

# *In vivo* behaviour of human muscle tendon during walking

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In the present study we investigated *in vivo* length changes in the fascicles and tendon of the human gastrocnemius medialis (GM) muscle during walking. The experimental protocol involved real-time ultrasound scanning of the GM muscle, recording of the electrical activity of the muscle, measurement of knee- and ankle-joint rotations, and measurement of ground reaction forces in six men during walking at 3 km h<sup>-1</sup> on a treadmill. Fascicular lengths were measured from the sonographs recorded. Musculotendon complex length changes were estimated from anatomical and joint kinematic data. Tendon length changes were obtained combining the musculotendon complex and fascicular length-change data. The fascicles followed a different length-change pattern from those of the musculotendon complex and tendon throughout the step cycle. Two important features emerged: (i) the muscle contracted near-isometrically in the stance phase, with the fascicles operating at *ca.* 50 mm; and (ii) the tendon stretched by *ca.* 7 mm during single support, and recoiled in push-off. The behaviour of the muscle in our experiment indicates consumption of minimal metabolic energy for eliciting the contractile forces required to support and displace the body. On the other hand, the spring-like behaviour of the tendon indicates storage and release of elastic-strain energy. Either of the two mechanisms would favour locomotor economy.

**Keywords:** elasticity; mechanical properties; muscle architecture; locomotion; energy

## 1. INTRODUCTION

In terrestrial locomotion, muscles in the legs and feet of bipeds and quadrupeds contract while the limb is on the ground to support body weight and displace the body ahead. Accurate information of these muscles' lengths and their changes is of crucial importance for gaining insight into mechanical and energetic aspects of locomotion (for a review, see Taylor & Heglund 1982; Alexander 1988).

To obtain information on locomotor muscle length changes, joint kinematic and anatomical data have traditionally been used (e.g. Alexander & Vernon 1975; Grieve *et al.* 1978; Prilutsky *et al.* 1996). This approach, however, provides length changes in the whole musculotendon complex, and thus it does not allow examination of interaction mechanisms between the contractile component and the tendon. Recordings of tendon-force changes from implanted force transducers can show whether and when a tendon lengthens or shortens during locomotion (Komi 1990; Prilutsky *et al.* 1996; Roberts *et al.* 1997; Carrier *et al.* 1998), but this does not provide any information on the muscle contractile component behaviour. Assuming that the contractile component follows a similar length change to the tendon or the whole musculotendon complex could lead to invalid conclusions (Hoffer *et al.* 1989; Griffiths 1991; Maganaris *et al.* 1998). Thus, direct muscle fibre length measurements during locomotion are needed.

Sonomicrometry has made this possible (Griffiths 1987; Caputi *et al.* 1992). Unfortunately, however, this technique is highly invasive and thus applicable to animals only

(Hoffer *et al.* 1989; Griffiths 1991; Roberts *et al.* 1997; Carrier *et al.* 1998). Hence, the mechanical behaviour of fibres and interaction mechanisms between fibres and tendons in intact human muscles during locomotion have, so far, remained obscure.

This unknown aspect is investigated in the present study using real-time ultrasonography, a scanning method that allows reliable and non-invasive measurements of intact human fascicular kinematics (Kawakami *et al.* 1993; Narici *et al.* 1996; Maganaris *et al.* 1998). Here we present data of *in vivo* mechanical behaviour in the fascicles and tendon of the ankle plantarflexor gastrocnemius medialis (GM) muscle in walking men.

## 2. METHODS

Six healthy male volunteers (average (mean  $\pm$  s.d.) age, 25  $\pm$  3 yr; height, 169  $\pm$  3 cm; body mass, 69  $\pm$  8 kg; lower leg length, 38  $\pm$  2 cm) gave their consent to participate as subjects. The study was approved by the local ethics committee. Measurements of (i) muscle architecture, (ii) electromyographical (EMG) activity, (iii) joint kinematics and (iv) ground reaction forces, were taken during barefoot walking at 3 km h<sup>-1</sup> at a self-selected frequency on a motor-driven treadmill (ADAL, Lyon, France). The relatively slow walking velocity studied enabled us to acquire a sufficient amount of data per step cycle. Ground reaction forces of both limbs were measured to identify the several phases of a step cycle. All the other measurements refer to the right limb.

### (a) Muscle architecture

The GM muscle was scanned *in vivo* using real-time ultrasonography. Details of the methodology followed have been described elsewhere (Kawakami *et al.* 1998; Maganaris *et al.* 1998). A 7.5 MHz B-mode ultrasound probe (SSD-2000; Aloka, Tokyo,

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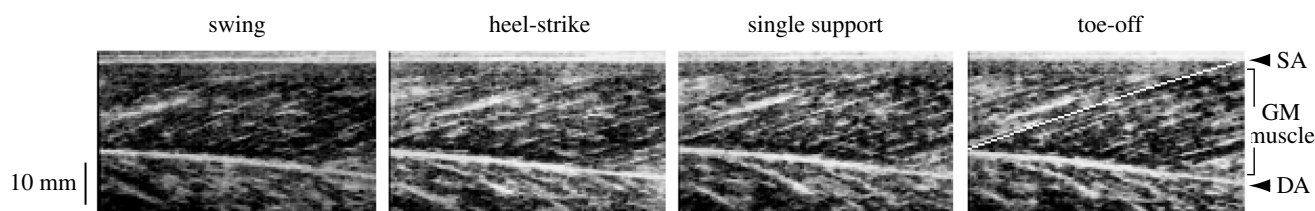


Figure 1. GM muscle sonographs in the beginning of swing, at heel-strike, in the middle of single support, and at toe-off. In the image at toe-off, the white line shows the course of a fascicle between the superficial aponeurosis (SA) and the deep aponeurosis (DA) of the GM muscle. The thin oblique white stripes parallel to the fascicle shown are inter-fascicular tissue echoes.

Japan; width and depth resolutions: 1 and 0.62 mm, respectively) was secured with adhesive on the skin in the central region along the longitudinal axis of the muscle. In this region, fascicular architecture is representative of that in several portions along and across the GM muscle belly (Narici *et al.* 1996; Kawakami *et al.* 1998; Maganaris *et al.* 1998). Images were recorded online at 30 Hz with the probe aligned in the plane of the fascicles. Typical muscle sonographs in several phases of a step cycle are shown in figure 1. The lengths of five fascicles along each image were digitized taking into account curvature effects between fascicular origin and insertion. Pennation angle measurements were taken at the insertions of these fascicles in the deep aponeurosis of the muscle. Average values of fascicular length and pennation angle in each image were used for further analysis.

### (b) EMG activity

The electrical activity of the GM muscle was recorded using bipolar Ag–AgCl surface electrodes of 5 mm diameter with a centre-to-centre distance of 25 mm. The recording electrodes were placed along the longitudinal axis of the muscle, below the scanning probe. The ground electrode was placed over the medial malleoli. The EMG signals were recorded by amplifiers with a gain of 1000 and a frequency band of 20–500 Hz. The analogue signals were sampled at 1000 Hz and converted to digital form.

### (c) Joint kinematics

Ankle- and knee-joint rotations were recorded by two electrogoniometers (Biometrics Ltd, Gwent, UK) attached over the lateral malleoli and popliteal crease, respectively. The analogue joint-rotation data were sampled at 1000 Hz and converted to digital form.

### (d) Kinetics

Ground reaction forces were recorded by two Kistler force-plates set under the treadmill. Analogue data were collected at 1000 Hz and converted to digital form.

### (e) Musculotendon and tendon length changes

Length changes in the GM musculotendon complex (muscle + free tendon and aponeurosis in both distal and proximal ends) in the whole step cycle were obtained from the joint displacement and lower-leg-length data using the equations reported by Grieve *et al.* (1978). To estimate changes in the GM tendon (free tendon and aponeurosis in both distal and proximal ends) length, the fascicular length change in every two consecutive scans during the whole step cycle was subtracted from the respective length-change estimate in the musculotendon complex, after accounting for the pennation angles measured (figure 2).

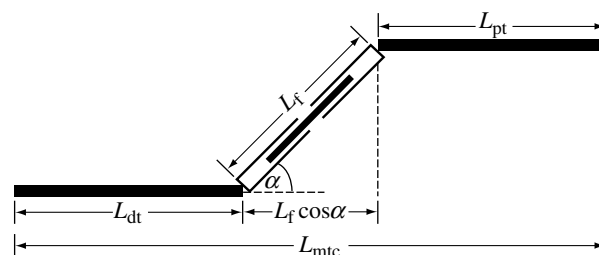


Figure 2. The musculotendon model used to estimate tendon length changes.  $L_f$  is the fascicular length,  $\alpha$  is the pennation angle,  $L_{pt}$  is the proximal tendon (free tendon and aponeurosis) length,  $L_{dt}$  is the distal tendon (free tendon and aponeurosis) length, and  $L_{mtc}$  is the musculotendon complex length. The entire tendon length ( $L_{pt} + L_{dt}$ ) equals  $L_{mtc} - L_f \cos \alpha$ . Data with a time-interval of *ca.* 33.3 ms (i.e. the time-interval corresponding to the ultrasound sampling frequency used) were used to obtain fascicular architecture, musculotendon complex and tendon length changes in the whole step cycle.

Data were recorded during three step cycles after familiarization for some minutes with the studied speed on the treadmill. Average data (means  $\pm$  s.d.) are presented.

## 3. RESULTS

Fascicular length followed a different change pattern from those of the musculotendon complex and tendon over the whole step cycle.

### (a) Fascicular length measurements

At toe-off the fascicular length was  $43 \pm 3$  mm. During swing the fascicles lengthened passively relative to toe-off, reaching at heel-strike a length of  $51 \pm 3$  mm. In the double and single support phases of stance the muscle was active and the fascicles maintained a length in the range from  $49 \pm 3$  to  $52 \pm 3$  mm. In push-off the fascicles shortened passively relative to heel-strike until reaching toe-off length levels.

### (b) Musculotendon complex and tendon length estimates

In the swing phase the musculotendon complex and the tendon lengthened by  $14 \pm 6$  mm and  $9 \pm 4$  mm, respectively, relative to toe-off. In the beginning of double support the musculotendon complex and tendon lengths decreased by  $6 \pm 2$  mm and  $8 \pm 2$  mm, respectively, relative to heel-strike. In the remaining part of double support the lengths at heel-strike were resumed. During

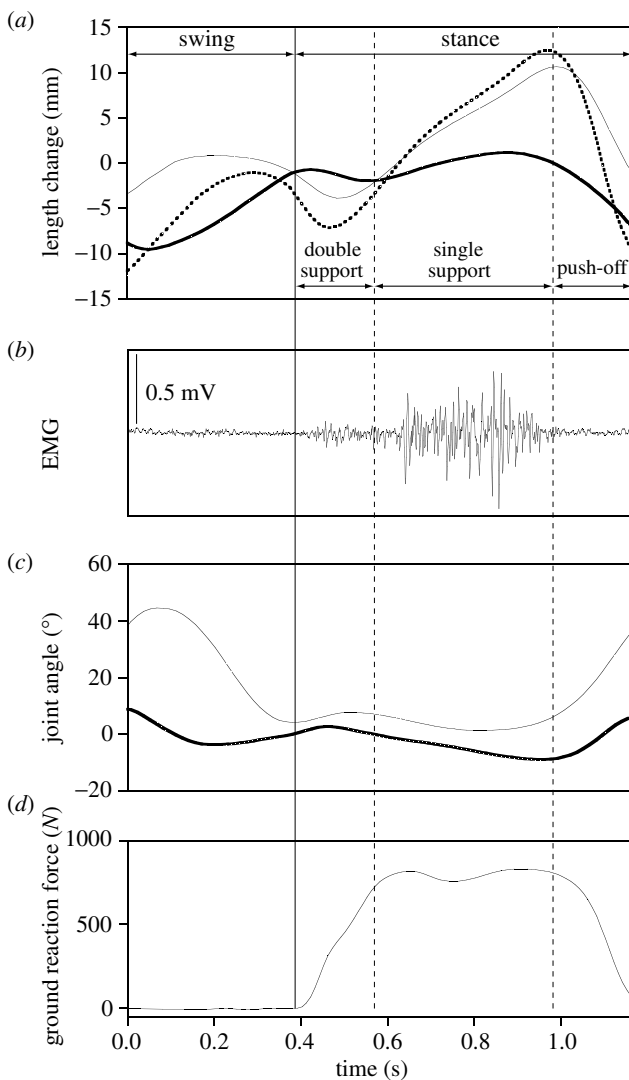


Figure 3. (a) Typical changes in GM fascicular length (thick line), musculotendon complex length (dashed line) and tendon length (thin line) from one subject in one step cycle. Raw data were fitted using a Stineman function. Positive and negative values indicate elongation and shortening, respectively. All values are given relative to heel-strike. (b) EMG recordings from the GM muscle in the same subject and step cycle. (c) Ankle-joint (thick line) and knee-joint (thin line) angles in the same subject and step cycle. (d) Vertical component of ground reaction force in the same subject and step cycle. The zero-degree joint position corresponds to the anatomically neutral ankle- and full knee-extension positions. For the ankle-joint, plantarflexion and dorsiflexion positions are indicated by positive and negative values, respectively.

single support the musculotendon complex and tendon lengths increased. Peak elongation values of  $8 \pm 3$  mm in the musculotendon complex and  $7 \pm 3$  mm in the tendon were reached at the end of single support. In push-off the musculotendon complex and the tendon shortened rapidly until reaching toe-off length levels (figure 3).

For each subject, the largest length-change differences across the three steps examined at any given phase of the step cycle were in the range 5–9%. A short cine-loop (electronic Appendix A) showing the *in vivo* behaviour of GM muscle during walking is available on The Royal Society Web site.

#### 4. DISCUSSION

Two important findings have emerged from our *in vivo* experiments. First, we showed that the GM muscle fascicles follow a different displacement pattern compared with the musculotendon complex and the tendon over the whole step cycle. Thus, erroneous conclusions with respect to the kinematics and energetics of the muscle contractile component during walking would have been obtained assuming that musculotendon, tendon, and fascicular length-change patterns coincide. This finding is consistent with results from *in vivo* animal experiments (Hoffer *et al.* 1989; Griffiths 1991). Second, and more importantly, we showed that (i) the fascicles maintain a near-constant length when the muscle is active and (ii) the tendon of the muscle stretches during a major part of stance and recoils in push-off. Each of these two mechanisms favours locomotor economy.

The near-isometric behaviour of the muscle allows no substantial mechanical work to be done by the contractile component. However, it allows the contractile component to operate around the highest force region of the force–velocity curve, thus supporting body weight economically (Hill 1938). This energy-saving effect would be maximized if the contractile component operated over the plateau region of its force–length curve. Dividing our shorter and larger fascicular length values of active muscle by an average number of  $1.77 \times 10^4$  in-series sarcomeres (Huijing 1985; Herzog *et al.* 1990), we estimated that the GM sarcomere working range in the step cycle would be from 2.75 to 2.92  $\mu$ m. These values are very close to the theoretical optimal length region of 2.64 to 2.81  $\mu$ m in human sarcomere (Walker & Schrodt 1973), indicating that tension development in the GM muscle during walking is associated with minimal energy cost.

Similar estimations to our *in vivo* results have been obtained from modelling studies of human walking (Hof *et al.* 1983). Results from *in vivo* experiments in animals, however, stand in opposition to our findings. Using sonomicrometry it has been shown that the cat GM muscle shortens in the stance phase of walking, thus generating mechanical work (Hoffer *et al.* 1989; Griffiths 1991). The reasons for this discrepancy between human and cat muscles during walking are not clear. Methodological differences in the studies and differences in the speeds examined could partly account for the lack of consensus between results. The possibilities, however, that differences in the results obtained reflect a species specificity (e.g. differences between cursorial and non-cursorial postures of the limbs), or a functional difference between bipedal and quadrupedal gaits should not be ruled out.

Our data indicate that the GM tendon acts as a spring in the transition from the beginning of single support to toe-off. The tendon high rebound resilience and the weak dependence of this parameter on loading frequency (Bennett *et al.* 1986) indicate that the tendon stretch and recoil in the stance period of walking yields elastic strain energy. Part of the strain energy released by the GM tendon upon recoil would be ‘dissipated’ to stretch the GM muscle during push-off. The rest of the tendon strain energy, however, would be used to plantarflex the ankle-joint and displace the body ahead. Storage and recovery

of elastic strain energy in tendinous structures is a mechanism of metabolic energy saving operating in bouncing locomotor paradigms, e.g. running and hopping (Cavagna *et al.* 1964, 1977; Alexander 1988; Minetti 1998). Our results, however, show that passive elastic mechanisms may operate in walking too. Other authors have reached similar conclusions using different *in situ* and *in vivo* methodologies (Elek *et al.* 1990; Griffiths 1991; Prilutsky *et al.* 1996).

Energy saving in walking is accomplished via a pendulum-like interchange between potential and kinetic energies within the stance phase of each step cycle (Cavagna *et al.* 1963, 1977; Cavagna & Margaria 1966). The amount of energy conserved depends on the interaction between the two energy-saving mechanisms described above. Consider that muscle length changes actively in stance. If the muscle is forcibly lengthened instead of maintaining a near-constant length around optimal values as shown here, less fibres will be recruited (or lower discharge frequencies will be attained (Henneman *et al.* 1965)) to support body weight (Katz 1939). This will decrease energy expenditure. However, for a given musculotendon complex length, tendon elongation during single support will be smaller under muscle lengthening conditions compared with isometric conditions. A smaller tendon stretch will result in less elastic energy recovered by passive recoil of the tendon in push-off. To make up for this loss, additional metabolic energy will be consumed. Conversely, if the muscle shortens in stance instead of contracting isometrically, the tendon will stretch more. This will yield a more effective operation of the elastic stretch-recoil mechanism of energy saving. As opposed to isometric contractions, however, concentric contractions are associated with shortening heat losses (Hill 1938), and thus additional metabolic energy will be required to bear body weight. This trade-off between elastic strain energy provision and metabolic cost of muscle contraction suggests that eliciting isometric tension at optimal muscle lengths may be an optimal mechanism for maximizing the overall energetic benefit in walking. Our data indicate that the human GM muscle deviates minimally only from this condition. It is challenging to investigate whether this is also the case in other locomotor muscles.

In conclusion, our data show that the *in vivo* human GM muscle maintains a near-constant length while active during walking, thus generating minimal power with minimal energetic cost. The tendon of this muscle, however, executes a stretch-recoil cycle in each step cycle. This would generate elastic strain energy that could further increase the economy of walking.

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