

# Muscle fascicle and series elastic element length changes along the length of the human gastrocnemius during walking and running

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## Abstract

Ultrasound imaging has recently been used to distinguish the length changes of muscle fascicles from those of the whole muscle tendon complex during real life movements. The complicated three-dimensional architecture of pennate muscles can however cause heterogeneity in the length changes along the length of a muscle. Here we use ultrasonography to examine muscle fascicle length and pennation angle changes at proximal, distal and midbelly sites of the human *gastrocnemius medialis* (GM) muscle during walking (4.5 km/h) and running (7.5 km/h) on a treadmill. The results of this study have shown that muscle fascicles perform the same actions along the length of the human GM muscle during locomotion. However the distal fascicles tend to shorten more and act at greater pennation angles than the more proximal fascicles. Muscle fascicles acted relatively isometrically during the stance phase during walking, however during running the fascicles shortened throughout the stance phase, which corresponded to an increase in the strain of the series elastic elements (SEEs) (consisting of the Achilles tendon and aponeurosis). Measurement of the fascicle length changes at the midbelly level provided a good approximation of the average fascicle length changes across the length of the muscle. The compliance of the SEE allows the muscle fascicles to shorten at a much slower speed, more concomitant with their optimal speed for maximal power output and efficiency, with high velocity shortening during take off in both walking and running achieved by recoil of the SEE.

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## 1. Introduction

The interaction of a muscle and associated tendon during dynamic activities such as locomotion is critical for both force production and economical movement. To understand the dynamics of muscle–tendon interaction it is necessary to distinguish the relative length changes of muscle's contractile parts (muscle fascicles) from those of the elastic parts (tendons, aponeurosis and other connective tissues). Within animal models it has

been possible to measure the length changes of muscle fascicles with sonomicrometry (Griffiths, 1991; Roberts and Scales, 2002, 2004). These studies have revealed that compliant tendons can store and return elastic energy to change the timing and rate of muscular work and allow the contractile components to act nearly isometrically, despite substantial length changes in the muscle–tendon unit. This produces higher forces and reduces the energetic requirements on the muscle fascicles. Similar results have been reported for human muscle fascicles using ultrasonography (Fukunaga et al., 2001, 2002).

The complex three-dimensional (3D) structure of pennate muscles complicates this measurement of muscular function. Most muscles are not homogenous in their architecture, typically consisting of muscle fascicles that act at different orientations to the line of

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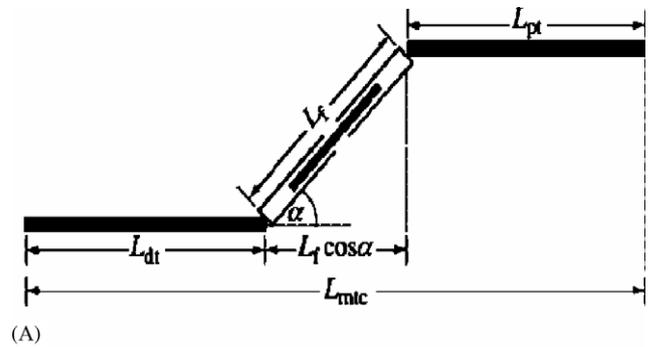
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action of the muscle; the pennation angle (Epstein and Herzog, 1998; Scott et al., 1993; Zuurbier and Huijing, 1993; Wickiewicz et al., 1983; Woittiez et al., 1984). The presence of additional elastic tissues that act in different directions when stretched, such as aponeurosis and perimysium, further complicates our understanding of muscle function (Scott and Loeb, 1995; Van Leeuwen, 1999; Zuurbier and Huijing, 1992). Models have previously been used to predict how muscle architecture changes during muscle contraction (Otten, 1988; Van Leeuwen and Spoor, 1992). However these models are muscle specific and are not necessarily subjected to the conditions that a muscle experiences during contraction in a real life activity such as locomotion and do not incorporate the interaction of the muscle with other biological structures (e.g. other muscles) (Maas et al., 2003; Yucesoy et al., 2003).

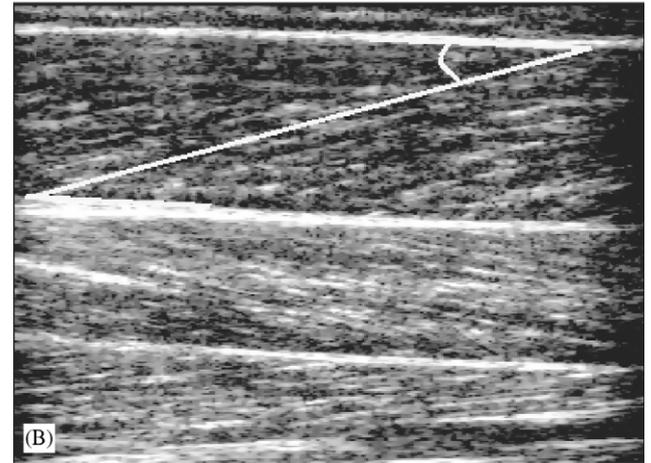
Recently, experimental work examining the human biceps brachii muscle has shown that the muscle fascicles act non-uniformly along the centreline of the muscle both proximally and distally (Pappas et al., 2002). Similar findings have been found to occur in the rat gastrocnemius muscle (Zuurbier and Huijing, 1993). Conversely, an ultrasound study looking at the fascicle length of the *triceps surae* muscle group during graded isometric contractions showed that fascicles of each of the three muscles that make up this complex were found to be homogenous in their length change (Maganaris et al., 1998). These conflicting results suggest that further examination of muscle homogeneity is required, particularly during movements where the muscle length changes during movements such as locomotion.

The assumption of muscle fascicle homogeneity during real-life muscle contractions has important implications in the modelling of muscle–tendon unit interaction. The model used by most investigators (Fukunaga et al., 2001, 2002) to calculate the changes in length of the series elastic element (SEE) makes the assumptions that the fascicles are homogenous and are therefore accurately represented by the action of fascicles from the midbelly of the muscle (Fig. 1A). However, these models do not take into account the complex architecture of muscle, nor the fact that muscle fascicles are linked and must obey the laws of conservation of volume and energy (Gans and Gaunt, 1991). To date, there has been little research that enables us to accurately predict architectural changes in muscle shape during muscle contractions that produce movement. In particular, very little is known about the way in which muscle architecture may react to changes in movement, such as a change in gait, where different forces and shortening trajectories are required.

Using a flat ultrasound probe which can be securely attached to the human leg without obstructing natural gait, we have been able to determine and compare muscle–tendon unit interaction during the real-life



(A)



(B)

Fig. 1. (A) The musculoskeletal model used by Fukunaga et al. (2001) to estimate tendon length changes. In this model, the total change in SEE length ( $\Delta L_{dt} + \Delta L_{pt}$ ) is equal to the change in muscle–tendon complex length ( $\Delta L_{mtc}$ ) minus the change in muscle fascicle length change in the direction of the SEE ( $\Delta(L_f \cos \alpha)$ ) which we will call the change in contractile component length ( $\Delta L_{cc}$ ). This model assumes that  $\Delta L_{cc}$  can be represented by a single fascicle's action ( $\Delta(L_f \cos \alpha)$ ). However if we consider multiple fascicles along the length of the muscle then  $\Delta L_{cc}$  is the average length change of each of these fascicles in the direction of the tendon (assuming that the fascicles are evenly distributed along the length of the muscle). (B) Ultrasound image of the GM muscle in the sagittal plane at the level of the midbelly. Muscle fascicle length was measured as the length of the white line from the upper fascia to the lower fascia and pennation angle was defined as the angle made between the upper fascia (the line of action of the tendon) and the direction of the muscle fascicles.

activities of both walking and running. Using this technique, we tested the hypotheses that:

1. the *gastrocnemius medialis* (GM) muscle fascicles undergo a homogenous length change across three sites along the length of the muscle (distal, middle and proximal) during walking and running;
2. the GM muscle fascicles perform differently during running and walking.

## 2. Materials and methods

Six healthy volunteers (three male, three female), average (mean,  $\pm$ SD), age  $31 \pm 1.67$  years, height

171±8 cm, and body mass 77±12 kg gave consent to participate in the study. The study was approved by a local ethics committee (RNOH JREC, 04/Q0506/11). Participants walked and ran on a treadmill at speeds of 4.5 and 7.5 km/h, respectively, whilst a variety of measurements were made. A 2 min warm-up period was allowed to familiarise participants with the setup.

### 2.1. Joint kinematics

Active CODA light-emitting diodes (LEDs) were attached the following body landmarks: head of the fifth metatarsal, calcaneus, lateral malleolus, head of the fibula, lateral epicondyle of the knee, iliotibial band (half-way between knee marker and greater trochanter) and the greater trochanter. The 3D position of these LEDs was determined with an accuracy of ±1 mm by using a CODA motion analysis system (Charwood Dynamics, UK) at rate of 100 Hz. Knee and ankle angles were determined in the sagittal plane. The markers on the fifth metatarsal and calcaneus were also used to determine the events of the stride cycle, as described in more detail below. Ankle dorsi-flexion was defined as ankle angles above 90°, whilst knee flexion was defined as angles above 0° (the approximate angles during quiet standing).

### 2.2. Muscle architecture

A PC-based ultrasound system (Echoblaster 128, UAB 'Telemed', Vilnius, Lithuania) was used to image the *medial gastrocnemius* muscle fascicles in the sagittal plane. In this experiment we used a 128-element, linear, multi-frequency ultrasound probe at a frequency of 7 MHz and with a field of view of 60 mm in B-mode. The probe, conventionally used for veterinary reproduction applications, is flat shaped with the cable exiting one end of the probe in line with the imaging face (unlike most probes where the cable is orthogonal to the imaging face). The probe was securely bandaged to the leg with Coban™ (3M, St. Paul, MN, USA). Images were collected by a PC and recorded in cineloop at 25 frames/s. The images were saved as a video file for further analysis.

The probe was taped to the GM muscle such that it imaged a transverse section of the leg (Fig. 1B). The probe was aligned to the midline of the muscle so that it was approximately in the same plane as the muscle fascicles. Measurements were made at three positions on the muscle: the midbelly and distally and proximally to this position. The proximal and distal positions were defined as 35 mm from the midbelly position.

Muscle fascicle length was defined as the straight line between the upper muscular fascia and the lower muscular fascia parallel to the lines of collagenous tissue visible on the image (Fig. 1B). This measurement was consistently made in the middle of image where the

full length of the fascicle could be imaged. The pennation angle was defined as the angle made between the upper fascia (the line of action of the tendon) and the direction of the muscle fascicles (Fig. 1B).

### 2.3. Synchronisation of motion analysis and ultrasound data

A digital output signal from the CODA motion analysis system that signified when data were being collected was passed to a signal generator. The signal generator then produced a 5 MHz pulse on a sonometry crystal (Sonometrics Ltd, Ont., Canada) attached to the end of the ultrasound probe. This produced a white signal on the edge of the ultrasound image and thus allowed synchronisation between the motion analysis and ultrasound data.

### 2.4. Determination of events

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. At the running speed measured here, all participants contacted the ground with the heel first. 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.

Measures of muscle fascicle length and orientation were made at 0%, 20%, 40%, 60%, 80% and 100% of both stance and swing phases (10 measures in all for each cycle). The stride was further divided up into the following specific events from the kinematics: T1—heel strike; T2—foot flat (approximate end of double support for walk); T3—heel off; T4—toe off; T5—heel strike. Three full stride cycles of ultrasound data were analysed for each participant at both walk and run for each of the three probe sites (proximal, midbelly and distal).

### 2.5. Muscle–tendon length measures

The ankle and knee angles were interpolated to 100 points across the time of a complete gait cycle. These 100 points were then averaged across five–ten strides (depending on how many occurred during 10 s collection time) for each subject and these were further averaged across all subjects. Length changes of the GM muscle–tendon unit length were estimated from the average joint angle data using the equations derived by Grieve et al. (1978). The average shank length of each of the six subjects (0.361±0.23 m) was used to determine the

absolute length change of the muscle–tendon complex (MTC) across the gait cycle (Grieve et al., 1978).

To estimate the SEE elongation, muscle fascicle lengths and the pennation angle from the ultrasound images were used along with the whole muscle–tendon length in the model proposed by Fukunaga et al. (2001) (see Fig. 1A). This was carried out for each of the measures at the proximal, middle and distal measurement sites and then a model combining the average length change of all three measurement sites was used to calculate an approximate tendon length change (described in Fig. 1A). The length corresponding to zero strain (or zero length) was approximated from the length of the tendon at the time of foot off; a time when zero force is applied through the tendon (Komi, 1990).

### 3. Results

The mean muscle fascicle length and pennation angles at each of the three sites along the muscle (distal,

midbelly and proximal) throughout the gait cycle are shown in Fig. 2 along with the average muscle fascicle length change trajectory. It is apparent that during both walking and running the muscle fascicles at each site perform a similar function; however, muscle fascicle function differs between running and walking. In both walking and running the midbelly position provides the best approximation to the average muscle fascicle length during the gait cycle.

During walking the muscle fibres were at their longest length at heel contact (T1). They then shortened rapidly from heel contact until the foot was flat on the treadmill surface (T2). During this time the ankle was plantar flexing and the whole MTC was also shortening (Fig. 3). From T2 to T3 (the moment when the heel leaves the ground), the muscle fibres acted relatively isometrically and showed little change in pennation angle. The distal muscle fascicles were approximately 4 mm shorter than the proximal and midbelly fascicles during this period. The fascicles then shortened by 9–18% at the different sites until the foot left the ground (T4). In addition the

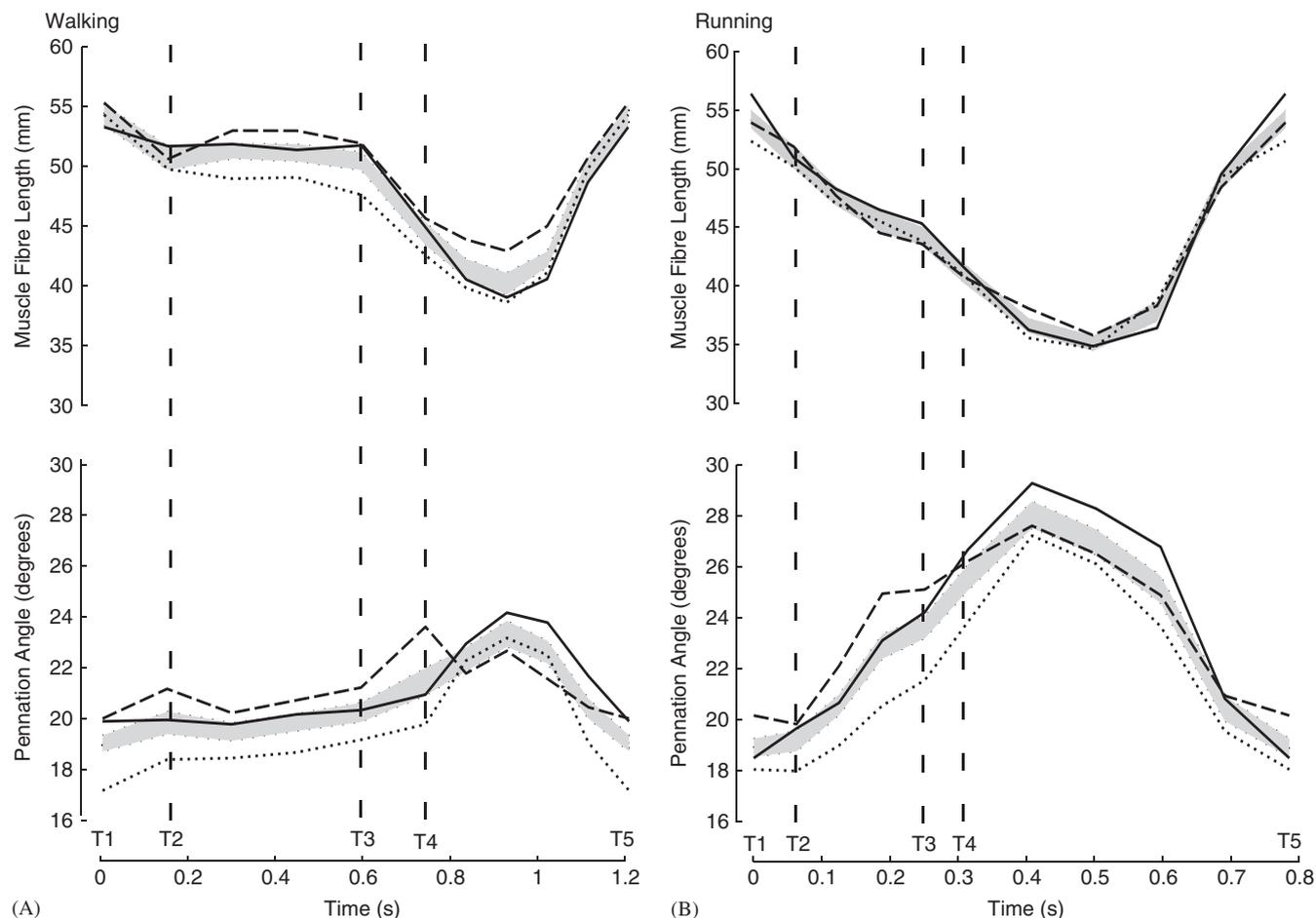


Fig. 2. Average length and pennation angle of muscle fascicles across one complete stride (heel on to next heel on) during walking (A) and running (B) for each of the three ultrasound sites (distal = dotted; medial = solid; proximal = dashed). The 95% confidence interval of the pooled data (as calculated with a general linear model) is demonstrated by the grey shaded area. The stride was divided up into the following specific events averaged from the kinematics: T1—heel strike; T2—foot flat; T3—heel off; T4—toe off; and T5—heel strike.

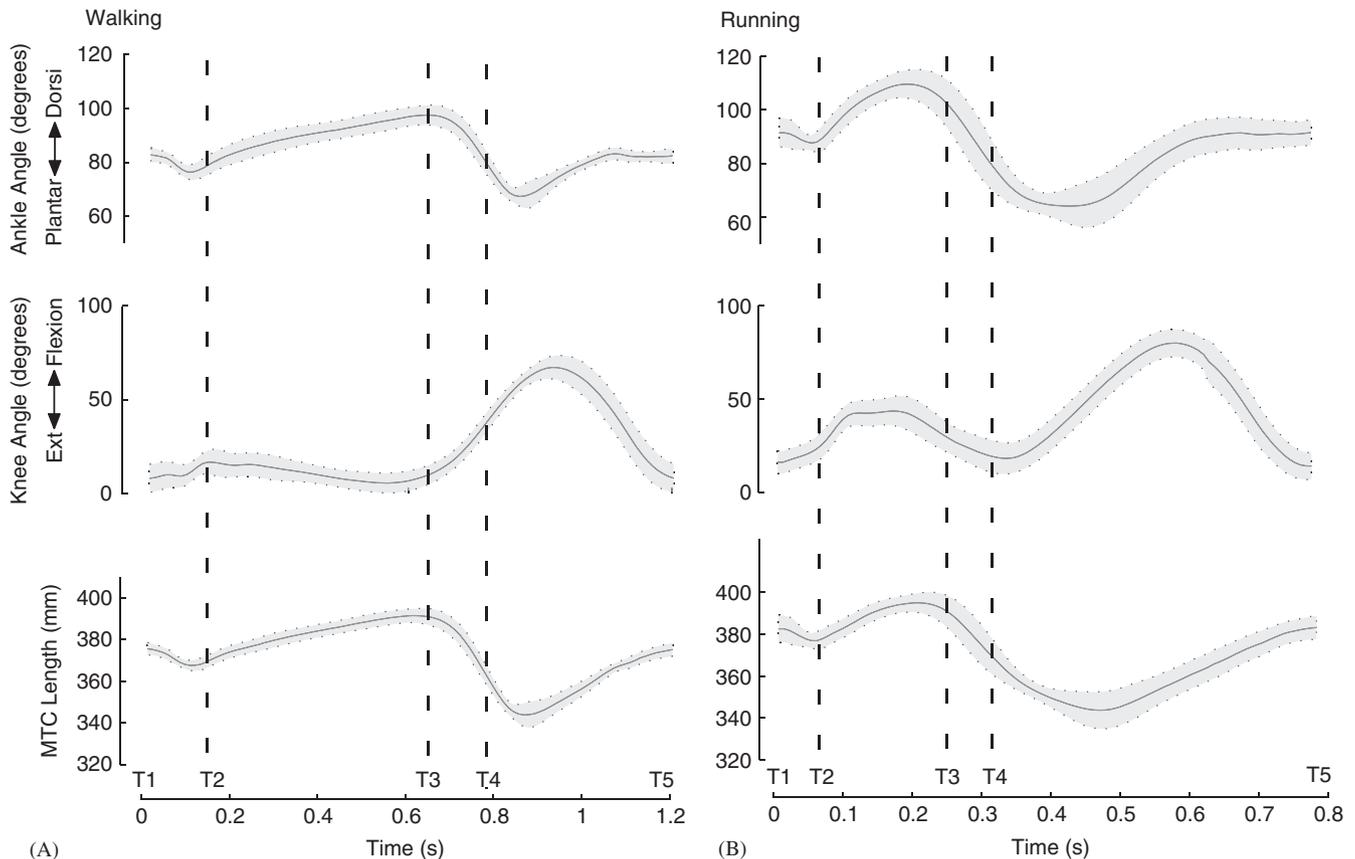


Fig. 3. Average ankle and knee angles for one complete stride and the corresponding estimation of gastrocnemius muscle–tendon complex length for walking (A) and running (B). The grey shaded area represents the 95% confidence interval. The stride was divided up into the following specific events averaged from the kinematics: T1—heel strike; T2—foot flat; T3—heel off; T4—toe off; and T5—heel strike. Ankle dorsi-flexion was defined as ankle angles above  $90^\circ$ , whilst knee flexion was defined as angles above  $0^\circ$ .

proximal fascicles acted at a greater pennation angle than the more distal fascicles. As the foot left the ground for the swing phase (T4) the fascicles continued to shorten until midway through the swing phase when they lengthened back to their starting length before heel contact (T5).

The major difference between walking and running occurred during the loading phase (T2–T3). The muscle fascicles shortened by approximately 23% from T1 to T4; however, only 40% of this length change occurred during the period when the whole foot was planted on the surface (T2–T3). The highest rates of shortening occurred from T1–T2 to T3–T4, where muscle fascicle lengths shortened at approximately 0.94 muscle lengths per second as opposed to 0.58 muscle lengths per second from T2 to T3. The shortening of the fascicles was also accompanied by increases in the pennation angle throughout the stance phase. Once the foot left the ground (T4) there was further shortening of the fascicles (and increases in pennation angle). During running, the muscle fascicles shortened to approximately 35 mm at foot off, which was 5 mm (9%) shorter than the minimum length during walking. Again the muscle

fascicles begin to lengthen midway during the swing phase, when the knee begins to extend and the ankle dorsi-flexes.

The influence of kinematic changes on GM MTC length across the gait cycle for walking and running is shown in Fig. 3. There was an increase in ankle dorsi-flexion and a decrease in knee flexion with the change of gait from walking to running. As a result, the MTC extended by up to 6 mm longer during the stance phase in running compared to walking. In both gaits, a rapid shortening of the MTC during the push off phase was apparent (T3–T4). During walking the maximum shortening speed at this period was up to six-muscle fascicle lengths per second, whereas it was only four and a half-muscle lengths per second in running.

The calculated SEE elongation for each of the three measurement sites and the elongation calculated using the averaged muscle model relative to the gait cycle are shown in Fig. 4. In both gaits the SEE lengthens during the loading period (T2–T3) and reached a peak elongation of 17.5 and 22 mm during walking and running, respectively. Throughout the push-off phase

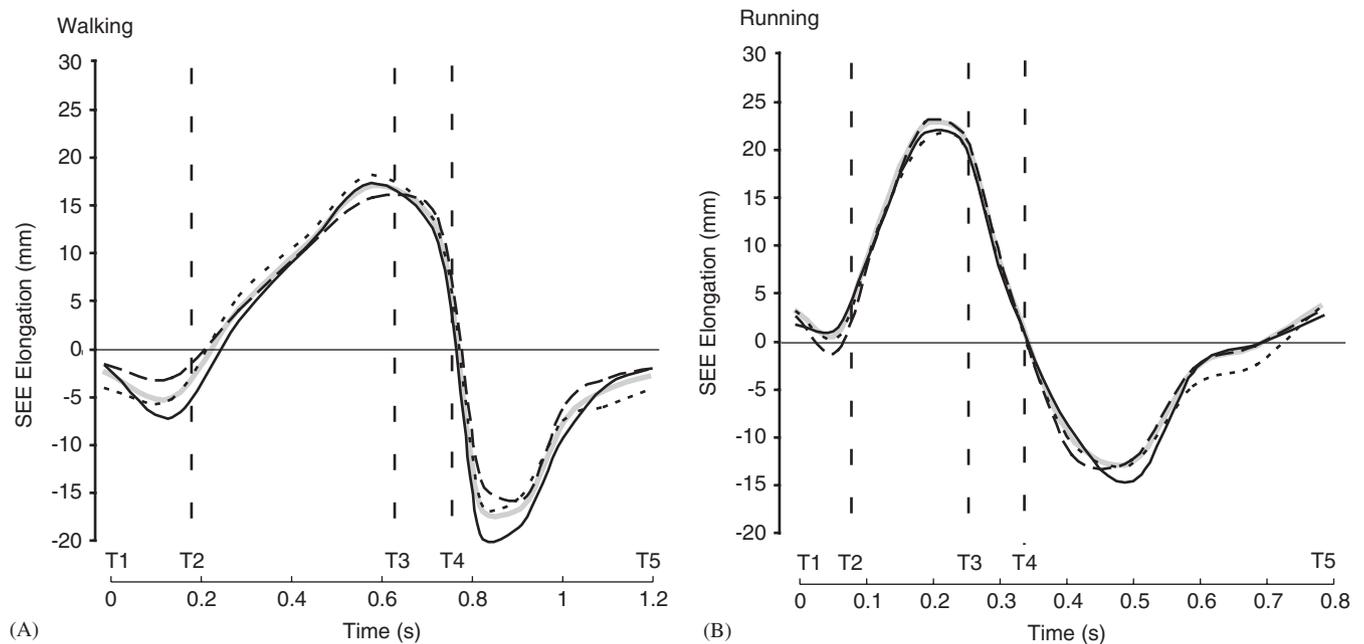


Fig. 4. Calculated SEE elongation during the gait cycle for walking (A) and running (B) using each of the three ultrasound sites (distal = dotted; medial = solid; proximal = dashed) and the average muscle fascicle length change (grey line). The stride was divided up into the following specific events averaged from the kinematics: T1—heel strike; T2—foot flat; T3—heel off; T4—toe off; and T5—heel strike. The length of zero strain (or zero length) was approximated from the length of the tendon at the toe off.

(T3–T4) the SEE rapidly shortened in both gaits such that it was slack within 0.12 s. The length of the SEE was shorter during the swing phase than at toe off. This corresponds to the tendon being ‘slack’. It is, however, difficult accurately to determine the slack length.

Although the three measurement sites differed in their predictions of SEE elongation, it is apparent that the midbelly site provided a good approximation of the SEE elongation compared to the average from all three sites. The largest discrepancies occurred during the initial period of foot contact (T1–T2) and also during the swing phase, times when the loading of the SEE was small.

#### 4. Discussion

Using ultrasound imaging to analyse muscle–tendon unit interaction during different gaits has provided valuable new insights into muscle mechanics. The results of this study have shown that muscle fascicles perform the same actions along the length of the human GM muscle during locomotion. However, the distal fascicles tend to shorten more and act at greater pennation angles than the more proximal fascicles during walking. The effect of the difference on calculation of SEE strain is minimal and the midbelly fascicles provide a good approximation. There is also a difference in the action of the muscle fascicles between running and walking, where the muscle fascicles shorten more to produce the greater

amount of work required during the stance phase of running.

The results of this investigation have demonstrated that the pennate GM muscle fascicles act in a similar way along the length of the muscle throughout the gait cycle for both walking and running. This supports the isometric data of Maganaris et al. (1998) from the same muscle. During walking there were small differences in muscle fascicle length at each level during the stance phase, although at all sites the muscle fascicles acted almost isometrically. The difference in length change is again likely to be due to differences in the local stresses applied to the muscle fascicles and also the internal pressure (Van Leeuwen and Spoor, 1993). This is less apparent in running, where the fibres perform very similar roles. Our data also suggests that in both walking and running, the change in length of the muscle fascicles in the midbelly accurately characterises those of the entire muscle.

The differences in muscle function between walking and running are also of interest. We have shown that the muscle fibres shorten during the stance phase of running, and hence produce positive work. This supports the estimations of muscle fibre action during running predicted by Hof et al. (2002), whose measurements showed that the contractile component of the muscle must shorten throughout the stance phase of the running cycle.

Energetically, it seems more expensive to have to shorten the muscle fascicles during running. However it

is apparent that the muscle fascicle never exceeds a shortening velocity of above 1.5 lengths per second during running. In fact, at the point of peak tendon stretch (peak force) the velocity of the muscle fascicles does not exceed 0.54 lengths per second at all levels of the muscle. This is a very slow speed for muscle to contract at considering that the maximum velocity of muscle contraction is about 10–13 lengths per second (Zajac, 1989). Therefore the muscle is in fact acting at a relatively optimal level to produce high forces with small amounts of work and high efficiency (Roberts and Scales, 2002). In contrast to the velocities of muscle fascicle shortening, the work done on the tendon allows MTC shortening velocities of up to six-muscle fascicle lengths per second to be achieved during recoil of the tendon at take-off. Therefore the complex interaction between the muscle fascicles and the attached tendon allows the muscle to operate with more optimal conditions. This is in agreement with the turkey ankle extensor data of Roberts et al. (1997).

The SEE strains predicted by the muscle model are at the higher end of the acceptable strains before tendon rupture as measured *ex vivo*. We measured SEE elongations of 22 mm during running, which equates to approximately 5.5% strain if total SEE length of 400 mm (accounting for all aponeurosis and both proximal and distal tendons) is assumed, despite the running speed being extremely slow compared to the participants' physiological maximum running speed. These large strains might be the result of the simplified model used to calculate the SEE strain; however, it is also possibly a physiological property of the GM connective tissue.

The length change of the SEE reported here is consistent with that of numerous other investigators during both dynamic activities and isometric contractions. Using the same muscle model has yielded estimates of up to 20 mm of stretch (~5% strain) during dynamic counter movements and up to 10 mm during slow walking (~2.5% strain) (Fukunaga et al., 2001; Kawakami et al., 2002). Although our data follow a similar length change trajectory to those of Fukunaga et al. (2001), our data estimate up to 16 mm elongation in the SEE during walking compared to 10 mm in the previous study. These differences are likely to be due both to the difference in speed and also the experimental setup. Here we have attached a flat ultrasound probe to the leg which is not cumbersome to participants during walking. As a result, higher speeds could be collected and a greater MG MTC length change was found (~7 mm).

Estimates of tendon strain in other animals such as horses have also yielded high estimates of tendon strain ranging from 5% to 9% during high speed locomotion (Dimery et al., 1986; Biewener, 1998). More direct measures of Achilles tendon strain which do not rely on this model also agree that during isometric contractions,

the Achilles tendon alone (without aponeurosis) can stretch by up to 15 mm (6% assuming an Achilles tendon length of 250 mm) (Maganaris and Paul, 2002). It has also been suggested that the aponeurosis strains significantly during gastrocnemius contraction (Muramatsu et al., 2002a, b) and this must be considered along with the Achilles tendon. Therefore, it is possible that the accepted estimates of SEE compliance based on *ex vivo* material testing of this tendon need to be revised.

We have also found that during running the SEE is loaded at the end of the swing phase so that the tendon is strained during initial foot contact. This corresponds with EMG data during running, which suggests that there is coactivation of the *tibialis anterior* and the gastrocnemius at the end of the swing phase, which is likely to load the SEE in preparation for foot contact (Modica and Kram, 2005). Invasive measures of tendon force during running in humans (Komi, 1990) and turkeys (Roberts et al., 1997) also support our findings.

Applying ultrasound-imaging techniques to measure muscle function during dynamic activities like running, where the probe is securely attached to body, has provided insight into how muscles function *in vivo*. However, in the current setup we were limited to a frame rate of 25 Hz. This is a relatively slow rate of data collection and limits the analysis of our results to averaging over numerous strides of data, and therefore subtle changes between strides cannot be measured. Future advances in ultrasound technology may enhance our knowledge in this field further.

In summary, the results of this study suggest that the GM muscle fascicles act similarly along the length of the muscle during locomotion, although significant differences in both length and pennation angle do occur (particularly under low force conditions such as walking). There are differences in the length change trajectories of both the muscle fascicles and also the whole muscle tendon unit when comparing between gaits, and these differences allow the SEE to stretch so that a greater force can be produced during running (equivalent to greater stretch). The compliance of the SEE allows the muscle fascicles to shorten at a much slower speed, which is more optimal for maximal power output and efficiency. SEE recoil also makes the high velocity shortening during take off in both walking and running possible. High strains that may be thought dangerous for elastic tissues such as tendon were estimated in this study, therefore further investigation into the nature of the stretch of the SEE and where this occurs is required.

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## References

- Biewener, A.A., 1998. Muscle–tendon stresses and elastic energy storage during locomotion in the horse. *Comparative Biochemistry and Physiology B-Biochemistry & Molecular Biology* 120, 73–87.
- Dimery, N.J., Alexander, R.M., Ker, R.F., 1986. Elastic extensions of leg tendons in the locomotion of horses (*Equus Caballus*). *Journal of Zoology London* 210, 415–425.
- Epstein, M., Herzog, W., 1998. *Theoretical Models of Skeletal Muscle*. Wiley, Chichester.
- Fukunaga, T., Kubo, K., Kawakami, Y., Fukashiro, S., Kanehisa, H., Maganaris, C.N., 2001. In vivo behaviour of human muscle tendon during walking. *Proceedings of the Royal Society of London B Biological Sciences* 268, 229–233.
- Fukunaga, T., Kawakami, Y., Kubo, K., Kanehisa, H., 2002. Muscle and tendon interaction during human movements. *Exercise and Sport Sciences Reviews* 30, 106–110.
- Gans, C., Gaunt, A.S., 1991. Muscle architecture in relation to function. *Journal of Biomechanics* 24 (Suppl. 1), 53–65.
- Grieve, D.W., Pheasant, S., Cavanagh, P.R., 1978. Prediction of gastrocnemius length from knee and ankle joint posture. *Proceedings of the Sixth International Congress of Biomechanics* 2A, 405–412.
- Griffiths, R.I., 1991. Shortening of muscle fibres during stretch of the active cat medial gastrocnemius muscle: the role of tendon compliance. *Journal of Physiology* 436, 219–236.
- Hof, A.L., van Zandwijk, J.P., Bobbert, M.F., 2002. Mechanics of human triceps surae muscle in walking, running and jumping. *Acta Physiologica Scandinavica* 174, 17–30.
- Kawakami, Y., Muraoka, T., Ito, S., Kanehisa, H., Fukunaga, T., 2002. In vivo muscle fibre behaviour during counter-movement exercise in humans reveals a significant role for tendon elasticity. *Journal of Physiology* 540, 635–646.
- Komi, P.V., 1990. Relevance of in vivo force measurements to human biomechanics. *Journal of Biomechanics* 23 (Suppl. 1), 23–34.
- Maas, H., Jaspers, R.T., Baan, G.C., Huijing, P.A., 2003. Myofascial force transmission between a single muscle head and adjacent tissues: length effects of head III of rat EDL. *Journal of Applied Physiology* 95, 2004–2013.
- Maganaris, C.N., Paul, J.P., 2002. Tensile properties of the in vivo human gastrocnemius tendon. *Journal of Biomechanics* 35, 1639–1646.
- Maganaris, C.N., Baltzopoulos, V., Sargeant, A.J., 1998. In vivo measurements of the triceps surae complex architecture in man: implications for muscle function. *Journal of Physiology* 512 (Pt 2), 603–614.
- Modica, J.R., Kram, R., 2005. Metabolic energy and muscular activity required for leg swing in running. *Journal of Applied Physiology* 98, 2126–2131.
- Muramatsu, T., Muraoka, T., Kawakami, Y., Fukunaga, T., 2002a. Superficial aponeurosis of human gastrocnemius is elongated during contraction: implications for modeling muscle-tendon unit. *Journal of Biomechanics* 35, 217–223.
- Muramatsu, T., Muraoka, T., Takeshita, D., Kawakami, Y., Fukunaga, T., 2002b. In vivo mechanical properties of proximal and distal aponeuroses in human tibialis anterior muscle. *Cells Tissues Organs* 170, 162–169.
- Otten, E., 1988. Concepts and models of functional architecture in skeletal muscle. *Exercise and Sport Sciences Reviews* 16, 89–137.
- Pappas, G.P., Asakawa, D.S., Delp, S.L., Zajac, F.E., Drace, J.E., 2002. Nonuniform shortening in the biceps brachii during elbow flexion. *Journal of Applied Physiology* 92, 2381–2389.
- Roberts, T.J., Scales, J.A., 2002. Mechanical power output during running accelerations in wild turkeys. *Journal of Experimental Biology* 205, 1485–1494.
- Roberts, T.J., Scales, J.A., 2004. Adjusting muscle function to demand: joint work during acceleration in wild turkeys. *Journal of Experimental Biology* 207, 4165–4174.
- Roberts, T.J., Marsh, R.L., Weyand, P.G., Taylor, C.R., 1997. Muscular force in running turkeys: the economy of minimizing work. *Science* 275, 1113–1115.
- Scott, S.H., Loeb, G.E., 1995. Mechanical properties of aponeurosis and tendon of the cat soleus muscle during whole-muscle isometric contractions. *Journal of Morphology* 224, 73–86.
- Scott, S.H., Engstrom, C.M., Loeb, G.E., 1993. Morphometry of human thigh muscles. Determination of fascicle architecture by magnetic resonance imaging. *Journal of Anatomy* 182 (Pt 2), 249–257.
- Van Leeuwen, J.L., 1999. A mechanical analysis of myomere shape in fish. *Journal of Experimental Biology* 202, 3405–3414.
- Van Leeuwen, J.L., Spoor, C.W., 1992. Modelling mechanically stable muscle architectures. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 336, 275–292.
- Van Leeuwen, J.L., Spoor, C.W., 1993. Modelling the pressure and force equilibrium in unipennate muscles with in-line tendons. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 342, 321–333.
- Wickiewicz, T.L., Roy, R.R., Powell, P.L., Edgerton, V.R., 1983. Muscle architecture of the human lower limb. *Clinical Orthopaedics and Related Research*, 275–283.
- Woittiez, R.D., Huijing, P.A., Boom, H.B., Rozendal, R.H., 1984. A three-dimensional muscle model: a quantified relation between form and function of skeletal muscles. *Journal of Morphology* 182, 95–113.
- Yucesoy, C.A., Koopman, B.H., Baan, G.C., Grootenboer, H.J., Huijing, P.A., 2003. Effects of inter- and extramuscular myofascial force transmission on adjacent synergistic muscles: assessment by experiments and finite-element modeling. *Journal of Biomechanics* 36, 1797–1811.
- Zajac, F.E., 1989. Muscle and tendon: properties, models, scaling, and application to biomechanics and motor control. *Critical Reviews in Biomedical Engineering* 17, 359–411.
- Zuurbier, C.J., Huijing, P.A., 1992. Influence of muscle geometry on shortening speed of fibre, aponeurosis and muscle. *Journal of Biomechanics* 25, 1017–1026.
- Zuurbier, C.J., Huijing, P.A., 1993. Changes in geometry of actively shortening unipennate rat gastrocnemius muscle. *Journal of Morphology* 218, 167–180.