Journal of Physiology (2002), **539.2**, *pp.* 637–645
DOI: 10.1013/jphysiol.2001.012756
www.jphysiol.org

Change in length of relaxed muscle fascicles and tendons with knee and ankle movement in humans

R. D. Herbert, A. M. Moseley, J. E. Butler and S. C. Gandevia

Prince of Wales Medical Research Institute, University of New South Wales, Randwick 2031, Sydney, Australia

Ultrasonography was used to measure changes in length of muscle fascicles in relaxed human tibialis anterior and gastrocnemius during passively imposed changes in joint angle. Changes in the length of muscle fascicles were compared to changes in the length of the whole muscle–tendon units calculated from joint angles and anthropometric data. Relaxed muscle fascicles underwent much smaller changes in length than their muscle–tendon units. On average, muscle fascicles in tibialis anterior 'saw' 55 ± 13 % (mean ± s.d.) of the total change in muscle–tendon length. This indicates nearly half of the total change in muscle–tendon length was taken up by stretch of tendon. In gastrocnemius, which has relatively long tendons, only 27 ± 9 % of the total change in muscle–tendon length was transmitted to muscle fascicles. Thus, the tendency for passive movement to be taken up by the tendon was greater for gastrocnemius than tibialis anterior ($P = 0.002$). For these muscles, the relatively large changes in tendon length across much of the physiological range of muscle–tendon lengths could not wholly be explained by tendon slackness, changes in fibre pennation, or stretch or contraction history of the muscle. Our data confirm that when joints are moved passively, length changes 'seen' by muscle fascicles can be much less than changes in the distance between muscle origin and insertion. This occurs because tendons undergo significant changes in length, even at very low forces.

(Resubmitted 21 May 2001; accepted after revision 27 November 2001)

Corresponding author S. C. Gandevia: Prince of Wales Medical Research Institute, Barker St, Randwick NSW 2031, Australia. Email: s.gandevia@unsw.edu.au

Both animal studies and studies of humans *in vivo* have shown that tendons can undergo functionally important changes in length at high forces (Morgan *et al.* 1978; Walmsley & Proske, 1981; Rack & Westbury, 1984; Griffiths, 1991; Fukashiro *et al.* 1995). As a consequence, muscle fascicles need not experience the same changes in length as their muscle–tendon units (i.e. whole muscle length) during the performance of motor tasks. To the extent that this occurs, muscle spindles do not behave as linear transducers of muscle–tendon length or joint motion (Griffiths, 1991; but see Elek *et al.* 1990). Changes in tendon length may also influence stretch reflex latencies (Fellows & Thilmann, 1989) and the capacity of muscle fibres to produce active force (Hof *et al.* 1983), and they allow for the storage of elastic energy in tendons (e.g. Alexander & Bennet-Clark, 1977; Morgan *et al.* 1978).

Relatively few studies have directly measured the elongation of tendons at the low levels of tension typically experienced by relaxed muscles. Stolov & Weillep (1966) measured elongation of the muscle belly and of the extramuscular part of the tendon as the relaxed rat gastrocnemius muscle was extended over a physiological range of lengths. They reported that the tendon lengthened only slightly and that most of the increase in length occurred in the muscle belly. However, the tendon of the rat gastrocnemius extends into the belly of the muscle (e.g. Woittiez *et al.* 1984), so this does not rule out the possibility that the intramuscular tendon increased in length. In a more recent study, resting rabbit soleus muscles were passively extended through a physiological range of lengths, and the lengths of muscle fascicles and tendons (both the extramuscular and intramuscular parts) were measured with markers placed on the ends of muscle fascicles (Herbert & Crosbie, 1997). Muscle fascicles experienced strains that were about four times greater than strains in tendons but, because the tendon was nearly four times longer than the muscle fascicles, muscle fascicles 'saw' only about half of the total change in length imposed on the muscle–tendon unit. That is, in the rabbit soleus, changes in tendon length accounted for nearly half of the total change in muscle–tendon length.

Refshauge and colleagues (1998) were able to measure how movements at the human ankle and toe were transmitted to the bellies of the relaxed tibialis anterior and extensor hallicis longus muscles. By surgical exposure of the tendons in one subject they showed that, when the ankle was in a dorsiflexed position, movement at the ankle joint produced little change in the length of the muscle bellies. This suggests that the extramuscular part of the tendons is either slack or very compliant when the ankle is passively dorsiflexed. When, however, the ankle was plantarflexed, there was faithful transmission of joint movement to the muscle belly, suggesting that when this muscle is relaxed and held at relatively stretched lengths the extramuscular part of the tendons is not slack and does not undergo significant elongation. It was not possible in that study to determine how much movement was taken up by the long intramuscular tendons, or how much change in length of the muscle belly was transmitted to muscle fascicles.

Changes in the length and pennation of human muscle fascicles can be measured directly, reliably and non-invasively with ultrasonography (e.g. Rutherford & Jones, 1992; Herbert & Gandevia, 1995; Narici *et al.* 1996; Kawakami *et al.* 1998; Ito *et al.* 1998; Maganaris *et al.* 1998). In the present study, ultrasonography was used to examine length changes in muscle fascicles of two relaxed, human, lower limb muscles with changes in joint angle. The two muscles differed in the relative lengths of their tendons. The aim was to determine, in a passive muscle, how much of the total increase in muscle–tendon length is transmitted to the muscle fascicles and how much is taken up by elongation of the tendons. Ultrasonography was used to determine change in length of muscle fascicle and, by inference, change in length of the whole tendon; that is, both its extramuscular and intramuscular parts.

METHODS

Five experiments were performed on 11 medial gastrocnemius and 15 tibialis anterior muscles in 24 healthy volunteers (12 women and 12 men) aged between 24 and 44 years. An overview of the muscles and number of subjects for each experiment is given in Table 1. The procedures conformed with the Declaration of Helsinki and were approved by the University of New South Wales ethics review committee.

Expt 1. Change in length of medial gastrocnemius muscle fascicles and tendon

For this experiment subjects ($n = 9$) sat semi-reclined. The foot was strapped to a plate positioned at about the height of the seat. The footplate could be fixed in position with the ankle anywhere in its normal range, and the seat could slide forwards and backwards or be fixed to change the angle of the knee. Surface electrodes (diameter 1 cm) were placed longitudinally over the belly of the lateral gastrocnemius separated by a distance of approximately 4 cm (electrodes were placed over the lateral head of gastrocnemius to allow placement of the ultrasound transducer over the medial head). The EMG signal was amplified and displayed to the subject on an oscilloscope at high gain (bandpass 1 Hz to 1.0 kHz). Subjects were asked to remain completely relaxed throughout the experiment.

Muscle fibre lengths were measured with ultrasonography (e.g. Henriksson-Larsén *et al.* 1992; Fukashiro *et al.* 1995; Narici *et al.* 1996; Fukunaga *et al.* 1997; Ito *et al.* 1998; Kawakami *et al.* 1998; Maganaris *et al.* 1998; Maganaris & Baltzopoulos, 1999). An 8 cm linear-array soundhead (5 MHz) was placed over the belly of the medial gastrocnemius. The soundhead was tipped slightly medially or laterally to find the best image, which was presumed to coincide with the plane of the muscle fascicles (Herbert & Gandevia, 1995; Narici *et al.* 1996). With ultrasonography, muscle fascicles appear as dark (hypoechogenic) lines lying between light (echogenic) striations of fat or connective tissue (see Fig. 1 of Herbert & Gandevia, 1995). The fascicles could usually be followed from their attachments on the proximal tendon plate to their insertions on the distal tendon plate (see Fig. 1 of Kawakami *et al.* 1998). Muscle fascicle lengths were measured on-line by taking the straight line distance between origin and insertion of the most clearly visualised muscle fascicles in the middle of the field of view. Sometimes it was necessary to change the orientation or position of the transducer to obtain clear images as joint angles were changed, but these movements were usually slight.

Measurements were made with the gastrocnemius muscle positioned at a range of lengths between near-fully shortened (knee flexed, ankle plantarflexed) and fully stretched (knee extended, ankle dorsiflexed). Measurements of gastrocnemius fascicle lengths could not be taken with the knee fully flexed because the thigh interfered with positioning of the ultrasound head. Consequently the maximum angle of knee flexion at which measurements could be made was about 110 deg (maximum knee flexion is typically 120–130 deg). The angles subtended by the horizontal and each of the sole of the foot, the shank and the thigh were measured with a digital inclinometer placed on the base of the footplate, the anterior border of the tibia, and the anterior surface of the thigh, respectively. The ankle angle was given by the difference between the foot and shank angles, and the knee angle was the difference between leg and thigh angles.

Expt 2. Change in length of tibialis anterior muscle fascicles and tendon

A similar procedure was used to measure changes in length of tibialis anterior muscle fascicles in six subjects. The proximal edge of the ultrasound head was aligned with the proximal margin of the intramuscular tendon, which is easily observed on the ultrasound images. In the tibialis anterior, muscle fascicles course both deeply (from the superficial proximal tendon plate) and superficially (from a deep proximal tendinous origin) towards their insertions on the distal tendon plate (see Fig. 2 in Ito *et al.* 1998 or Fig. 1 in Maganaris & Baltzopoulos, 1999). Muscle fascicle lengths were measured as the straight line distance between origin and insertion of the most clearly visualised muscle fascicles in the middle of the field of view. Such measures are representative of those from fascicles in other regions of the muscle (Maganaris & Baltzopoulos, 1999). To rule out the possibility that observer bias distorted measurements of muscle fascicle length, these measurements were taken from the ultrasound image by a person who was unaware of to the position of the ankle. For all measurements, the knee was positioned between 15 and 30 deg of flexion, and the ankle angle was varied by adjusting the position of the footplate. Again, ankle and knee angles were measured with an inclinometer. To partially control for history effects (e.g. Jahnke *et al.* 1989), the tibialis anterior muscle was stretched by full passive plantarflexion of the ankle prior to every measurement. (This form of muscle conditioning is thought to produce greater slack lengths than contraction at the test angle, as described in the experiments below.) Subjects were asked to keep the tibialis anterior relaxed during the stretch and release of stretch, and during subsequent measurements. EMG was not routinely recorded in this experiment because preliminary tests indicated that very low levels of muscle activity could be detected by observation of bowing of the tendon on the dorsum of the ankle. This observation was formally confirmed in the last experiment, described below.

Expt 3. Effect of prior contraction at the test angle (part A)

Human skeletal muscles exhibit thixotropic behaviours, so that their mechanical properties are influenced by their history of stretch and contraction (e.g. Jahnke *et al.* 1989). An additional experiment was conducted to determine if the findings of the first experiment could be replicated when the gastrocnemius muscle was conditioned by prior contractions at the test angle. In three subjects, muscle fascicle lengths of medial gastrocnemius were measured in the same way as described above except that, prior to each measurement of muscle fascicle length, subjects performed moderate intensity isometric contractions of ~3 s duration at the test angle. These measurements were made by a blinded measurer.

Expt 4. Effect of prior contraction at the test angle (part B)

Three subjects participated in a further experiment to determine the effects of prior conditioning contractions at the test angle. In this experiment, on the tibialis anterior, the muscle was always stretched by full passive plantarflexion prior to each measurement but, in randomly selected trials, the subject subsequently performed a moderate intensity isometric contraction of ~3 s duration at the test angle immediately prior to measurement. Again, measurements were made by a blinded measurer.

Expt 5. Effect of ongoing contraction

We tested whether the relationship between changes in tibialis anterior muscle fascicle and muscle–tendon lengths was different at rest and during contraction. Nine subjects were seated with the knee flexed 60–90 deg and the foot strapped to the footplate of a strain-gauge-based isometric dynamometer. The dynamometer permitted measurement of ankle torque with the ankle fixed at any angle. Surface electrodes (diameter 1 cm, separation ~4 cm) were placed longitudinally over the lower part of the belly of the tibialis anterior. Both EMG and ankle torque were displayed to the subject on an oscilloscope. Prior to each measurement, the muscle was taken to its fully stretched position and returned to the test position. Measurements of muscle fascicle length were taken from the tibialis anterior muscle with the subject either completely relaxed, or during contractions to either 5 or 100 % of the maximal isometric torque the subject could produce with the ankle dorsiflexed to 90 deg. In the relaxed condition, the subject was instructed to minimise the amplitude of the electromyogram, and in the 5 % maximum voluntary force (MVC) condition the subject was instructed to increment the torque signal displayed on the oscilloscope to the target intensity. (However, as the contribution of passive synergist muscles and the effects of the force–angle relation were not controlled, the tension in tibialis anterior was not constant across joint angles.) The order of ankle angles and of the three conditions was randomised. Again, the person who measured muscle fascicle lengths was unaware of contraction intensity and joint angle. As the ultrasound image looks different during a maximal voluntary contraction (e.g. the striations become more prominent; Herbert & Gandevia, 1995), effective blinding to contraction intensity was not assured in maximal contractions. However, the measurer did not know the joint angle for any trial or whether the subject was relaxed or contracting to 5 % of MVC for any measurements.

Analysis

The relative compliance of muscle fascicles and tendon was determined by comparing measured changes in muscle fascicle length with changes in muscle–tendon length. Changes in muscle–tendon length were obtained from measured changes in joint angle using published anthropometric data derived from 27 cadaveric legs (Grieve *et al.* 1978; Spoor *et al.* 1990; Visser *et al.* 1990; Spoor & van Leeuwen, 1992; Klein *et al.* 1996). The data pooled from five studies are presented in Fig. 1. The figure was constructed from the regression equations provided by Grieve *et al.* (1978) and Visser *et al.* (1990), and by polynomial regression of digitised data from the graphs of Spoor *et al.* (1990) and Spoor and van Leeuwen (1992). Klein *et al.* (1996) provided regression equations for moment arms, rather than change in muscle–tendon length, so their equations were integrated with respect to joint angle to give change in length. To correct for differences in leg lengths, data for tibialis anterior from Grieve *et al.* (1978), Spoor *et al.* (1990), Spoor and van Leeuwen (1992) and Visser *et al.* (1990) were linearly scaled to a leg length of 36 cm (the distance between

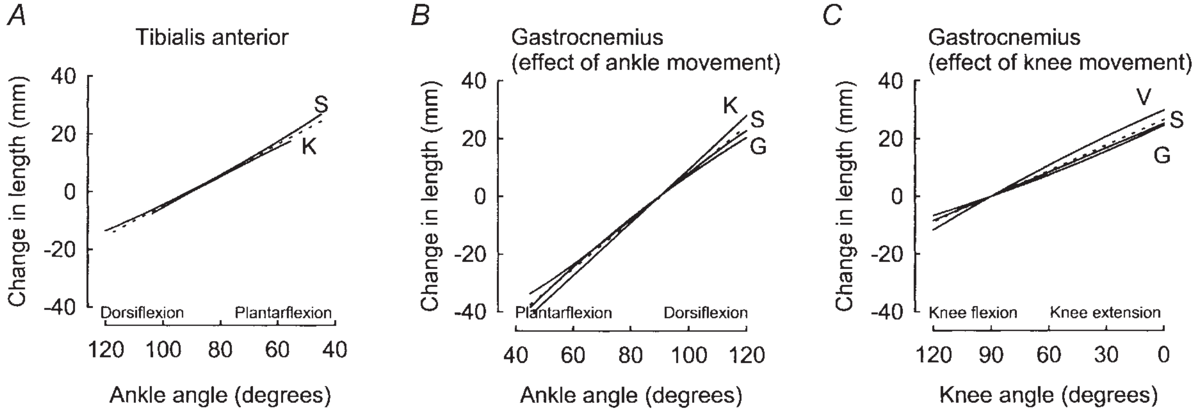

Figure 1. Relationship between change in length of muscle–tendon units and joint angle

Data on changes in length of whole muscle–tendon units were obtained from measurements in cadavers. *A,* change in tibialis anterior length with ankle angle. *B,* change in gastrocnemius length with ankle angle. *C,* change in gastrocnemius length with knee angle. Continuous lines are polynomial regressions through the data from Spoor *et al.* (1990) (S in *A* and *B*); Spoor & van Leeuwen (1992) (S in *C*); Klein *et al.* (1996) (K); Grieve *et al.* (1978) (G); and Visser *et al.* (1990) (V). Dotted lines are best fit linear regressions to all data. The absolute values of the slopes of the three linear regressions are 0.53 mm deg^{-1} (tibialis anterior), 0.83 mm deg^{-1} (gastrocnemius at ankle) and 0.29 mm deg^{-1} (gastrocnemius at knee). See text for details.

Table 1. Summary of experiments

	Muscle	*n*	Conditioning	Slope[a] at rest
1.	Medial gastrocnemius	9	None	0.27
2.	Tibialis anterior	6	Stretch	0.55
3.	Medial gastrocnemius	3	Contract at test angle	0.21
4.	Tibialis anterior	3	Stretch/stretch then contract at test angle	0.44/0.61
5.	Tibialis anterior	9	Stretch	0.44 (0.66/0.60[b])

The table shows, for each of the five experiments, the nature of the conditioning applied to the muscle before fascicle lengths were measured from the resting muscle. [a]Slopes were obtained from the linear regression of muscle fascicle length on change in muscle–tendon length (i.e. 'whole' muscle length). The slope can be interpreted as the proportion of the total change in length due to lengthening of resting muscle fascicles (see Discussion). [b]In Expt 5, measurements were taken from the resting muscle and as it contracted to 5 % and 100 % of MVC force. The numbers in brackets are slopes at 5 %MVC/100 %MVC. *n* is the number of subjects.

the axes of rotation of the ankle and knee) because the mean leg length for subjects in our studies of tibialis anterior was 36 cm. Gastrocnemius data were linearly scaled to a leg length of 39 cm, the mean leg length for subjects in our study of gastrocnemius. Klein *et al.* (1996) did not provide data on leg length, so their data were not scaled. Data from these five studies were remarkably similar, and the relationships between change in muscle–tendon length and change in joint angle was nearly linear (i.e. moment arms were nearly constant; Fig. 1), so linear regression was performed on the pooled data. For a subject with a 36 cm leg length, this gave changes in tibialis anterior muscle tendon length of 0.53 mm deg^{-1} of ankle displacement, and for the medial gastrocnemius of a subject with a 39 cm leg length, 0.83 mm deg^{-1} of ankle displacement and 0.30 mm deg^{-1} of knee displacement. Change in tendon length was determined by subtracting change in muscle fascicle length from change in muscle–tendon length. Estimates of the rest lengths of medial gastrocnemius and tibialis anterior were obtained by measurement of the distance from the presumed site of origin to the presumed site of insertion in one subject with the ankle and knee joints positioned so that the muscles were at their shortest *in vivo* lengths. These estimates of the rest lengths of medial gastrocnemius and tibialis anterior were scaled by leg length to give estimates of muscle–tendon rest lengths for other subjects.

Statistics

Linear regression was used to determine the slope of the relationship between muscle fascicle length and change in muscle–tendon length. As the slope of the regression is the ratio of changes in muscle fascicle and muscle–tendon lengths, it provides an estimate of the contribution of change in muscle fascicle length to total change in muscle–tendon length.

Linear regression provides an unbiased estimate of the slope of the linear relation between two variables when the predictor variable is measured without error. When there is random measurement error in the predictor variable, statistical regression causes the true slope to be underestimated. It is possible to correct for this bias if the reliability of the measure is known ('true' slope = estimated slope/coefficient of determination; cf. Armitage & Berry, 1994). The reliability of measured change in muscle–tendon length was estimated by comparing the measurements of two independent measurers and was found to be very high ($r^2 > 0.99$), implying that statistical regression biased the estimate of the slope of the regression between change in muscle–tendon length and fascicle length by less than 1 %.

Non-parametric tests were used to determine if there were differences in the slopes of the linear regressions of muscle fascicle length on change in muscle–tendon length between the medial gastrocnemius and tibialis anterior muscles (Mann–Whitney test) or between stretch-conditioned and stretch-and-contraction-conditioned tibialis anterior muscles (Wilcoxon's test). The non-parametric Friedman's test was used to compare the slope of linear regressions obtained in resting, 5 % MVC and MVC conditions. Additional analyses are described in the Results. A probability of less than 5 % was considered significant. Unless otherwise stated, data are given as means ± S.D.

RESULTS

Estimates of the rest lengths of muscle fascicles and tendons were obtained by assuming that rest lengths lay close to the shortest *in vivo* lengths. With this assumption, rest lengths of muscle fascicles were, on average, about one-third greater in tibialis anterior than in gastrocnemius (39 ± 8 mm in tibialis anterior; 29 ± 7 mm in medial gastrocnemius). In contrast, the tendon is about one-third shorter in tibialis anterior (230 ± 31 mm in tibialis anterior; 302 ± 28 mm in medial gastrocnemius). Thus the proportion of tendon, as measured by the ratio of rest lengths of tendon and muscle fascicles, is 77 % greater in the medial gastrocnemius (5.9 in tibialis anterior; 10.4 in medial gastrocnemius).

A summary of the five studies designed to look at muscle and tendon compliance is given in Table 1. The key finding is that much less of the passive change in whole muscle–tendon length is taken up by muscle fascicles than would occur if the tendons were inextensible. This finding holds irrespective of the 'history' of the muscle.

Expt 1. Change in length of medial gastrocnemius muscle fascicles and tendon

The relationship between muscle fascicle length and change in muscle–tendon length for the medial gastrocnemius of one subject is shown in Fig. 2*A*. The relationship is approximately linear (see below). Thus, even though the stiffness of both tendon and muscle fascicles increases with tension (Alexander & Bennet-Clark, 1977), the ratio of

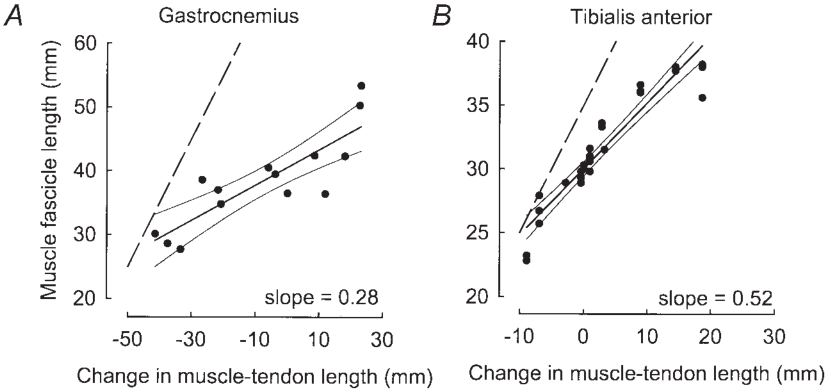

Figure 2. Relationship between muscle fascicle length and change in length of muscle–tendon units

Each panel shows data from one subject. *A*, medial gastrocnemius. *B*, tibialis anterior. Continuous lines are least-squares linear regressions and 95 % confidence intervals. The dashed lines indicate a slope of 1. (Scales differ in panels *A* and *B*, but the ratio of horizontal and vertical scales is the same.)

their stiffnesses remains nearly constant. The slope of the linear regression is less than one, indicating that muscle fascicles do not lengthen as much as the muscle–tendon unit. For this subject, the slope was 0.28, meaning that 28 % of the total change in muscle–tendon length occurred in the muscle fascicles; the remaining 72 % of the total change in muscle–tendon length is presumed to have occurred primarily in the tendon (see below). The mean slope for all nine subjects was 0.27 (S.D. = 0.09; mean $r = 0.77$; Fig. 3*A*). This indicates that in the passive muscle, just over one-quarter of the total change in muscle–tendon length was transmitted to muscle fascicles.

Expt 2. Change in length of tibialis anterior muscle fascicles and tendon

The relationship between muscle fascicle length and change in muscle–tendon length for the tibialis anterior of one subject is shown in Fig. 2*B*. For this subject, the slope of the regression was 0.52. Similar results were obtained for all six subjects. The mean slope for all subjects was 0.55 ± 0.13 (mean $r = 0.89$; Fig. 3*B*), indicating that, on average, approximately one-half of the total change in muscle–tendon length was transmitted to muscle fascicles. This slope was significantly greater than the slope for the medial gastrocnemius ($P = 0.002$).

We considered several potential sources of error in our measurements. First, tendon length was estimated by subtracting change in muscle fascicle length from change in muscle–tendon length. This ignores the pennation of muscle fascicles. At rest, pennation of tibialis anterior varies from 13 deg at short lengths to 9 deg at stretched lengths, and pennation of medial gastrocnemius varies from 45 deg at short lengths to 22 deg at stretched lengths (Kawakami *et al.* 1998; Maganaris & Baltzopoulos, 1999). Neglecting pennation produces errors in estimates of tendon length that are approximately:

$$100 \times (l_f - l_f \cos\theta)/(l_{mt} - l_f \cos\theta),$$

where l_f is fascicle length, l_{mt} is muscle–tendon length, and θ is the angle of pennation. Consequently, actual tendon length is of the order of 0.4 % (tibialis anterior, shortest length) to 2.7 % (medial gastrocnemius, shortest length) greater than estimated by subtracting fascicle length from muscle–tendon length. These errors are of little practical significance. Ignoring change in pennation, however, produces larger errors in estimates of change in length. The error is approximately

$$100 \times \frac{\Delta l_f - [l_{f,max}\cos\theta_{max} - l_{f,min}\cos\theta_{min}]}{\Delta l_{mt} - [l_{f,max}\cos\theta_{max} - l_{f,min}\cos\theta_{min}]},$$

where the subscripts ‘max’ and ‘min’ refer to the stretched and shortened lengths, respectively, and l_{mt} is muscle–tendon length. Thus change in tendon length has been overestimated (in relative terms) by approximately 2.1 % for tibialis anterior and 14.4 % for medial gastrocnemius. The slope of the relationship between muscle fascicle length (y axis) and change in muscle–tendon length (x axis) is underestimated by:

$$(l_{f,max}\cos\theta_{max} - l_{f,min}\cos\theta_{min} - \Delta l_f)/\Delta l_{mt},$$

which equates to an underestimation of slope of approximately 0.009 for tibialis anterior and 0.091 for medial gastrocnemius. This does not materially change the interpretation of the results (see Discussion).

Although a linear regression was fitted to the data, we also considered the possibility that the relationship between changes in

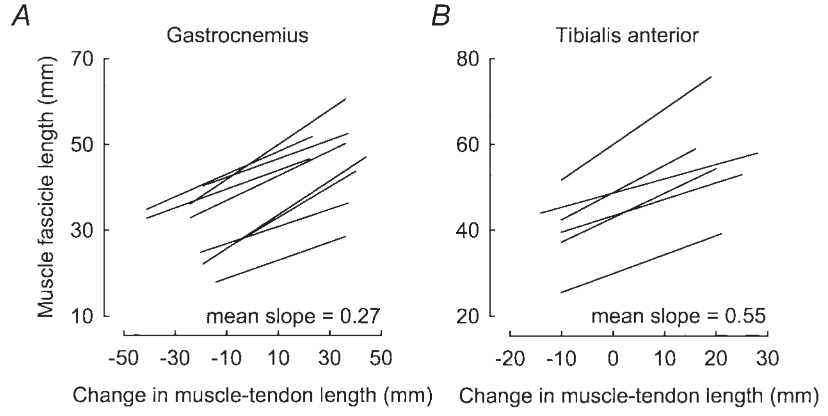

Figure 3. Linear regressions of muscle fascicle length on change in muscle–tendon length

Each line is the linear regression through all data for one subject (mean of 22 measurements per subject; see Fig. 2). The regression line for each subject has been extended from the smallest to the largest muscle–tendon length measured. *A*, medial gastrocnemius. *B*, tibialis anterior. (Note that scales and ratio of horizontal and vertical scales differ in *A* and *B*.)

muscle fascicle and muscle–tendon lengths is actually non-linear. If the relationship curved upwards this would indicate that the contribution of tendon was greatest at short lengths and became progressively smaller at longer lengths. To investigate this possibility we pooled the data from the medial gastrocnemius muscles of nine subjects and, separately, the tibialis anterior muscles of six subjects by expressing both change in muscle fascicle length and change in muscle–tendon length as a percentage of the shortest muscle–tendon length (this provided greater statistical precision in the subsequent analysis). For the medial gastrocnemius, the slope appeared to increase slightly with increasing muscle–tendon length, but for the tibialis anterior the slope appeared to decrease slightly. When the data were analysed with polynomial regression, second and third order terms increased the proportion of explained variance by less than 2 % for tibialis anterior and 5 % for medial gastrocnemius, suggesting that curved regression lines do not provide better fits to the data and that there was no flattening of the curve at short lengths.

If the tendon fell fully slack at short lengths, the relationship between muscle fascicle length and change in muscle–tendon length would have a zero slope at short lengths and a positive slope only at lengths greater than slack length. In that case, the slope we estimated with linear regression would underestimate the true slope above slack length. The failure of curvilinear regression to provide a better fit to the pooled data argues against this possibility. A further test was provided by fitting a linear regression to the data obtained at the shortest muscle lengths (initially just the shortest five measurements). The slope of this regression was not significant (this might occur either because there the slope of the regression was truly zero or because the small number of data points provided insufficient statistical precision to detect a true positive slope). Then the regression was fitted to progressively longer lengths until the slope became significant. This provided an approximate upper limit to the range of lengths over which the muscle could possibly be slack. A second linear regression was fitted to the remaining data, which must have been obtained at lengths greater than slack length. The slope of this regression was 0.37 for medial gastrocnemius (95 % confidence interval 0.28 to 0.46) and 0.44 for tibialis anterior (95 % confidence interval 0.37 to 0.51) indicating that the slope was clearly less than 1 even at lengths that must be greater than slack length, if indeed the muscles fall slack at short lengths.

Expt 3. Effect of prior contraction at the test angle (part A)

In three subjects who performed isometric contractions of the medial gastrocnemius at the test angle prior to measurement of medial gastrocnemius muscle fascicle length, the relationship between muscle fascicle length and change in muscle–tendon length was, again, approximately linear. The mean slope of the relationship was 0.21 (range 0.19 to 0.23), just a little less than the slope of 0.27 obtained when muscles were not pre-conditioned by prior contraction. Thus essentially the same findings were obtained when the muscle was pre-conditioned with a contraction at the test angle.

Expt 4. Effect of prior contraction at the test angle (part B)

A second experiment, on the tibialis anterior muscle, also investigated whether prior contraction at the test angle influenced the slope of the relationship between muscle fascicle length and change in muscle–tendon length. When the muscle was stretched prior to measurement the mean slope was 0.44 (range 0.41 to 0.47), but when the muscle was first stretched and then contracted at the test angle prior to measurement the mean slope was 0.61 (range 0.34 to 0.80). This difference was not significant ($P = 0.50$), but as the sample was small we cannot rule out the possibility that prior contraction does produce small increases in the slope of the relationship. Nonetheless, the slope is still clearly much less than 1.

Expt 5. Effect of ongoing contraction

In nine subjects, when the tibialis anterior muscle contracted (even to only 5 % MVC), the contribution of

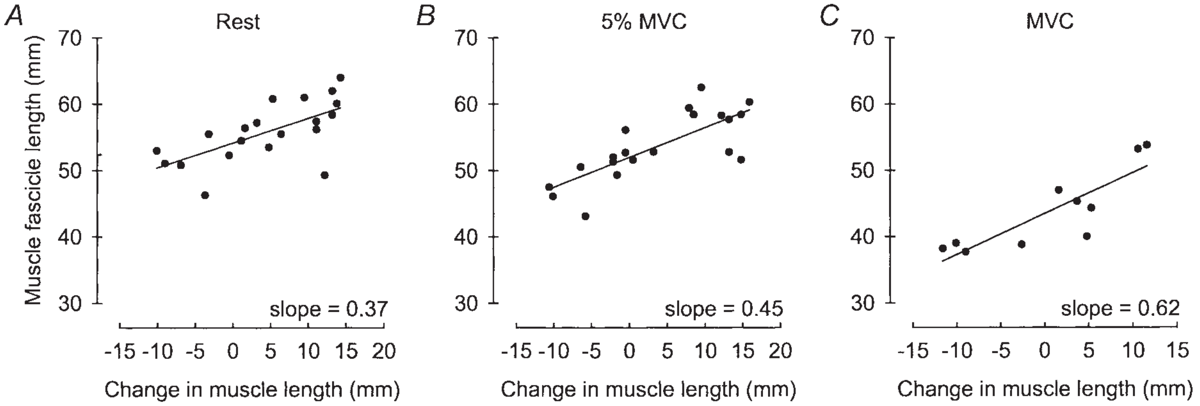

Figure 4. Effect of muscle contraction on relationship between muscle fascicle length and change in muscle–tendon length for tibialis anterior

Data from one subject. *A*, subject relaxed. *B*, subject contracting the ankle dorsiflexor muscles to 5 % of the maximal isometric torque that could be produced with the ankle dorsiflexed to 90 deg. *C*, subject contracting the ankle dorsiflexor muscles to 100 % of the maximal isometric torque that could be produced with the ankle dorsiflexed to 90 deg. The slope of the regressions is greater during contraction than at rest, indicating that muscle fascicles undergo relatively greater changes in length during contraction.

muscle fascicles to total change in length (as reflected in the slope of the regression of muscle fascicle length on change in muscle–tendon length) tended to increase (Fig. 4). The mean slope of the regression was 0.44 ± 0.19 at rest (cf. 0.55 ± 0.13 in Expt 2 above), 0.66 ± 0.26 at 5 % MVC, and 0.60 ± 0.22 with MVC (Friedman's test, $P = 0.06$).

DISCUSSION

Ultrasonographs of relaxed human tibialis anterior and medial gastrocnemius muscles were used to quantify changes in muscle fascicle length produced by movement of the ankle and knee. With passive movement, muscle fascicles underwent much smaller changes in length than whole muscle–tendon units (i.e. origin-to-insertion length). Muscle fascicles lengthened only half as much (in the tibialis anterior) or one-quarter as much (in the gastrocnemius) as their muscle–tendon units. Thus when resting muscles are stretched (e.g. by contraction of their antagonists) much of the increase in muscle–tendon length occurs in the tendon.

These findings rely on the accuracy of estimations of changes in muscle–tendon length with joint angle. This has been carefully evaluated (Methods, see Fig. 1). The five sources of data on change in muscle–tendon length with joint angle (Grieve *et al.* 1978; Spoor *et al.* 1990; Visser *et al.* 1990; Spoor & van Leeuwen, 1992; Klein *et al.* 1996) gave similar estimates of change in muscle–tendon length, and this justifies their use here. Even large errors in these estimates would not alter substantially our main finding.

There are several possible explanations for the observation that muscle fascicles appear to contribute surprisingly little to total changes in resting muscle–tendon length. First, muscles may fall slack at short lengths. Indeed some passive muscles may be slack across major parts of their physiological range, as assessed by ultrasonography in humans (e.g. Herbert & Gandevia 1995) and by recordings of the discharge of primary muscle spindle endings in cats (Burgess *et al.* 1982). Slack would produce a horizontal region in the relationship between muscle fascicle length and change in muscle–tendon length at short lengths, although it may have been obscured by scatter in our data. While we cannot rule out the possibility that there is slack at very short lengths, particularly in medial gastrocnemius, slack would not wholly explain why changes in muscle fascicle length are less than changes in muscle–tendon length. Even if we assume the largest possible slack length that could be consistent with our data, the slope of the relationship at longer lengths is still less than 0.45 for both muscles.

A small part of the total change in muscle–tendon length is due to changes in muscle pennation. Pennation decreases with increasing muscle–tendon unit length, increasing the effective length of muscle fascicles. Our calculations, based on published data of changes in pennation in these muscles, suggest this mechanism accounts for only 9 % of the total change in length of relaxed medial gastrocnemius and only 1 % for relaxed tibialis anterior.

The remainder of the total change in length (~44 % of total change in muscle–tendon length for medial gastrocnemius and 56 % for tibialis anterior) must be due to elongation of the tendon. At the low tensions in relaxed muscles, both muscle fascicles and tendons are highly compliant. Tendons are intrinsically less compliant than muscle (i.e. tendon experiences smaller strains than muscle fascicles at a given tension) but, because the tendons of tibialis anterior and medial gastrocnemius are much longer than their muscle fascicles (by about 10-fold for medial gastrocnemius), the tendons experience relatively large changes in length.

The need for compliant tendons is illustrated in Fig. 2*A*. Medial gastrocnemius muscle fascicles are ~29 mm long when the ankle is plantarflexed and the knee is flexed. Dorsiflexion by 77 deg increases muscle–tendon length by 65 mm. The muscle fascicles could not lengthen from 29 mm to (29 + 65 =) 94 mm without being damaged. If muscle fascicle strain is to be less than 100 %, muscle fascicles must contribute less than 45 % of change in muscle–tendon length. As pennation may contribute ~9 % of the total length change (see above), tendon must contribute more than 46 % of total change in muscle–tendon length.

Significant tendon compliance at resting tensions is consistent with data from a study on rabbit soleus muscle (Herbert & Crosbie, 1997). In the rabbit soleus, muscle fascicle strains are about four times greater than tendon strains, but because the tendons are about four times as long as the muscle fascicles, approximately half of the increase in muscle–tendon length occurs in muscle fascicles and half in tendon. The present study extends these findings to passive human muscles *in vivo*. However, the present data are difficult to reconcile with a recent study on cat medial gastrocnemius, in which an indirect estimate of muscle fibre length was used (Whitehead *et al.* 2001). The authors argued that for lengths beyond optimum, their data favoured the muscle fibres rather than the tendon as the site of lengthening when the muscle was passively extended. The cause of these important discrepancies requires further investigation.

The present data are similar to some, but not all, ultrasound data on resting human ankle muscles. Three studies have described resting fascicle lengths of medial gastrocnemius at short and stretched lengths (Narici *et al.* 1996; Kawakami *et al.* 1998; Maganaris *et al.* 1998). Our analysis of these data gives slopes of 0.46 (Narici *et al.* 1996), 0.43 (Kawakami *et al.* 1998) and 0.46 (Maganaris *et al.* 1998). These values are higher than our value of 0.27, but still much less than 1.0. The smaller slope could be explained if there was slack at short lengths, as we measured fascicle lengths over a greater range. In contrast, Maganaris & Baltzopoulos (1999) report a slope of 0.92 for tibialis anterior, higher than that of 0.55 in our study. It is not clear why these data differ from our data and from the medial gastrocnemius data of Narici *et al.,* Kawakami *et al.* and Maganaris *et al.* but failure to obtain full relaxation could be critical. Several ultrasonographic studies on human muscles have attempted to estimate length–tension properties of tendon by measuring muscle fascicle length changes during isometric contraction (e.g. Fukashiro *et al.* 1995). While this approach may provide estimates of tendon length changes induced by contraction, the data in such studies may not be comparable with the present data if, as has been suggested, contraction changes the mechanical properties of the intramuscular tendon (Ettema & Huijing, 1989; Lieber *et al.* 2000).

Elek *et al.* (1990) performed elegant experiments to determine the extent of 'extramysial displacement' (primarily elongation of tendon) in cat medial gastrocnemius during gait. They recorded spindle discharge while the passive muscle–tendon unit was subjected to gait-like changes in length. Subsequently, the muscle was contracted by selectively stimulating alpha motoneurones, and changes in muscle–tendon length were adjusted until the same pattern of spindle discharge was obtained under passive and active conditions, whereupon it was assumed that muscle fascicles were undergoing the length changes. Elek *et al.* estimated that extramysial displacements were small (~0.5 % of total muscle–tendon length), which suggests there was little elongation of tendon in the transition from passive to active conditions. However, this method could underestimate the extramysial (or tendon) displacement with contraction because some spindles lie partly or wholly in series with extrafusal muscle fibres (Binder & Stuart, 1980; Cameron *et al.* 1983).

In one subject, who had also participated in an experiment in which the tendon of tibialis anterior was surgically exposed, we were able to compare estimates of changes in muscle–tendon length with direct measures of displacement of the extramuscular tendon of tibialis anterior (Refshauge *et al.* 1998). Displacement of a marker on the extramuscular tendon (~10 cm proximal to the distal insertion) was measured when the ankle was moved passively during relaxation. At ankle angles of $\geqslant -10$ deg (i.e. at all but the most dorsiflexed positions) the marker moved 0.60 mm deg^{-1} (calculated from Fig. 5 in Refshauge *et al.* 1998), a value that is exactly equal to the estimated change in tibialis anterior muscle–tendon length for this subject. This indicates that there is little stretch in the most distal 10 cm of the tendon of tibialis anterior and that most stretch occurs in more proximally in the tendon. Perhaps this is not surprising, as strains in the intramuscular tendons of isolated muscles greatly exceed those in extramuscular tendon (Lieber *et al.* 1991; Trestik & Lieber, 1993; Zuurbier *et al.* 1994; cf. Scott & Loeb, 1995). In contrast, at high tensions, strains in the intramuscular and extramuscular tendon are nearly identical (cat soleus muscle; Morgan, 1977).

There was a tendency, albeit not quite significant ($P = 0.06$), for ankle displacement to produce larger changes in muscle fascicle length at higher forces. The slope remains less than one, which probably indicates that the contribution of synergistic muscles to the dorsiflexion torque is not constant across joint angles. Regardless of the mechanism, an intriguing consequence is that the stretch 'seen' by muscle fascicles and their spindles might be modulated by muscle contraction. Contraction of only 5 % MVC increases the change in muscle fascicle length associated with a change in joint angle by about 50 %, suggesting even this low level of muscle contraction increases the 'sensitivity' of tibialis anterior muscle spindles to changes in ankle angle by half. This provides an additional mechanism which would alter the sensitivity of muscle spindles. Furthermore, this adds extra complexity to central 'interpretation' of spindle afferent discharge, as is required for proprioceptive judgements; for tibialis anterior, the sensitivity of muscle spindles to joint displacement can be increased indirectly by excitation of alpha motoneurones as well as by fusimotor neurones.

In summary, this study suggests that for a range of movement and contraction 'histories' the tendon of long human muscles acting across the ankle (and in particular its intramuscular portion) may undergo surprisingly large changes in length.

REFERENCES

Alexander, R. M. & Bennet-Clark, H. C. (1977). Storage of elastic strain energy in muscle and other tissues. *Nature* **265**, 114–117.

Armitage, P. & Berry, G. (1994). *Statistical Methods in Medical Research*, 3rd edn, pp. 288–290. Blackwell Science, Oxford.

Binder, M. D. & Stuart, D. G. (1980). Responses of Ia and spindle group II afferents to single motor-unit contractions. *Journal of Neurophysiology* **43**, 621–629.

Burgess, P. R., Wei, J. Y., Clark, F. J., Simon, J. B. (1982). Signaling of kinesthetic information by peripheral sensory receptors. *Annual Review of Neuroscience* **5**, 171–187.

Cameron, W. E., Binder, M. D., Botterman, B. R., Reinking, R. M. & Stuart, D. G. (1983). "Sensory partitioning" of cat medial gastrocnemius muscle by its muscle spindles and tendon organs. *Journal of Neurophysiology* **46**, 32–47.

Elek, J., Prochazka, A., Hulliger, M. & Vincent, S. (1990). In-series compliance of gastrocnemius muscle in cat step cycle: do spindles signal origin-to-insertion length? *Journal of Physiology* **429**, 237–258.

Ettema, G. J. & Huijing, P. A. (1989). Properties of the tendinous structures and series elastic component of EDL muscle-tendon complex of the rat. *Journal of Biomechanics* **22**, 1209–1215.

Fellows, S. J. & Thilmann, A. F. (1989). The role of joint biomechanics in determining stretch reflex latency at the normal human ankle. *Experimental Brain Research* **77**, 135–139.

Fukashiro, S., Ito, M., Ichinose, Y., Kawakami, Y. & Fukunaga, T. (1995). Ultrasonography gives directly but noninvasively elastic characteristic of human tendon *in vivo*. *European Journal of Applied Physiology* **71**, 555–557.

Fukunaga, T., Ichinose, Y., Ito, M., Kawakami, Y. & Fukashiro, S. (1997). Determination of fascicle length and pennation in a contracting human muscle *in vivo*. *Journal of Applied Physiology* **82**, 354–358.

Grieve, D. W., Pheasant, S. & Cavanagh, P. R. (1978). Prediction of gastrocnemius length from knee and ankle joint posture. In *Biomechanics-VI-A, International Series on Biomechanics*, 2A, ed. Asmussen, E. & Jorgensen, K., pp. 405–412. University Park Press, Baltimore.

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.

Henriksson-Larsén, K., Wretling, M.-L., Lorentzon, R. & Oberg, L. (1992). Do muscle fibre size and fibre angulation correlate in pennated human muscles? *European Journal of Applied Physiology* **64**, 68–72.

Herbert, R. D. & Crosbie, J. (1997). Rest length and compliance of non-immobilised and immobilised rabbit soleus muscle and tendon. *European Journal of Applied Physiology* **76**, 472–479.

Herbert, R. D. & Gandevia, S. C. (1995). Changes in pennation with joint angle and muscle torque: *in vivo* measurements in human brachialis muscle. *Journal of Physiology* **484**, 523–532.

Hof, A. L., Geelen, B. A. & Van den Berg, J. (1983). Calf muscle moment, work and efficiency in level walking; role of series elasticity. *Journal of Biomechanics* **16**, 523–537.

Ito, M., Kawakami, Y., Ichinose, Y., Fukashiro, S. & Fukunaga, T. (1998). Nonisometric behavior of fascicles during isometric contractions of a human muscle. *Journal of Applied Physiology* **85**, 1230–1235.

Jahnke, M. T., Proske, U. & Struppler, A. (1989). Measurements of muscle stiffness, the electromyogram and activity in single muscle spindles of human flexor muscles following conditioning by passive stretch or contraction. *Brain Research* **493**, 103–112.

Kawakami, Y., Ichinose, Y. & Fukunaga, T. (1998). Architectural and functional features of human triceps surae muscles during contraction. *Journal of Applied Physiology* **85**, 398–404.

Klein, P., Mattys, S. & Rooze, M. (1996). Moment arm length variations of selected muscles acting on talocrural and subtalar joints during movement: an in vitro study. *Journal of Biomechanics* **29**, 21–30.

Lieber, R. L., Leonard, M. E., Brown, C. G. & Trestik, C. L. (1991). Frog semitendinosis tendon load-strain and stress-strain properties during passive loading. *American Journal of Physiology* **261**, C86–92.

Lieber, R. L., Leonard, M. E. & Brown-Maupin, C. G. (2000). Effects of muscle contraction on the load-strain properties of frog aponeurosis and tendon. *Cells Tissues Organs* **166**, 48–54.

Maganaris, C. N. & Baltzopoulos, V. (1999). Predictability of *in vivo* changes in pennation angle of human tibialis anterior muscle from rest to maximum isometric dorsiflexion. *European Journal of Applied Physiology* **79**, 294–297.

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**, 603–614.

Morgan, D. L. (1977). Separation of active and passive components of short-range stiffness of muscle. *American Journal of Physiology* **232**, C45–49.

Morgan, D. L., Proske, U. & Warren, D. L. (1978). Measurements of muscle stiffness and the mechanism of elastic energy storage in hopping kangaroos. *Journal of Physiology* **282**, 253–261.

Narici, M. V. T., Binzoni, T., Hiltbrand, E., Fasel, J., Terrier, F. & Cerretilli, P. (1996). *In vivo* human gastrocnemius architecture with changing joint angle at rest and during graded isometric contraction. *Journal of Physiology* **496**, 287–297.

Rack, P. M. H. & Westbury, D. R. (1984). Elastic properties of the cat soleus tendon and their functional importance. *Journal of Physiology* **347**, 479–495.

Refshauge, K. M., Taylor, J. L., McCloskey, D. I., Gianoutsos, M., Mathews, P. & Fitzpatrick, R. C. (1998). Movement detection at the human big toe. *Journal of Physiology* **513**, 307–314.

Rutherford, O. M. & Jones, D. A. (1992). Measurement of fibre pennation using ultrasound in the human quadriceps in vivo. *European Journal of Applied Physiology* **65**, 433–437.

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.

Spoor, C. W. & van Leeuwen, J. L. (1992). Knee muscle moment arms from MRI and from tendon travel. *Journal of Biomechanics* **25**, 201–206.

Spoor, C. W., van Leeuwen, J. L., Meskers, C. G. M., Titulaer, A. F. & Huson, A. (1990). Estimation of instantaneous moment arms of lower leg muscles. *Journal of Biomechanics* **23**, 1247–1259.

Stolov, W. C. & Weillep, T. G. (1966). Passive length-tension relationship of intact muscle, epimysium, and tendon in normal and denervated gastrocnemius of the rat. *Archives of Physical Medicine and Rehabilitation* **47**, 612–620.

Trestik, C. L. & Lieber, R. L. (1993). Relationship between Achilles tendon mechanical properties and gastrocnemius muscle function. *Journal of Biomechanical Engineering* **115**, 225–230.

Visser, J. J., Hoogkamer, J. E., Bobbert, M. F. & Huijing, P. A. (1990). Length and moment arm of human leg muscles as a function of knee and hip-joint angles. *European Journal of Applied Physiology* **61**, 453–460.

Walmsley, B. & Proske, U. (1981). Comparison of stiffness of soleus and medial gastrocnemius muscles in cats. *Journal of Neurophysiology* **46**, 250–259.

Whitehead, N. P., Gregory, J. E., Morgan, D. L. & Proske, U. (2001). Passive mechanical properties of the medial gastrocnemius muscle of the cat. *Journal of Physiology* **563**, 893–903.

Woittiez, R. D., Huijing, P. A., Boom, H. B. K. & 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.

Zuurbier, C. J., Everard, A. J., van der Wees, P. & Huijing, P. A. (1994). Length-force characteristics of the aponeurosis in the passive and active muscle condition and in the isolated condition. *Journal of Biomechanics* **27**, 445–453.

Acknowledgements

This research was supported by the National Health and Medical Research Council. We thank Dr Kathryn Refshauge and colleagues for allowing us to use their raw data.