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Title: 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 (4.5km/h) and running (7.5km/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 (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 series elastic element 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.

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; Roberts and Scales, 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; Fukunaga *et al.*, 2002).

The complex three-dimensional 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 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 length (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; Fukunaga *et al.*, 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 (Figure 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 accurately to 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 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.

Materials and Methods

Six healthy volunteers (three male, three female) average (mean, +/- SD) age, 31+/- 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 4.5km/h and 7.5km/h respectively whilst a variety of measurements were made. A two minutes warmup period was allowed to familiarise participants with the setup.

Joint Kinematics

Active CODA light emitting diodes (LEDs) were attached the following body landmarks: head of the 5th metatarsal, calcaneous, lateral malleolus, head of the fibula, lateral epicondyle of the knee, iliotibial band (halfway between knee marker and greater trochanter) and the greater trochanter. The 3D position of these LEDs was determined with an accuracy of +/- 1mm by using a CODA motion analysis system (Charwood Dynamics, UK) at rate of 100Hz. Knee and ankle angles were determined in the sagittal plane. The markers on the 5th 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).

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, multifrequency ultrasound probe at a frequency of 7 MHz and with a field of view of 60mm 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/second. The images were saved as a video file for further analysis.

The probe was taped to the *gastrocnemius medialis* (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 35mm 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).

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 5MHz

pulse on a sonomicrometry crystal (Sonometrics Ltd, Ontario, Canada) attached to the end of the ultrasound probe. This produced a white signal on the the edge of the ultrasound image and thus allowed synchronisation between the motion analysis and ultrasound data.

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 5th 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 (ten 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).

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 to ten strides (depending on how many occurred during 10 second collection time) for each subject and these were further averaged across all subjects. Length changes of the *gastrocnemius medialis* (GM) muscle-tendon unit length were estimated from the average joint angle data using the equations derived by Grieve and colleagues (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 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 Figure 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 Figure 1A). The length of 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).

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 Figure 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 is plantar flexing and the whole muscle tendon complex (MTC) is 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 4mm 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 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-T4; however, only 40% of this length change occurred during the period when the whole foot is planted on the surface (T2-T3). The highest rates of shortening occurred from T1-T2 and 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-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 35mm at foot off, which was 5mm (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 muscle tendon complex length across the gait cycle for walking and running is shown in Figure 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 is 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 Figure 4. In both gaits the SEE lengthens during the loading period (T2-T3) and reaches a peak elongation of 17.5 mm and 22 mm during walking and running respectively. Throughout the push-off phase (T3-T4) the SEE rapidly shortens in both gaits such that it is slack within 0.12 seconds. The length of the SEE is 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.

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 (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 and colleagues (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 doesn't 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 and colleagues (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 tendon elongations of 22mm during running, which equates to approximately 5.5% strain if total SEE length of 400mm (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 tendon 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 20mm of stretch (~5% strain) during dynamic counter movements and up to 10mm 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 and colleagues (2001), our data estimate up to 16mm elongation in the SEE during walking compared to 10mm 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 (~7mm).

Estimates of tendon strain in other animals such as horses have also yielded high estimates of tendon strain ranging from 5-9% 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 15mm (6% assuming an Achilles tendon length of 250mm) (Maganaris, 2002). It has also been suggested that the aponeurosis strains significantly during gastrocnemius contraction (Muramatsu *et al.*, 2002a; Muramatsu *et al.*, 2002b) 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 have been limited to a frame rate of 25Hz. 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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Figure 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 (ΔL_{mtc}) minus the change in muscle fascicle length change in the direction of the SEE ($\Delta(L_f \cdot \cos.\alpha)$) which we will call the change in contractile component length (ΔL_{cc}). This model assumes that ΔL_{cc} can be represented by a single fascicle's action ($\Delta(L_f \cdot \cos.\alpha)$). However if we consider multiple fascicles along the length of the muscle then ΔL_{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) Ultrasonound image of the *gastrocnemius medialis* 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.

Figure 2: A) 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; T5 – Heel strike.

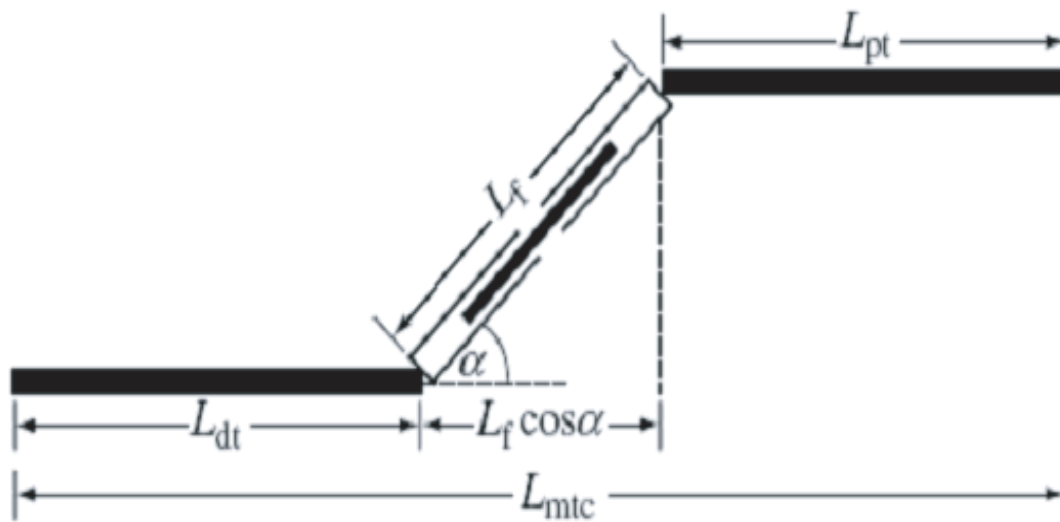
Figure 3: Average ankle and knee angles for one complete stride and the corresponding estimation of gastrocnemius muscle-tendon complex length for walking (A) and running (B). The grey shaded area represents the 95% confidence interval. The stride was divided up into the following specific events averaged from the kinematics: T1-Heel strike; T2 – Foot flat;

T3 – Heel off; T4 - Toe off; T5 – Heel strike. Ankle dorsi-flexion was defined as ankle angles above 90° , whilst knee flexion was defined as angles above 0° .

Figure 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; T5 – Heel strike. The length of zero strain (or zero length) was approximated from the length of the tendon at the toe off.

Figure 1

A.



B.

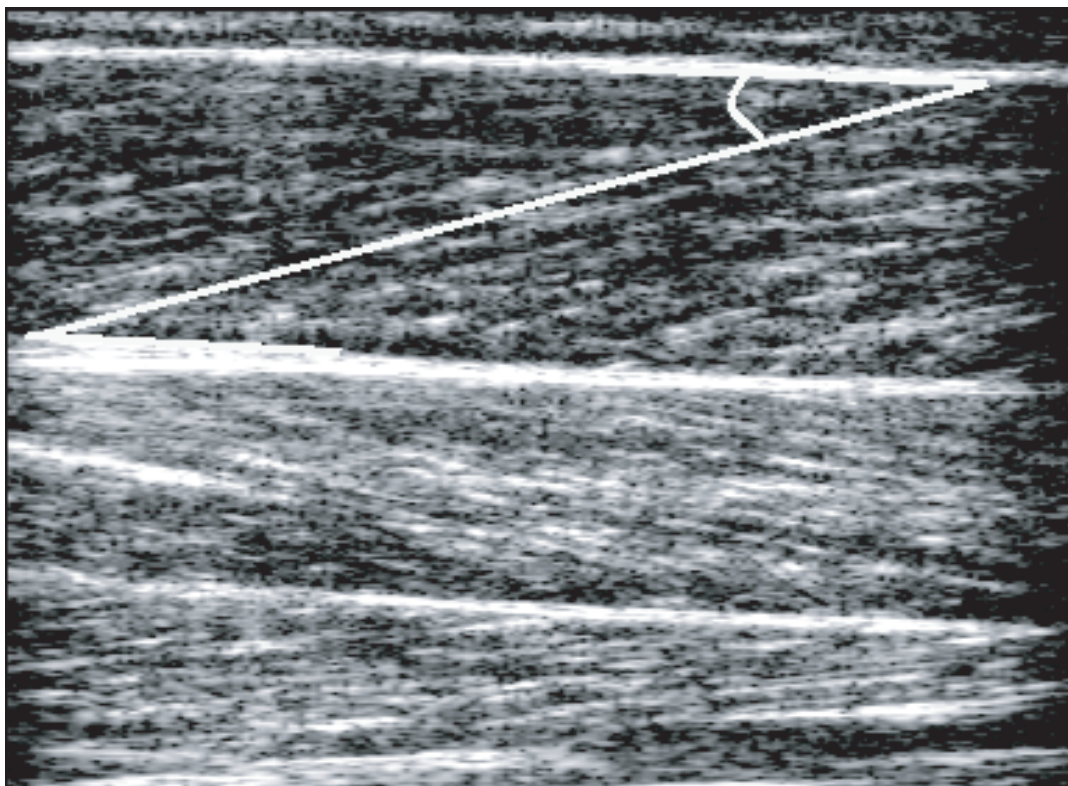


Figure 2

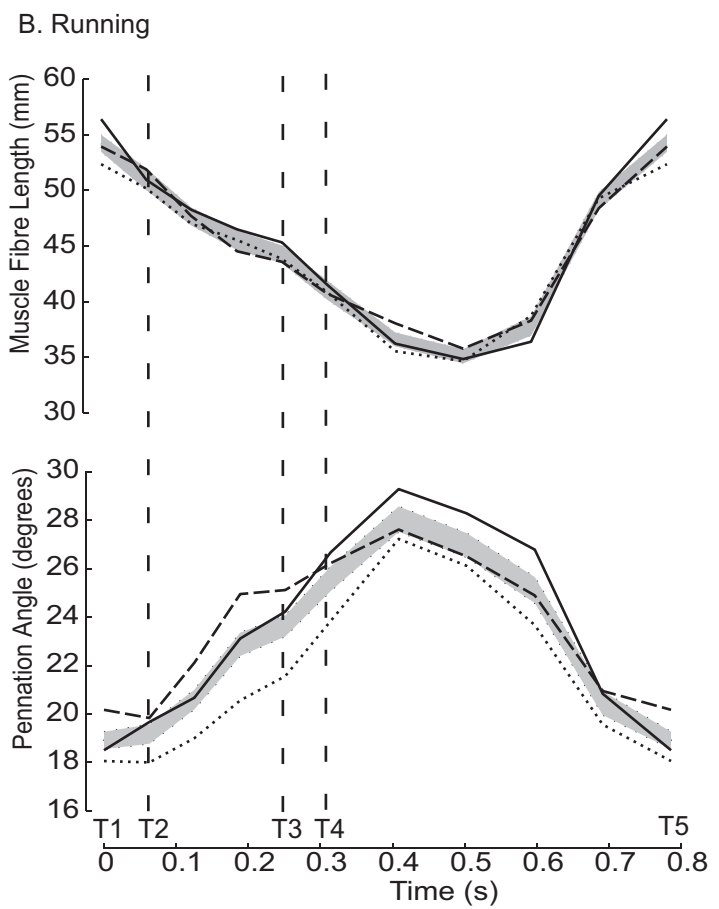
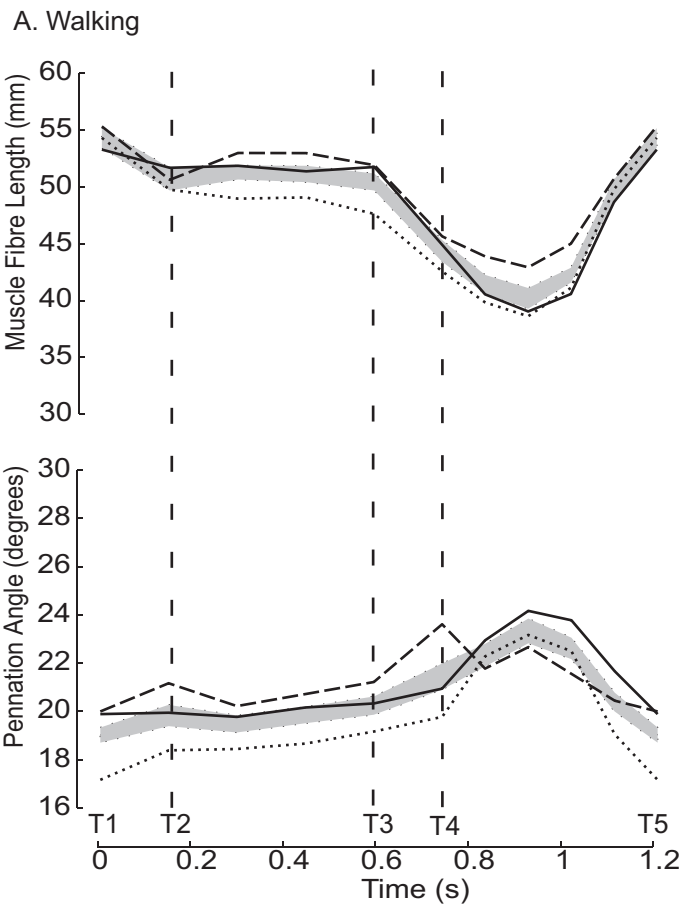


Figure 3

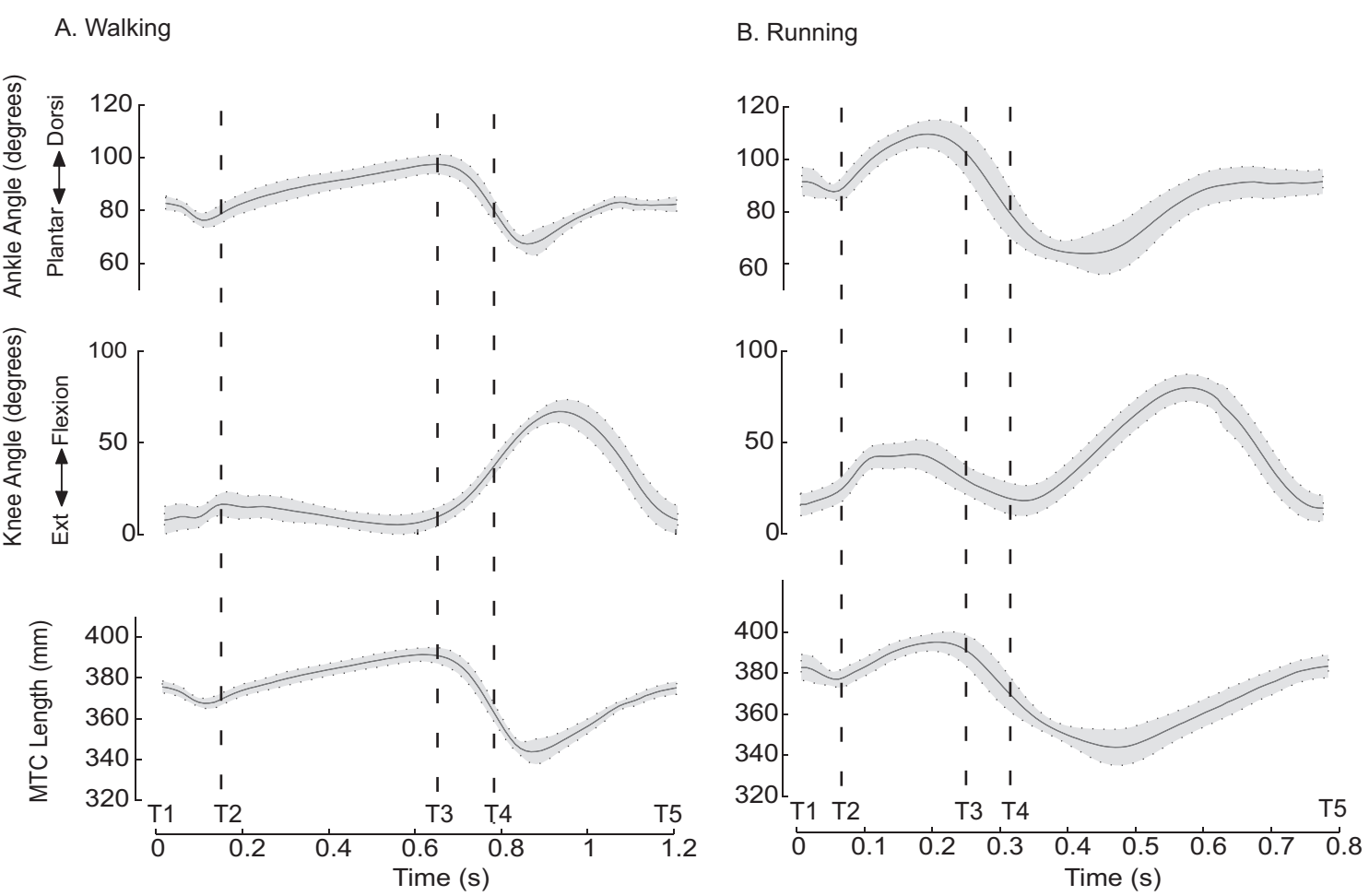


Figure 4

