced by the body (Gabaldon et al., 2004) and hence been able to study how GM muscle mechanics alter under these different conditions. We hypothesised that the GM muscle fascicles will interact differently with the AT as a result of changes in the required external work.

Materials and methods

Participants and protocol

Six healthy male participants, average age 28 ± 3.68 years, height 182 ± 12 cm, and weight 82 ± 12 kg, gave written consent to participate in this study. The study was approved by a local ethics committee (RNOH JREC, 04/Q0506/11). No participants had any history of AT pain and had a clinically normal gait pattern.

Participants were asked to walk (at 5 km h^{-1}) and run (at 10 km h^{-1}) on a treadmill at different grades while measurements were made. Participants walked at grades of -10 , 0 and 10% (negative grades indicate decline/downhill) and ran at grades of 0 and 10% . A walking warm-up period of 2 min was initially used and a period of 1 min was allowed at each condition for the participant to normalise their gait. This period preceded two 10 s data collection periods for walking and one 10 s collection period for running, which ensured that at least ten strides of good data were collected for each individual. The order of the walking and running and the grades of incline were randomised between subjects. This protocol was applied twice in the same session so that muscle fascicle and tendon length measurements could be made using one ultrasound machine.

Kinematics and muscle activity

Active CODA light emitting diodes (LEDs) were attached to the following body landmarks: head of the fifth metatarsal, calcaneus, lateral malleolus, head of the fibula, lateral epicondyle of the knee, iliotibial band (halfway between knee marker and greater trochanter) and the greater trochanter (Fig. 1B). The three dimensional (3D) position of these LEDs was determined with an accuracy of ± 1 mm by using a CODA motion analysis system (Charwood Dynamics, Rothley, Leics, UK) at rate of 100 Hz. Simultaneous muscle activity was measured using EMG and collected with a sampling frequency of 2000 Hz into the 16-bit A/D board of the CODA system.

Sagittal plane knee and ankle angles were determined. Length changes of the GM muscle–tendon unit length were estimated from the average joint angle data using the equations derived by Grieve and colleagues (Grieve et al., 1978), with shank length defined as the length of the lower length segment as defined above. This calculation assumes a rigid foot and ignores any shape change or compression of the foot during the stance phase.

The vertical velocity of the calcaneus marker was used to determine when the foot contacted the ground. Foot contact was defined as the time when the vertical velocity crossed from negative to positive. The beginning of swing phase was defined as the time when the calcaneus marker had a positive vertical velocity and the fifth metatarsal marker changed from a negative to a positive horizontal velocity. This technique provided a consistent predictor of the time of foot on and foot off under the conditions of both walking and running.

Electromyography (EMG) was used to assess the muscle activity of the GM and its antagonist, the tibialis anterior. Surface electrodes were placed on the muscle bellies of the GM and TA using round bipolar electrodes (12 mm diameter, 18 mm spacing) with reference electrodes placed in between. The EMG signals were preamplified at the source with a frequency bandwidth of 20 Hz–20 kHz (MA-310–surface EMG, Motion Lab Systems, Inc, Los Angeles, CA, USA) and synchronously collected with the motion analysis data at 2000 Hz. The EMG data were rectified and low pass filtered

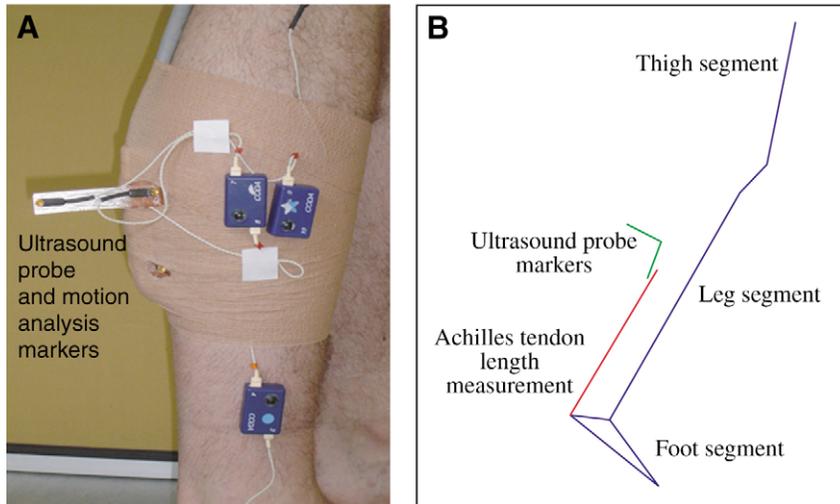


Fig. 1. (A) Picture of the flat ultrasound probe attached to the leg with 3-motion analysis (CODA) markers rigidly attached to the probe head. The ultrasound probe images the leg in the sagittal plane. (B) A stick figure representing the leg used in the measurements. The blue lines represent the leg and foot, the green lines represent the lines joining the three markers attached to the ultrasound probe to measure its position and orientation relative to the leg, and the red line indicates the measured Achilles tendon length (from the calcaneous insertion to insertion on the MG, as determined with the ultrasound images). For an animation, see Animation 1 in supplementary material.

with a fourth order, 5 Hz low pass Butterworth filter to create an EMG envelope.

Ultrasound measurement 1 – muscle fascicle and angle

A PC based ultrasound system (Echoblaster 128, UAB ‘Telemed’, Vilnius, Lithuania) was used to image the GM muscle fascicles and also the muscle–tendon junction. We used a 128-element, linear, multifrequency ultrasound probe at a frequency of 7 MHz and with a field of view of 60 mm in B-mode. Images were collected at 25 frames s^{-1} .

The probe was attached to the GM muscle such that it imaged a sagittal section to the leg. The probe was aligned to the midline of the muscle so that it was approximately in the same plane that the muscle fascicles ran in (Fig. 1A). Measurements of muscle fibre length and pennation angle were made at a mid-belly position as described in previous work (Lichtwark and Wilson, 2005d). During measurements the rotation of the probe was minimised due to the flat shape of the probe (approximate range of 10° rotation relative to the leg axis frame) and the image plane stayed in good alignment with the muscle fascicles. This was assessed by continuous, clear fascicle images obtained throughout the entire period of each stride. A digital output signal from the CODA motion analysis system that signified when data were being collected was passed to a control signal generator. The signal generator produced a 5 MHz pulse (amplitude 2.5 V) that was fed to a sonomicrometry crystal attached to the probe (Sonometrics Corp., London, ON, Canada) along the cable of the ultrasound probe. This produced a white signal on the bottom of the ultrasound image for a short period of time and thus allowed synchronisation between the motion analysis and ultrasound data.

Ultrasound measurement 2 – Achilles tendon length

AT length was measured as the distance from the calcaneous marker to the projected 3D position of the GM muscle–tendon junction (MTJ) (Fig. 1B). This was done by using the same ultrasound probe as previously mentioned to image the two dimensional position of the MTJ and tracking

the movement of the probe so that the two dimensional measurement could be projected into the 3D laboratory space (Fig. 1A). This technique, including accuracy determination, is detailed elsewhere (Lichtwark and Wilson, 2005c). The position and orientation of the probe was determined using three CODA markers rigidly attached to the probe. The position of the image relative to these markers was predetermined such that measurements made in this plane could be embedded back into the 3D laboratory space – the projected 3D position of the GM MTJ. This measurement was made in separate trials to those of the muscle fascicle length and pennation angle for all conditions. A stick figure animation of the leg and the AT length measurement during walking is shown in supplementary material (Animation 1).

The AT length change was measured relative to the slack length. The slack length of each individual was defined as the average length (across all strides) of the AT at toe-off for the level walking condition. This was calculated for each participant. This event was chosen because the Achilles tendon force should have dropped to zero at foot-off and hence there will be both zero stress and zero strain (Ishikawa et al., 2005; Komi, 1990). AT strain was calculated from the length change of the tendon divided by the slack length.

Series elastic element and aponeurosis length measurement

The length of the series elastic elements (SEE, including tendon and aponeurosis) was determined by subtracting the length of the muscle fascicles in the direction of the tendon from the change in whole muscle–tendon unit length:

$$L_{SEE} = L_{MTC} - L_{Fascicle} \cdot \cos\alpha, \quad (1)$$

where L_{SEE} is the length of the SEE, $L_{Fascicle}$ is the length of the muscle fascicle and α is the pennation angle (Fukunaga et al., 2001; Lichtwark and Wilson, 2005d). Length change of the SEE was reported relative to the average length of the SEE at toe-off for each condition.

An approximation of the total stretch of the combined proximal tendon and the aponeurosis in series with the muscle was also made as follows:

$$\Delta L_{\text{APO}} = \Delta L_{\text{SEE}} - \Delta L_{\text{AT}}, \quad (2)$$

where ΔL_{APO} is the length change of the aponeurosis plus the proximal tendon and ΔL_{AT} is the length change of the AT using the previously described ultrasound method.

Statistical analysis and force estimations

Muscle fascicle length and pennation angle were recorded for three strides for each participant and each incline condition. AT length was recorded simultaneously with joint angles, whole muscle length and EMG data for five complete strides for each participant and each incline condition. All of these data were interpolated to 100 points across each individual stride (from one heel contact to the next) and an average for each participant and each condition was determined at each one percent of the stride. The data from each participant were then pooled to get a group average and standard error for each variable across one complete stride.

Individual mean values for each condition were evaluated using a general linear model in Statistica v 6.0 (Statsoft Inc, Tulsa, OK, USA). Gait and incline were analysed as fixed factors and subject as a random factor since the mean value of dependent variables varied between subjects, but we were not interested in determining the actual properties for the individual subjects. In the analysis comparing walking and running we only used data collected on flat and incline (and had slope as a fixed factor). In the analysis of slope, we created two separate models; one using the data for walking and one using the data for running. For the walking state we then undertook two *post hoc* paired *t*-tests comparing the data for incline and decline to the data for level walking. Dependent variables were evaluated independently. A *P*-value of 0.05 was taken as indicating statistical significance except in the *post hoc* tests, where a *P*-value of 0.025 was taken to indicate significance, since two comparisons were performed.

An approximate average AT force (F_{AT}) was estimated for each condition using the average length change of the AT (ΔL_{T}) and the average stiffness of the AT ($k \sim 180 \text{ N mm}^{-1}$) as calculated elsewhere (Lichtwark and Wilson, 2005c) using the same method of length measurement:

$$F_{\text{AT}} = k_{\text{T}} \cdot \Delta L_{\text{T}}. \quad (3)$$

The contribution of the GM to the total AT force was estimated based on the physiological cross-sectional area (PCSA) of this muscle relative to all other plantar flexors (Kurokawa et al., 2003). An average PCSA of 15.4% of the total PCSA has been estimated (Fukunaga et al., 1992) and therefore the force contribution of the GM (F_{GM}) was calculated as follows:

$$F_{\text{MG}} = 0.154 F_{\text{AT}}. \quad (4)$$

The average force applied by the muscle fascicles (F_{Fascicle}) was then calculated in the direction of the muscle fascicles as

measured by the pennation angle (α) at each time instant and therefore the GM fascicle force were calculated as follows:

$$F_{\text{Fascicle}} = F_{\text{MG}} (\cos \alpha)^{-1}. \quad (5)$$

Fascicle length was normalised (L_{F0}) to a resting fascicle length of 60 mm (mean fascicle length at foot contact during walking trials) and average fascicle force was normalised (F_{F0}) to a maximum isometric force of 1200 N, based on a physiological cross-sectional area of 42 cm² and an average pennation angle of 15° (Narici, 1996). The average instantaneous velocity of the muscle fascicles (V_{Fascicle}) was also calculated by differentiating the average relative fascicle length with respect to time ($L_{\text{F0}} \text{ s}^{-1}$).

Results

Kinematics and muscle lengths

A comparison between the average kinematics and the calculated GM MTU length change for each condition is shown in Fig. 2. Although stance time varied slightly between incline conditions [Walking: 0.601 s (−10%), 0.604 s (0%), 0.618 s (+10%); Running: 0.300 s (0%), 0.288 s (+10%)], this was not significantly different within either ($P=0.35$ and $P=0.29$ for walking and running, respectively). Therefore, average stance times for walking and running across all conditions are indicated in the figures by grey shading.

Slope was found to have a significant effect on maximum MTU length in both walking and running ($P=0.04$ and $P=0.03$, respectively). For walking, the average maximum length changes (\pm s.e.m.) were 23.5 \pm 1.33 mm, 24.9 \pm 1.35 mm and 27.0 \pm 1.6 mm in the downhill, flat and uphill conditions, respectively. A *post hoc* paired *t*-test revealed no significant difference between the downhill and flat conditions ($P=0.4$); however, a significant difference was found between the flat and uphill conditions ($P=0.03$). For running, the MTU length change increased from 24.5 \pm 1.3 mm to 26.9 \pm 1.7 mm from flat to uphill. There was also an increase in ankle dorsi-flexion and knee flexion during the stance phase of running compared to walking; however, this did not result in a significantly different maximum MTU length change ($P=0.8$). This is likely to be due to the opposite effect that each has on whole muscle length.

Muscle fascicle length, pennation angle and excitation

The average change in muscle fascicle length and pennation angle for each grade during both walking and running is shown in Fig. 3. In both walking and running stance phase, incline seemed to make little difference to how the muscle fascicles changed length and pennation angle. The results indicate that slope had no significant effect on the length of the muscle fascicles at mid stance phase for both walking and running ($P=0.2$ and $P=0.3$, respectively, at 50% stance). Mean (\pm s.e.m.) walking muscle fascicle length at mid stance was 56.8 \pm 2.3 mm, 57.7 \pm 2.3 mm and 58.1 \pm 2.3 mm for downhill, flat and uphill walking, respectively, while running fascicle lengths were 53.4 \pm 1.7 mm and 54.5 \pm 1.5 mm for flat and uphill running, respectively.

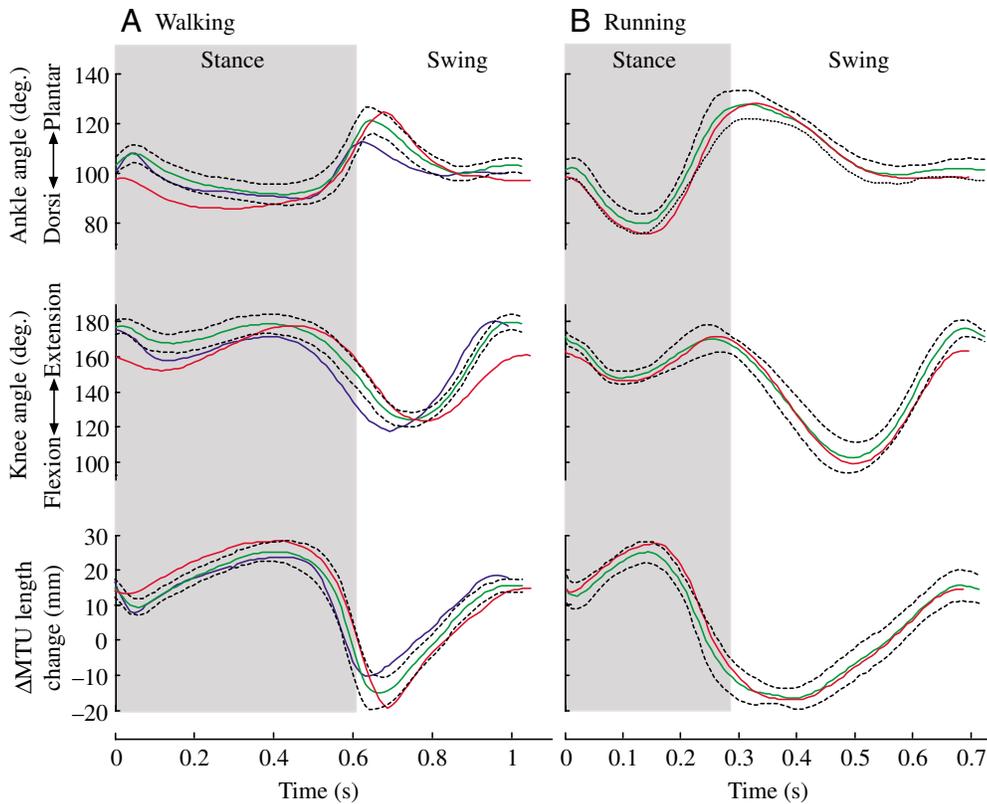


Fig. 2. Average ankle and knee angle and GM MTU length changes (Δ MTU length) with respect to time during walking (A) and running (B) for downhill (-10% ; blue), level (0% ; green) and uphill (10% ; red) conditions. The shaded areas mark the average stance time across each condition and the pooled 95% confidence interval (± 2 s.e.m.) across all grades for both walking and running is shown with respect to the level condition as the area within the dotted lines. The average standard error across each grade condition was equivalent.

During the running conditions the muscle fascicles were on average 4 mm shorter at heel strike and 6.5 mm shorter at toe-off than for walking; however, this was not statistically significant ($P=0.07$ and $P=0.09$, respectively). The fascicles also shortened more through the stance phase, in contrast to the walking conditions where muscle fibres acted relatively isometrically except at initial heel strike and just prior to toe-off. The muscle fascicles shortened to a mean of 40.1 ± 0.6 mm during the swing phase for both running conditions, whilst the shortest mean muscle fascicle length for the walking conditions was 44.1 ± 1.0 mm ($P=0.02$).

The GM muscle fascicles actively shortened while the whole MTU lengthened during the first half of the stance phase. When the GM began to deactivate, the muscle fascicles shortened along with the MTU in both walking and running. In both gaits, the EMG signal from the GM increased throughout stance until the MTU began to shorten. In walking the total GM EMG level increased with incline, whilst the maximum EMG level was similar in both running conditions. The tibialis anterior EMG signal showed some coactivation with the GM muscle at the beginning of the stance phase in both walking and running, and also at the end of the swing phase during running.

There was little variation in pennation angle with the change in incline for both walking and running ($P=0.12$ and $P=0.20$, respectively). However, the muscle fascicles acted at a significantly higher pennation angle during running than for walking ($P=0.001$), with a maximum pennation angle of

$20.8 \pm 1.0^\circ$ in running compared to $17.5 \pm 1.2^\circ$ in walking. During walking at all grades the muscle fascicles acted at a relatively constant pennation angle throughout stance with a mean range of $4.4 \pm 0.8^\circ$, compared to a running range of $5.8 \pm 0.7^\circ$. The relationship between muscle fascicle length and pennation angle is shown in Fig. 4. We found an inverse linear relationship between muscle fascicle length and pennation angle; however, there were differences between shortening and lengthening of the muscle fascicles and also some difference between walking and running conditions.

Muscle velocity

Table 1 compares the maximum shortening velocity of the muscle fascicles with that of the whole MTU. The maximum velocity of the MTU was faster for running than for walking ($P=0.002$). A similar effect was apparent in the muscle fascicle velocity data, with the maximum shortening velocity during running being higher than that during walking ($P=0.002$). Change in grade did not result in a significant difference in either MTU shortening velocity or maximum muscle fascicle shortening velocity in either gait. In all cases, however, the maximum shortening velocity of the muscle fascicles was substantially lower than that of the MTU, averaging under 30% of the MTU shortening in all conditions. The maximum shortening velocity of both the muscle fascicles and the MTU occurred at the end of the stance phase in all conditions. The maximum muscle fascicle shortening velocity was always less than $3 L_0 s^{-1}$.

Achilles tendon and SEE length changes

The length change of the AT across the gait cycle for all conditions (Fig. 5) showed that a greater stretch is achieved during running than walking. There was little difference, however, between maximum length changes with changes in grade. The average maximum strain measured during the walking conditions was 4.6% (10.9 ± 1.7 mm, mean \pm s.e.m.), whilst it averaged 5.8% (13.8 ± 1.4 mm) during the running conditions, which was not found to be significant ($P=0.11$). The uphill conditions for both walking and running, however, showed a longer length of the AT throughout the first half of

stance phase compared to the level results ($P=0.002$ and $P=0.01$ for walking and running, respectively, at 25% of stance). The *post hoc t*-test found this difference to be significant only between the flat and uphill conditions ($P=0.01$). The AT length shortened to below the slack length before the approximate toe-off in both running conditions. The results also show that the AT was strained during the swing phase with an average maximum strain of 2.9% during walking and 3.8% during running ($P=0.14$).

Fig. 5 also shows the estimated change in length of the SEE for each condition. The SEE stretched in a similar way to that

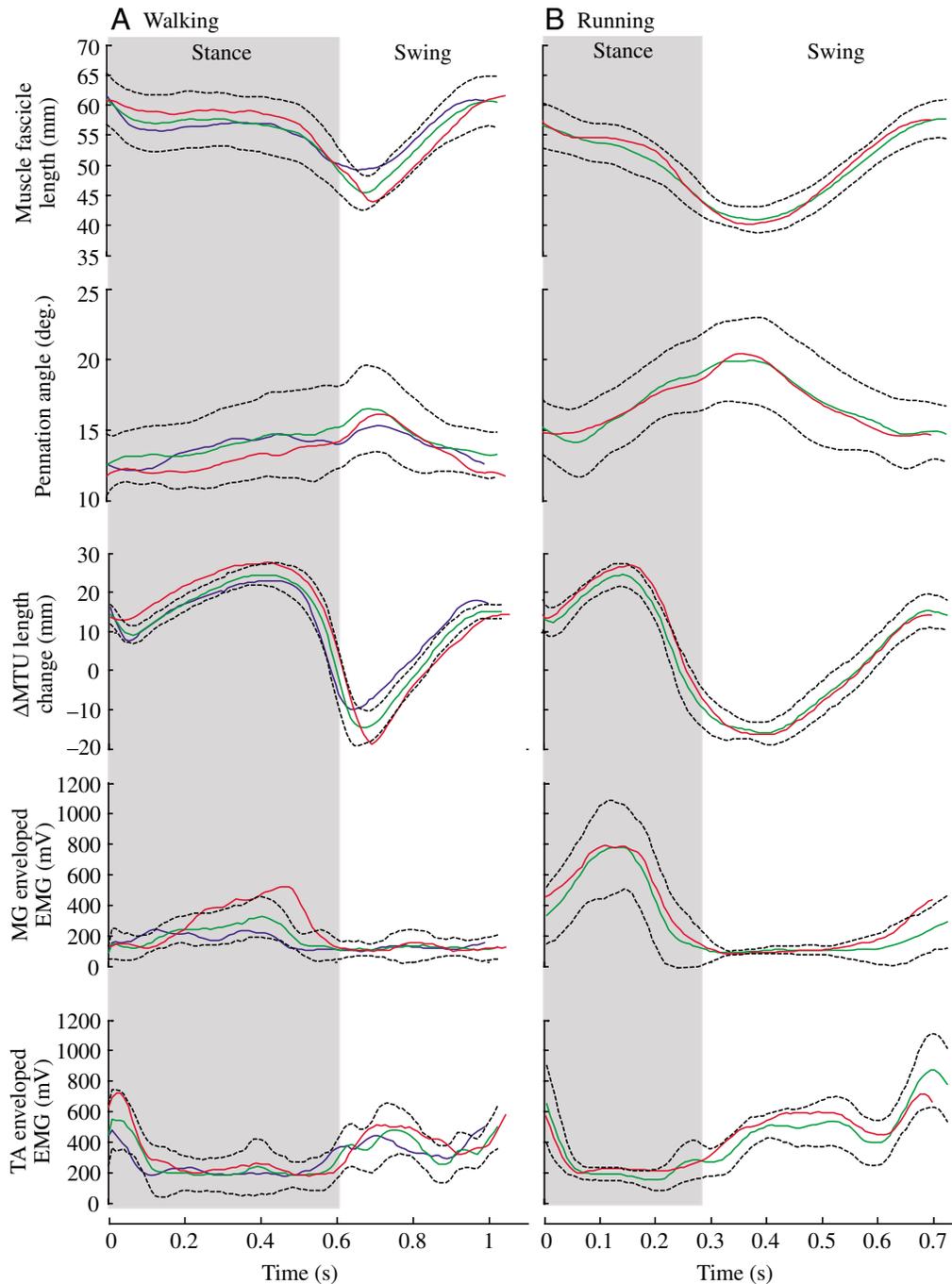


Fig. 3. Average GM fascicle length, pennation angle, MTU length change (Δ MTU length) and enveloped GM and tibialis anterior (TA) EMG signals with respect to time during walking (A) and running (B) for downhill (-10%; blue), level (0%; green) and uphill (10%; red) conditions. The shaded areas mark the mean stance time across each condition and the pooled 95% confidence interval (± 2 s.e.m.) across all grades for both walking and running is shown with respect to the level condition as the area within the dotted lines. The mean standard error across each grade condition was equivalent.

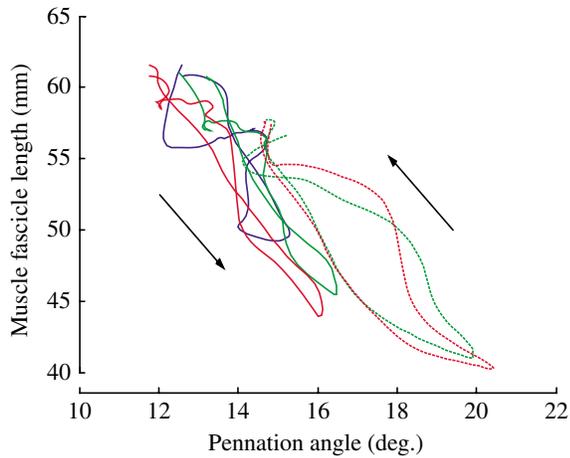


Fig. 4. The average relationship between muscle fascicle length and muscle fascicle angle for walking (solid lines) and running (dotted lines) during downhill (–10%; blue), level (0%; green) and uphill (10%; red) conditions.

of the AT; however, the amplitude of the total length change was greater in the SEE. The maximum stretch for all grade conditions in both walking and running was similar, with a higher strain achieved during the running trials. The maximum length change estimated with the model was 23.4 mm during walking and 25.2 mm during running. This estimate is based on a zero length for each condition, defined as the length measured at toe-off under that condition, rather than a fixed zero length for the SEE. Subtraction of the AT length change from the overall SEE length change gave an estimate of other elastic strain (aponeurosis, proximal tendon, other muscle fascia), termed aponeurosis strain for simplicity. The estimated maximum length changes in the aponeurosis were similar for both walking and running, with an average maximum elongation of 13.8 mm and 12.8 mm, respectively (Fig. 5).

Muscle work

The average length change of the muscle fascicle relative to the average length change of the tendon during the stance phase for each condition is shown in Fig. 6. The approximate force applied by the muscle fascicles, calculated using the stretch of the AT and Eqn 3–5, is also shown. The length of the muscle fascicles during the rise of force was different for each

condition. As grade increased for both gait types, the muscle fascicle length during force production increased. The muscle fascicles were, however, shorter during force production in running than walking and developed force before heel contact. In all cases, force development was associated with little change in length of the muscle fascicles and is hence isometric during this period. Shortening of the fascicles occurred during force decline in all conditions.

Discussion

The results of this study have shown that the human GM muscle fascicles produce force in a consistent fashion, despite changes in gait and incline. In each condition the Achilles tendon length (and hence force) increased with no change in muscle fascicle length. The change in locomotion condition did however alter the GM muscle fascicles' length and velocity at which force was produced during the stance phase. Positive work was done by the GM fascicles in all conditions. This was achieved because the muscle fascicles all shortened during force decline.

In the present study we demonstrate that when the MTU trajectory changes with change in grade and gait (speed), the muscle fascicle length trajectory also changes. In particular, the length of the muscle fascicles during force development varies as a function of grade and gait. As has previously been demonstrated, the muscle fascicles act relatively isometrically during the stance phase of walking (Fukunaga et al., 2001), and shorten during the stance phase of running (Lichtwark and Wilson, 2005d). Here we have found, however, that there is an increase in muscle fascicle length associated with the increase in grade. This is likely to be due to the increase in whole MTU length occurring as a result of the increased dorsi-flexion throughout stance. The force–length properties of the muscle fascicle, including the contribution of parallel elastic elements, may therefore be important in determining the muscle power output.

In all conditions the AT strain and hence force was developed with very little change in muscle fascicle length; the contractile element acted almost isometrically during this period (Fig. 6). The results demonstrate that the muscle fascicles shortened at speeds below 1/3 of the estimated maximum muscle shortening velocity [assuming a maximum shortening velocity of between 8 and 14 L_0 s^{-1} (Epstein and

Table 1. Average maximum GM muscle–tendon unit (MTU) shortening velocity and maximum muscle fascicle shortening velocity for the stance cycle for each condition

Maximum velocity (L_0 s^{-1})	Walking (–10%)	Walking (0%)	Walking (+10%)	Running (0%)	Running (+10%)
Fascicle	1.73±0.18	1.69±0.27	1.59±0.18	1.94±0.16	2.63±0.34
MTU	5.26±0.46	5.98±0.60	5.94±0.60	7.75±0.50	8.54±0.49

Values are means ± s.e.m. ($N=6$).

L_0 =length of fascicle at the start of stance in level walking. Gait (walking or running) had a significant effect on the maximum fascicle shortening velocity ($P=0.002$) and maximum MTU shortening velocity ($P=0.002$).

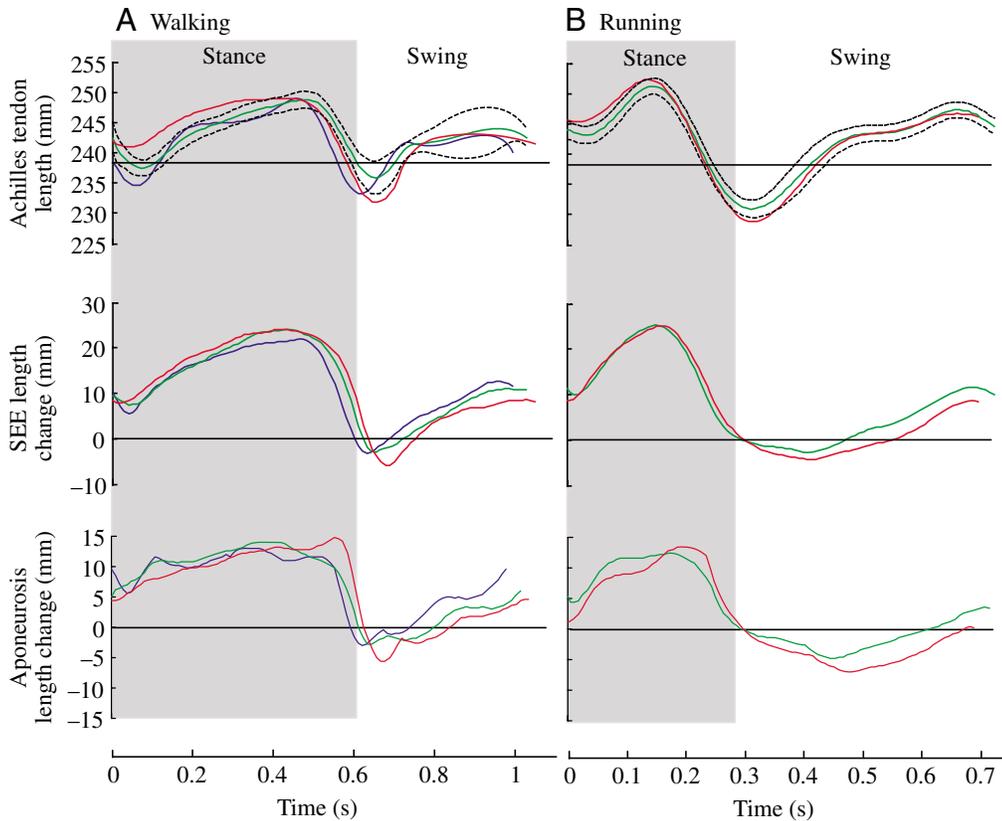


Fig. 5. The average Achilles tendon (AT) length change measured directly using the projected MTJ measurement and the corresponding estimates of series elastic element (SEE) length change during walking (A) and running (B) for downhill (–10%; blue), level (0%; green) and uphill (10%; red) conditions. The AT slack length is estimated from the average length of AT during walking on the level at the average time of toe-off. The estimated aponeurosis length change (which includes the proximal GM tendon) is calculated as the difference between the AT length change (relative to the slack length) and the SEE length change. The shaded areas mark the average stance time across each condition.

Herzog, 1998)]. This is both energetically efficient and is also advantageous in being able to produce high forces (Roberts, 2002; Woledge et al., 1985). A similar result has previously been predicted using indirect methods (Hof et al., 2002); however, that study estimated the entire contractile component length change (which is largely influenced by muscle shape

changes) rather than length measurements of individual fascicles.

Most of the work done by the muscle fascicles was done during deactivation, when the elastic tissues were also recoiling and doing the majority of the work of the MTU. The rate of muscle fascicle shortening increased with an increase in speed; however, the rate of shortening was typically around 25–30% of the total MTU shortening speed. Therefore the elastic recoil of the tendon and aponeurosis contributed most of the MTU shortening. A similar finding has been demonstrated during walking (Fukunaga et al., 2001; Ishikawa et al., 2005). This raises the question as to why the muscles do not deactivate at a faster rate, remain isometric, and allow the tendon to do all of the work whilst recoiling. Perhaps if the muscle were to relax too fast then the high forces would stretch the muscle and absorb some of the work of the whole MTU, which is an inefficient method of performing whole muscle work. Also, perhaps the muscle must maintain a short length during the swing phase so as to ensure foot clearance, and therefore the muscle fascicles must be at a shorter length. Alternatively, this may be an efficient way to perform muscular work (Woledge et al., 1985) or perhaps the neuromuscular system is unable to control such a precise method of deactivation.

During walking there was an increase in the muscle excitation (based on EMG) with an increase in incline. However, there was not an increase in muscle fascicle force or a significant change in the area under the GM fascicle length–AT length curve. Throughout the stance phase,

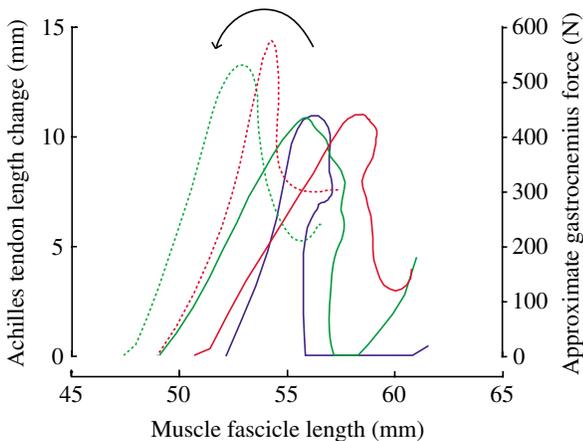


Fig. 6. Average work loops for walking (solid lines) and running (broken lines) during downhill (–10%; blue), level (0%; green) and uphill (10%; red) conditions during the stance phase of the gait cycle. Approximate medial gastrocnemius fascicle force is calculated using Eqn 3–5.

however, the muscle fascicles act at a longer length during force development as incline increases. Therefore, perhaps the muscle moves along the descending limb of the force–length curve here and requires more activation to produce the required force and stretch the AT. This is probably unlikely, however, due to the effect of parallel elasticity. Alternatively, the muscle fascicles also contract at a higher velocity in the uphill conditions, which would require a higher activation to achieve the same force according to the force–velocity relationship of muscle. In contrast to walking, the running conditions showed a higher excitation but this level was very similar between grade conditions. Again, the muscle fascicle lengths were much shorter and the contraction velocities were greater uphill running condition. The differences in excitation level (EMG) may also be due to variations in the force sharing between the other muscles of the triceps surae (Arndt et al., 1998).

During both walking and running the AT length was greater than its slack length at heel strike (Fig. 5). This suggests that some force was developed in the AT during the swing phase. During walking this occurred during periods of inactivity in the GM muscle and is likely to be due to parallel elastic structures, other muscles or measurement errors in this portion of the stride (probe rotations etc.). However in the running condition, where greater strain was developed and maintained throughout the heel contact period, the GM was co-activated with an antagonist, the tibialis anterior. This suggests that there is indeed some requirement for tension to be developed in the AT during foot contact. This may act to stabilise the ankle joint for impact with the ground. Activating the GM muscle before foot strike also alters the length of the muscle fascicle in preparation for force development during stance, and may optimise the length of the muscle for force production during stance.

During steady state locomotion on the level, the requirement for whole body work is zero across the period of a stride; however, here we have demonstrated that the GM muscle does positive work even when travelling downhill. This is in contrast to the findings of Gabaldon and colleagues (Gabaldon et al., 2004), who found that the work output of the lateral gastrocnemius and peroneous longus muscles of the turkey more closely resemble that of the whole body work output. Perhaps the role of the human GM is different to that of the muscles examined in the turkey. It is not possible to present accurate and validated calculations that compare the external work and power output of the body to that of the muscle fascicles from this data set (due to estimations of individual muscle forces and errors likely associated with the ultrasound technique). Perhaps future studies will explore these relationships.

In our estimates of muscle fascicle force, we assumed that the three muscles of the triceps surae contribute equally to the whole tendon force based on PCSA. This may not be the case, however, and the contribution to whole tendon force may vary with different conditions (as mentioned above). Direct measures of AT strain suggest that the strain distribution of the muscles attaching to the tendon may not be equal and can cause

differential strain patterns in the tendon and aponeurosis (Finni et al., 2003; Bojsen-Moller et al., 2004; Arndt et al., 1998). The large variation in Achilles tendon stiffness between individuals is also likely to have an effect on individual estimates of muscle fascicle force (Lichtwark and Wilson, 2005c; Hof, 1998; Maganaris and Paul, 2002).

Previously it has been suggested that the primary function of biarticular muscles with opposite actions at each joint, such as the GM, is to transfer energy from the more powerful and proximal muscles of the knee and hip and hence may not be required to produce large amounts of work (Bobbert and Ingen Schenau, 1988; Neptune et al., 2004). However the action at both joints must be considered in examining the amount of energy that can be transferred. It has recently been demonstrated in human running, that although the maximum plantar flexion ankle joint moment does not vary between level and uphill running, the knee extensor moment actually decreases when running uphill (Roberts and Belliveau, 2005). Therefore the GM, which acts as a knee flexor, may produce less force in counteracting the knee extensors during uphill running. The results from this study are therefore consistent of those of Roberts and Belliveau, who concluded that the extra power for uphill running is generated mostly at the hips; not the knee and ankle (Roberts and Belliveau, 2005).

This study has also demonstrated the importance of strain of other elastic tissues (e.g. aponeurosis) in producing muscular force. The large difference between the strain of the AT and the calculated SEE length (Fig. 5) demonstrates that other tissues must be stretching. This was shown experimentally by Magnusson and colleagues (Magnusson et al., 2003), who demonstrated that the aponeurosis strain is significant, although it appears to be stiffer than the AT. Hof and coworkers (Hof, 1998) have also argued that series elastic tissue such as the aponeurosis may be selectively recruited based on muscle activation levels and that this may alter the stiffness of the entire elastic component. This again would influence our estimations of fascicle force, work and power output.

In conclusion, the interaction of the GM muscle with the AT and other elastic tissues varies with both gait and grade of incline. Force is typically developed isometrically and work is done by the fascicles during force decline. The fascicle length at which force is developed, however, does vary with incline. This is likely due to the change in force requirements and the change in whole MTU length trajectory resulting from kinematic changes. To achieve this pattern of muscle contraction, the AT and other elastic elements are strained substantially, which allows the muscle fascicles to act at velocities that maximise power output of the muscle. Our results also indicate that the GM produces positive work during all incline conditions.

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