Passive mechanical properties of human gastrocnemius muscle–tendon units, muscle fascicles and tendons *in vivo*

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Summary

This study provides the first *in vivo* measures of the passive length–tension properties of relaxed human muscle fascicles and their tendons. A new method was used to derive passive length–tension properties of human gastrocnemius muscle–tendon units from measures of ankle stiffness obtained at a range of knee angles. Passive length–tension curves of the muscle–tendon unit were then combined with ultrasonographic measures of muscle fascicle length and pennation to determine passive length–tension curves of the muscle fascicles and tendons. Mean slack lengths of the fascicles, tendons and whole muscle–tendon units were 3.3±0.5 cm, 39.5±1.6 cm and 42.3±1.5 cm, respectively (means ± s.d., *N*=6). On average, the muscle–tendon units were slack (i.e. their passive tension was zero) over the shortest 2.3±1.2 cm of their range. With combined changes of knee and ankle angles, the maximal increase in length of the gastrocnemius muscle–tendon unit above slack length was 6.7±1.9 cm, of which 52.4±11.7% was due to elongation of the tendon. Muscle fascicles and tendons underwent strains of 86.4±26.8% and 9.2±4.1%, respectively, across the physiological range of lengths. We conclude that the relaxed human gastrocnemius muscle–tendon unit falls slack over about one-quarter of its *in vivo* length and that muscle fascicle strains are much greater than tendon strains. Nonetheless, because the tendons are much longer than the muscle fascicles, tendons contribute more than half of the total compliance of the muscle–tendon unit.

Key words: gastrocnemius, muscle, strain, tendon.

Introduction

Relaxed muscle–tendon units display spring-like properties. When lengthened beyond a threshold length (sometimes called the slack length) they develop passive tension (Hill, 1952; Swanstrom et al., 2005; Whitehead et al., 2001).

The passive length–tension properties of whole muscle–tendon units are often explained in terms of a simple mechanical model in which muscle fibres (or, perhaps more accurately, muscle fascicles) are arranged in series with tendons. According to this model, as muscle–tendon units are lengthened, muscle fascicles and tendons contribute to the total change in muscle–tendon length in proportion with their compliances (Zajac, 1989).

It has often been assumed that relaxed muscle fascicles are much more compliant than tendons and that therefore, when muscle–tendon units are lengthened, most of the increase in length occurs in the muscle fascicles (e.g. De Deyne, 2001; Tardieu et al., 1982). But this view may be incorrect for several reasons. First, in many muscles, the tendons are very long compared to the muscle fascicles, so at any given strain the tendons typically experience much greater changes in length than do muscle fascicles. Second, while it has often been claimed that tendons undergo only small strains, and fail at strains of about 10% (Zajac, 1989), the true strains experienced by whole tendons *in vivo* may actually be quite large. Estimates of failure strains are usually based on measurements made on extramuscular tendon, but it is possible that intramuscular tendon experiences greater strains than does extramuscular tendon (Lieber et al., 2000; Zuurbier et al., 1994). Also, studies of failure properties of tendons often measure gauge lengths with the tendon under significant tension (Ker, 1981), causing the strain numerator to be underestimated and the strain denominator to be overestimated (Herbert and Crosbie, 1997). A further complication, articulated recently by Epstein and Herzog (Epstein et al., 2006), is that muscle fascicles and tendons are not arranged simply in series but instead are arranged partly in series and partly in parallel. This may explain why the tendons of contracting muscles appear to be shorter and possibly stiffer than the tendons of relaxed muscles (Ettema and Huijing, 1989; Lieber et al., 2000).

Elegant methods have been used to quantify contributions of changes in tendon length to changes in length of *contracting* muscle–tendon units (Biewener et al., 1998; Elek et al., 1990; Griffiths, 1991; Morgan, 1977; Rack and Westbury, 1984; Roberts et al., 1997) but relatively few studies have examined contributions of changes in tendon length to changes in length of *relaxed* muscle–tendon units. Herbert and Crosbie measured displacement of markers placed on the ends of the muscle

fascicles of rabbit soleus muscle–tendon units and showed that when the relaxed muscle–tendon unit was stretched through a physiological range of lengths about half of the total change in length occurred in the tendon (Herbert and Crosbie, 1997).

In humans, ultrasonography can be used to obtain non-invasive measures of muscle fascicle length (De Monte et al., 2006; Fukashiro et al., 1995; Fukunaga et al., 1997; Herbert et al., 2002; Lichtwark et al., 2007; Loram et al., 2004; Maganaris et al., 1998; Magnusson et al., 2001; Muraoka et al., 2002; Narici et al., 1996), and several groups have measured muscle fascicle lengths of relaxed human lower limb muscles at a range of joint angles (De Monte et al., 2006; Herbert et al., 2002; Kawakami et al., 1998; Maganaris et al., 1998; Muraoka et al., 2005; Muraoka et al., 2002; Narici et al., 1996). The change in length of muscle fascicles that occurs as the relaxed gastrocnemius or tibialis anterior muscle is lengthened through its physiological range is much less than the total change in muscle–tendon unit length. This suggests that the tendon contributes substantially to the total length changes in these muscle–tendon units (De Monte et al., 2006; Herbert et al., 2002).

Ultrasonography can provide descriptions of length changes in human muscle fascicles, but unless ultrasonographic measures of muscle fascicle lengths are combined with measures of muscle tension they cannot be used to determine length–tension properties. Some authors have estimated tension in a single human muscle by dividing joint torque by the moment arm of the muscle (Muraoka et al., 2002), but, because many structures usually contribute to passive joint torque, this approach is likely to overestimate tension in the muscle. Without a measure of tension it is not possible to measure slack length, so it is difficult to estimate strains. Slack length is usually assumed to be the length measured with the joint in its mid-position (Magnusson et al., 2003) or when the net joint torque is zero (De Monte et al., 2006; Muraoka et al., 2002), but there is no compelling reason to believe that either joint position should correspond to the true slack length.

In the present study, we combine ultrasonographic measures of fascicle lengths and measures of the length–tension properties of the human gastrocnemius muscle–tendon unit obtained with a recently developed method (Hoang et al., 2005). By combining these methods it is possible to obtain non-invasive measures of the length–tension properties and strains of relaxed human muscle fascicles and tendons without having to assume that the passive torque is entirely attributable to the gastrocnemius and without making arbitrary assumptions about which joint angles correspond to slack length.

Materials and methods

The right legs of nine healthy subjects (two females and seven males, aged between 24 and 48 years) were studied. Subjects had no history of significant orthopaedic problems in the lower limbs, nor were they currently involved in a physical training program. Anthropometric data are given in Table 1. All subjects gave written consent to the experimental protocol, which had been approved by the Human Research Ethics Committees of the University of New South Wales and University of Sydney. Studies were conducted according to the Declaration of Helsinki.

Table 1. *Measures of body mass, foot length, length of the lower leg and reference length of all nine subjects*

Subject	Body mass (kg)	l_{foot} (cm)	l_s (cm)	l_{ref} (cm)
1	90	17.0	42.7	44.0
2	81	17.6	43.5	45.5
3	81	17.0	41.5	43.5
4	75	16.5	40.0	42.0
5	75	16.0	43.5	46.5
6	71	18.5	46.0	49.0
7	92	18.0	44.5	48.0
8	55	15.0	39.0	42.0
9	73	17.0	42.0	45.0
Mean ± s.d.	77±11	17.0±1.1	42.5±2.2	45.1±2.5

l_{foot}, foot length, defined as the distance between the middle of the lateral malleolus and the tip of the second metatarsal; l_s, segment length, defined as the distance between the middle of lateral epicondyle of the femur and the middle of lateral malleolus; l_{ref}, reference length of the gastrocnemius, defined as the distance between the middle of the lateral epicondyle and the tip of the lateral malleolus.

Testing equipment

Subjects lay prone on a device designed to enable both the knee and ankle to move freely within their available ranges without moving the lower leg (Fig. 1B). The axes of the device were aligned with the presumed axes of the subject's ankle and knee, using laser pointers built into the device's axes (Fig. 1A). Potentiometers recorded knee and ankle angles. The foot was strapped to a footplate that 'floated' on a footplate balance mechanism to accommodate changes in location of the ankle axis of rotation as well as the subjects' different foot shapes (an enhancement of the device initially described for this application (Hoang et al., 2005). A calibrated force transducer measured passive ankle torque (XTran, Melbourne, Australia: linear to 250 N). The analogue outputs from the force transducer and potentiometers were sampled at 50 Hz.

An ultrasound unit (Acuson 128XP4, Mountain View, CA, USA) was used to generate simultaneous images of the medial gastrocnemius. Images were obtained with an 80 mm 5 MHz linear transducer placed longitudinally on the belly of the medial gastrocnemius. The position of the transducer was adjusted so that optimal images of the muscle fascicles and the intramuscular tendons (superficial and deep) of the medial gastrocnemius could be visualised. Measurements were made over the mid-belly of the muscle, as changes at this site are relatively uniform and they approximate the average changes in fascicle length observed during walking and running (Lichtwark et al., 2007). Once the images were considered optimal, the transducer was manually stabilized while the ankle was rotated. To maintain optimal images, markers were placed on the skin to maintain a constant orientation of the ultrasound head with respect to the muscle fascicles. The images were displayed in real time and digitally sampled at 25 Hz.

Surface electromyography was used to monitor muscle relaxation during ankle movement. Bipolar surface electrodes (Ag–AgCl, 10 mm diameter) were placed over the muscle bellies of the lateral gastrocnemius, soleus and tibialis anterior with an inter-electrode distance of 3 cm. The signals were
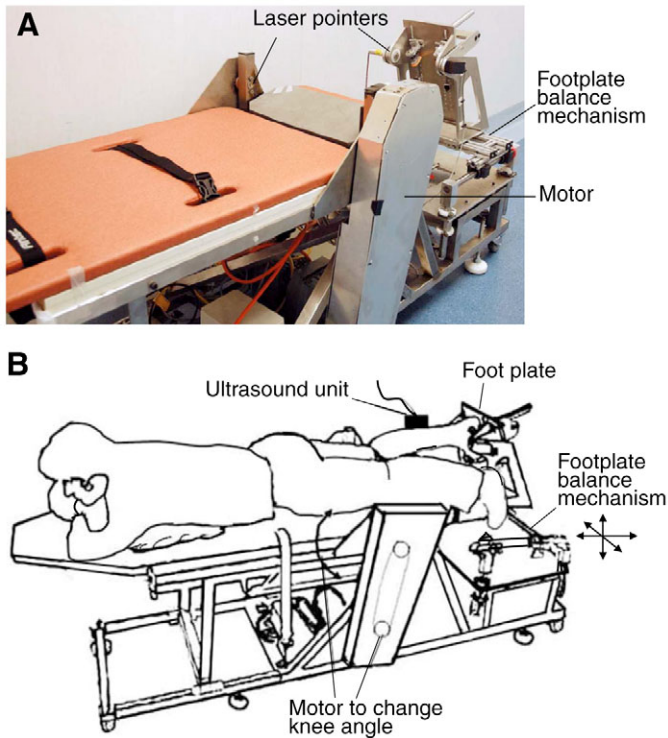
Fig. 1. Testing equipment and experiment set up. (A) Testing equipment. (B) Schematic diagram of the testing equipment and experimental set up. The subject lies prone, strapped to the lying board, with the assumed axes of rotation of the knee and ankle aligned with potentiometers by laser pointers. The right foot, strapped to the footplate, is manually rotated through the ankle's range of movement. The footplate is controlled by a 'floating' balance mechanism to accommodate slight changes in the location of the ankle axis during rotation as well as the subjects' differing foot shapes. The lying board can be moved up and down by a motor to change the knee angle without moving the lower leg. An ultrasound transducer was stabilized over the midbelly of the medial gastrocnemius to generate images of muscle fascicles during ankle rotation. Passive ankle torque, ankle and knee angles and ultrasound images were recorded simultaneously.

amplified ($\times$1000), bandpass filtered (100–1000 Hz; Grass, IP 511, West Warwick, RI, USA) and sampled at 2000 Hz.

Measurement

Passive ankle torque-angle relations were measured at eight knee angles (0°, 10°, 20°, 50°, 60°, 70°, 90° and 100° in random order; 0° represents full knee extension). With the subject's right foot firmly strapped to the footplate, the footplate was manually cycled from plantarflexion to dorsiflexion and back at ~0.05 Hz (average angular speed of 6 deg. s^{-1}) (Fig. 1B). Subjects were asked to remain as relaxed as possible throughout measurements. Occasionally, brief bursts of electromyographic activity were observed [see fig. 3 of Hoang et al. (Hoang et al., 2005)], but these were small: typically of the order of 1–3% of the amplitude observed during a maximal voluntary contraction. Such low-level contractions have little effect on passive length–tension curves (data not shown). Nonetheless, all passive ankle torque-angle data associated with observable electrical activity were excluded from the analyses.

To minimize the effect of time-dependent deformation, including thixotropic effects, the ankle was rotated for five full cycles before data were recorded. Passive ankle torque, ankle angle, knee angle and ultrasound images of muscle fascicles of the medial gastrocnemius were then recorded for three cycles of dorsiflexion–plantarflexion. This procedure was repeated at each knee angle.

Data analysis and statistics

Here, we use the term 'tendon' to mean both intramuscular tendon (aponeuroses) and extramuscular tendon (free tendon) and the term 'gastrocnemius' to mean both medial and lateral parts of the muscle. The gastrocnemius is treated as a functional unit, although there are some anatomical differences between the two components (Huijing, 1985).

Passive length–tension relation of the muscle–tendon unit

The analysis used to derive the passive length–tension relation of the gastrocnemius muscle–tendon unit has been presented in detail (Hoang et al., 2005). Key features of the analytical approach are repeated here.

The method is based on the assumption that the passive torque measured at the ankle depends on torques due to (1) single-joint structures such as single-joint muscles and ligaments that cross the plantar (posterior) and dorsal (anterior) aspects of the ankle joint but not the knee joint and (2) the two-joint muscle, gastrocnemius, which crosses the plantar aspect of the ankle and the posterior aspect of the knee (see Fig. 2A for a schematic diagram of these structures). The key proposition is that, therefore, differences in the passive ankle torques measured at different knee angles are due to changes in the length of the gastrocnemius (Fig. 2B). Contributions to the passive ankle torque from other two-joint structures such as the plantaris muscle, nerves and blood vessels were assumed to be negligible. For discussion of the assumptions, see Hoang et al. (Hoang et al., 2005).

Torque-angle properties of the single-joint structures and the gastrocnemius were assumed to be exponential functions at lengths greater than slack length. Under this assumption, the total passive torque measured at the ankle is:

$$\tau_{ankle}\{\theta_a,\theta_k\} = a_p e^{k_p(\theta_a-\theta_P)} - a_p \quad | \quad \theta_a > \theta_P$$
$$+ a_d e^{k_d(\theta_D-\theta_a)} - a_d \quad | \quad \theta_a < \theta_D$$
$$+ m_g[a_g e^{k_g(l_g-l_G)} - a_g] \quad | \quad l_g < l_G , \quad (1)$$

where $\tau_{ankle}\{\theta_a,\theta_k\}$ is the passive torque at the ankle, which is a function of both ankle and knee joint angles; $a_p e^{k_p(\theta_a-\theta_P)}$–$a_p$ is the torque due to single-joint structures on the plantar aspect of the ankle; $a_d e^{k_d(\theta_D-\theta_a)}$–$a_d$ is the torque due to single-joint structures on the dorsal aspect of the ankle; $m_g[a_g e^{k_g(l_g-l_G)}$–$a_g]$ is torque due to the gastrocnemius; θ_a and θ_k are ankle angle and knee angle, respectively; a_p, k_p, a_d, k_d, a_g and k_g are parameters that determine the stiffness of structures that cross the plantar aspect (a_p, k_p) and dorsal aspect (a_d, k_d) of the ankle, and the gastrocnemius (a_g, k_g); θ_P and θ_D are ankle angles at which ankle plantar flexors and dorsiflexors, respectively, are slack; m_g is the moment arm of the gastrocnemius at the ankle; l_g is the
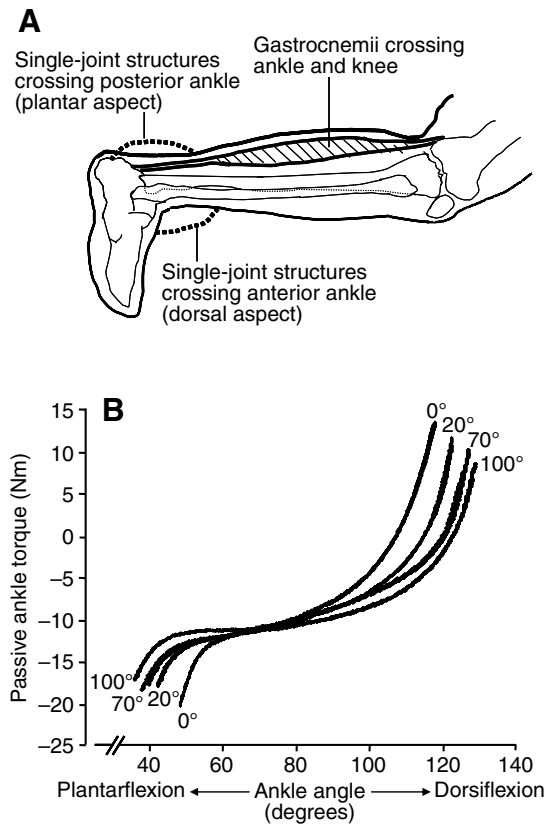
Fig. 2. (A) Schematic diagram of single joint structures crossing plantar and dorsal aspects of the ankle and the gastrocnemius crossing both ankle and knee. Passive ankle torque is assumed due to resistive forces from these structures. (B) Raw data of passive ankle torques when the ankle was rotated from full plantarflexion to full dorsiflexion from one subject measured at four of the eight different knee angles (0°, 20°, 70° and 100°). Differences in torque-angle relations are assumed to reflect changes in the length of the gastrocnemius (see Materials and methods).

length of the gastrocnemius muscle–tendon unit; and l_G is the slack length of the gastrocnemius muscle–tendon unit.

In Eqn 1, two variables – ankle torque (τ_{ankle}) and ankle angle (θ_a) – were known from measurement. Two further variables – the moment arm (m_g) and length (l_g) of the gastrocnemius – were derived using published anthropometric data. The length of the gastrocnemius varied as a function of knee and ankle angles (Grieve et al., 1978), and the moment arm at the ankle was calculated by differentiation of the gastrocnemius length with respect to ankle angle. The remaining parameters in Eqn 1 (a_g, k_g, l_G, a_p, k_p, θ_P, a_d, k_d and θ_D) are unknown and were estimated during the analysis process. Of these parameters, the three of interest were a_g, k_g and l_G, as they determine the gastrocnemius length–tension properties.

Before analysis, raw data of passive ankle torque-ankle angle relations were transformed as follows. First, torques due to the weight of the footplate and estimated weight of the foot (both functions of ankle angle) were subtracted from the measured ankle torques. The weight of the foot was estimated using anthropometric data (Winter, 1990). Second, we used data from the dorsiflexion half of each cycle. We focused on the

dorsiflexion portion of the curve as this direction mimics clinical examination of the ankle to assess the plantarflexor muscles, and dorsiflexion is the direction that lengthens the gastrocnemius. This also avoids the complexity associated with the hysteretic behaviour of the muscle–tendon unit.

Derivation of passive length–tension properties of the gastrocnemius muscle–tendon unit involved two steps. First, the parameters in Eqn 1 were estimated using the quasi-Newton algorithm with Statistica [StatSoft, Inc., Tulsa, OK, USA, version 6; for details see Hoang et al. (Hoang et al., 2005)]. The quasi-Newton class of algorithms involves iterative estimation of parameters. The parameter search is guided by approximations to the first and second derivatives of an error function. The approach is generally robust but shares with other non-linear optimization techniques the risk that it may fail to converge or may converge on local rather than global minima. Second, estimated values of the three gastrocnemius parameters a_g, k_g and l_G were used to construct passive length–tension curves of the gastrocnemius using the formula:

$$F\{l_g\} = a_g e^{k_g(l_g-l_G)} - a_g \qquad |\quad l_g > l_G$$
$$F\{l_g\} = 0 \qquad\qquad\qquad |\quad l_g \leq l_G . \qquad (2)$$

Passive length–tension curves of gastrocnemius muscle–tendon units measured in this way are reproducible [average root mean square error of 3% and 6% of maximal passive tension for pairs of measurements within a day and a week apart respectively (Hoang et al., 2005)].

Sensitivity analysis

As passive length–tension curves rely on the precision of the estimated parameters a_g, k_g and l_G, we assessed the sensitivity of the curves from one randomly selected subject to errors in model parameters by analyzing changes in length–tension curve associated with a 5% error in each of the model parameters. For each sensitivity analysis, we fixed one parameter at its new value (its initial value ±5%) and then used the quasi-Newton algorithm to estimate the values of the remaining eight parameters. The new values of parameters a_g, k_g and l_G were used to re-plot the length–tension curves. In addition, we tested the sensitivity of the length–tension curve of the same subject to biases in passive ankle torques or weight torques of the foot or ankle. To do this, we re-ran the analysis after systematically adding biases (±2% or 5%) to recorded ankle torques and after adding 5% to the weight torque of the footplate and 25% to the weight torque of the foot. In all of the above analyses, differences between the re-plotted curves and the initial curve were calculated as root-mean-square errors (RMSEs) and expressed as a percentage of the maximal tension of the initial length–tension curve. The new values of l_G obtained from all of the above sensitivity analyses were also used to estimate the sensitivity of measures of strains of the whole muscle–tendon unit, the muscle fascicles and the tendon.

Calculation of slack lengths and changes in the length of muscle fascicles and tendon

Muscle fascicles lengthen and shorten during ankle rotation. Changes in the length of muscle fascicles were tracked
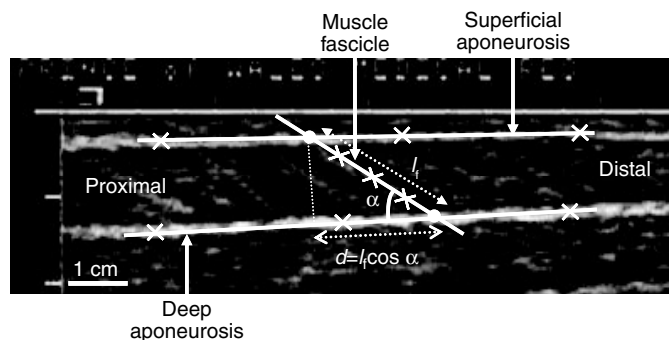
Fig. 3. Single frame ultrasound image of the medial gastrocnemius from one subject. Three sets of three points (white crosses) were marked on the first frame to identify the lines of the superficial aponeurosis (top white line), the deep aponeurosis (bottom white line) and a muscle fascicle (diagonal white line). The length of the fascicles (l_f) is defined by the intersections of the three lines (white circles). The pennation angle of the fascicles (α) is the acute angle between the fascicle line and the deep aponeurosis line. The longitudinal displacement of the fascicle (d) is used to calculate the length of the tendon (length of the muscle–tendon unit – d).

automatically using the following procedure. Three video files of the images of muscle fascicles of the medial gastrocnemius (each with the knee at a different angle: 20°, 60° or 90°) were analysed. In the first frame of each file, three sets of three points were identified: one set lay along the superficial aponeurosis, one set lay along the deep aponeurosis and one set lay along an identifiable muscle fascicle (Fig. 3). The DgeeMe program (freeware available at www.geeware.com) was used to track the coordinates of the three sets of points on the video files during ankle rotation. The tracking was then checked manually frame by frame.

Subsequently, three lines were fitted to the three sets of points. The regression equations were used to identify the coordinates of the intersections of the muscle fascicle line and the two aponeurosis lines, and therefore also both the (straight line) length of the muscle fascicles and fascicle pennation (α, the acute angle between the muscle fascicles and the deep aponeurosis) (Fig. 3).

The relationship between the length of muscle fascicles and the length of the muscle–tendon units was modeled as a third-order polynomial:

$$l_f = l_F + [b(l_g - l_G) + c(l_g - l_G)^2 + d(l_g - l_G)^3 \qquad | \quad l_g \geq l_G$$
$$l_f = l_F \qquad\qquad\qquad\qquad\qquad\qquad\qquad | \quad l_g < l_G \; , \qquad (3)$$

where l_f is the length of the muscle fascicle, l_F is the slack length of the muscle fascicles, l_g is the length of the gastrocnemius and l_G is the slack length of the gastrocnemius muscle–tendon unit estimated from Eqn 1. The form of this equation means that the muscle fascicles and muscle–tendon unit fall slack together (i.e. $l_f = l_F$ when $l_g = l_G$). The parameters l_F, b, c and d in Eqn 3 were estimated using the quasi-Newton algorithm. In this way, an estimate of l_F was obtained, and it was possible to determine fascicle length at any muscle–tendon length (see Fig. 4).
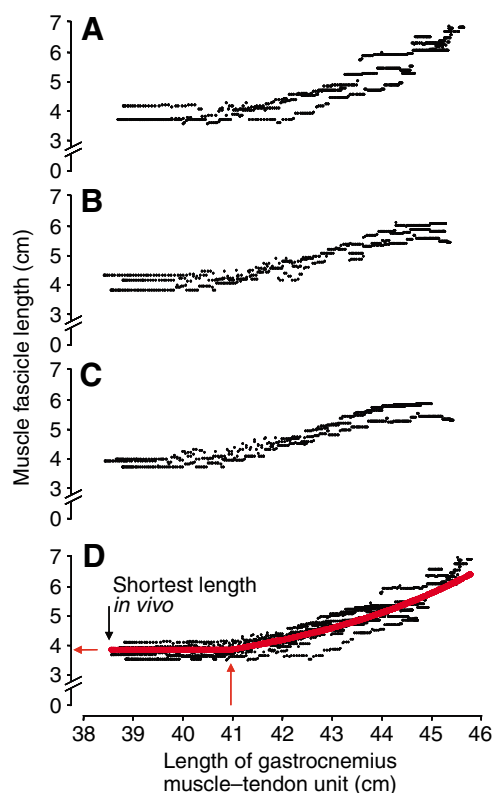

Fig. 4. Relationship between changes in the length of muscle fascicles and the whole muscle–tendon unit during muscle lengthening in one subject. (A–C) The relationship between changes in the lengths of muscle fascicles and the whole muscle–tendon unit when the knee was at 20°, 60° and 90°, respectively. The relationship at the three different knee angles are very similar. (D) The three relationships superimposed, and the fitted line (in red) using Eqn 3 (see Materials and methods). The vertical red arrow shows slack length of the whole muscle–tendon unit, and the horizontal red arrow indicates the slack length of the muscle fascicles.

The slack length of the tendon (l_T) was calculated by subtracting the longitudinal displacement of the muscle fascicles [$l_F \cos(\alpha_s)$, where α_s is fascicle pennation at slack length] from the slack length of the muscle–tendon unit (l_G). The maximal tendon length was calculated by subtracting the maximal longitudinal displacement of the muscle fascicles [$l_{f,max} \cos(\alpha_{max})$, where the 'max' subscript indicates the longest *in vivo* length] from the maximal muscle–tendon length. The contribution of tendon lengthening to the maximal change in muscle–tendon length above slack length was calculated by dividing the maximal change in tendon length by the maximal change in muscle–tendon length. Maximal strains of the muscle–tendon unit, muscle fascicles and tendon were calculated by dividing maximal changes in lengths by slack lengths. Passive length–tension curves of the fascicles and tendon were derived by plotting l_f and $L_g - l_f \cos(\alpha)$ against tension. All data are presented as means ± s.d.

Results

The relationship between ultrasonographically derived changes in muscle fascicle length and muscle–tendon unit

Table 2. *Lengths, strains, and contribution to total change of lengths of muscle–tendon units, muscle fascicles and tendons*

	Muscle–tendon unit	Muscle fascicles	Tendons
Shortest *in vivo* length (cm)	40.1±1.8	–	–
Slack length (cm)	42.3±1.5	3.3±0.5	39.5±1.6
Pennation at slack length (deg.)	–	32.2± 7.7	–
Maximum length (cm)	49.1±2.2	6.2±1.1	43.1±2.0
Pennation at maximum length (deg.)	–	17.2±4.8	–
Maximum change in length (or, for muscle fascicles, longitudinal displacement) from slack length (cm)	6.7±1.9	3.1± 0.9	3.6±1.6
Maximum strain (%)	16.0±4.5	86.4±26.8	9.2±4.1
Contribution to total change in muscle–tendon length (%)	100	47.6±11.7	52.4±11.7

Data are means ± s.d. of the six subjects for whom muscle fascicle slack lengths could be measured.

length from one subject is shown in Fig. 4. The relationship did not change when the knee angle was changed. This was observed in all subjects. The significance of this observation is explained in the Discussion.

In Table 2, we present complete results for only six of the nine subjects because the slack lengths of the gastrocnemius muscle–tendon unit in the remaining three subjects were shorter than the minimum length of muscle–tendon unit that we were able to attain *in vivo*. In these three subjects, we could not use Eqn 3 to derive the slack length of muscle fascicles.

The shortest *in vivo* length of the gastrocnemius muscle–tendon unit in the six subjects was 40.1±1.8 cm (mean ± s.d.). The slack lengths of the muscle–tendon units, muscle fascicles and tendons were 42.3±1.5 cm, 3.3±0.5 cm and 39.5±1.6 cm, respectively. The slack length of the muscle–tendon unit exceeded the shortest *in vivo* length by 2.3±1.2 cm, or about one-quarter of the total length range (maximum *in vivo* length minus minimum *in vivo* length) of the muscle–tendon unit.

The mean maximal change in length of the whole gastrocnemius muscle–tendon unit, from slack length to the longest length measured *in vivo*, was 6.7±1.9 cm. The mean maximal change in the longitudinal displacement of the muscle fascicles (with correction for changes in pennation angle) was 3.1±0.9 cm, and the mean maximal change in the length of the tendon from slack length was 3.6±1.6 cm. This indicates that tendon contributes slightly more than muscle fascicles (means of 52.4% for tendon and 47.6% for muscle fascicles) to the maximal change in length of the whole muscle–tendon unit under passive conditions. Changes in fascicle pennation (32.2±7.7° at slack length, 17.2±4.8° at the maximal length) were accounted for in these calculations, but they make little difference to estimates of the contribution of muscle fascicles and tendons to total changes in muscle–tendon unit length.

Fig. 5 shows a typical example of passive length–tension curves of the gastrocnemius muscle–tendon unit, muscle fascicles and tendon from one subject, and length–tension curves of the muscle fascicles and tendons of the six subjects. Most of the change in length of the whole muscle–tendon units, muscle fascicles and tendons occurs at low tensions.

Maximal strains of the whole muscle–tendon unit, muscle fascicles and tendon were 16.0±4.5%, 86.4±26.8% and 9.2±4.1%, respectively.

The potential errors in our analysis have been quantified. Fig. 6 shows that forcing errors into any one of the estimated parameters produces small to moderate changes in the length–tension curves (RMSEs of 1.2–8.9% of initial maximal tension). Adding biases to either ankle torque data or weight torques of the footplate and the foot produces only small changes in length–tension curves. For the subject randomly chosen for the sensitivity analysis, adding 5% errors to the parameters and biases to the ankle torque and weight torques produced only small changes in the maximum strains of the muscle–tendon unit, the fascicles and the tendon. The means of
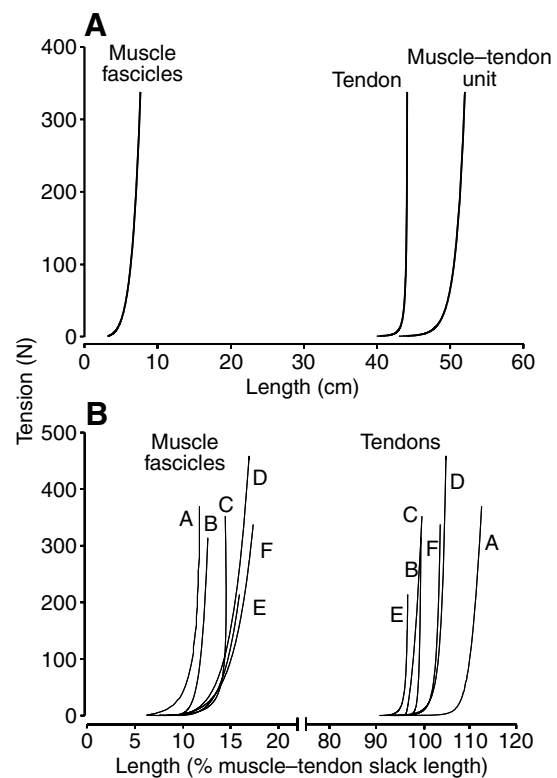

Fig. 5. (A) An example of passive length–tension relationships of the muscle–tendon unit, muscle fascicles and tendon of the gastrocnemius of one subject. (B) Length–tension curves of muscle fascicles and tendons of six subjects.
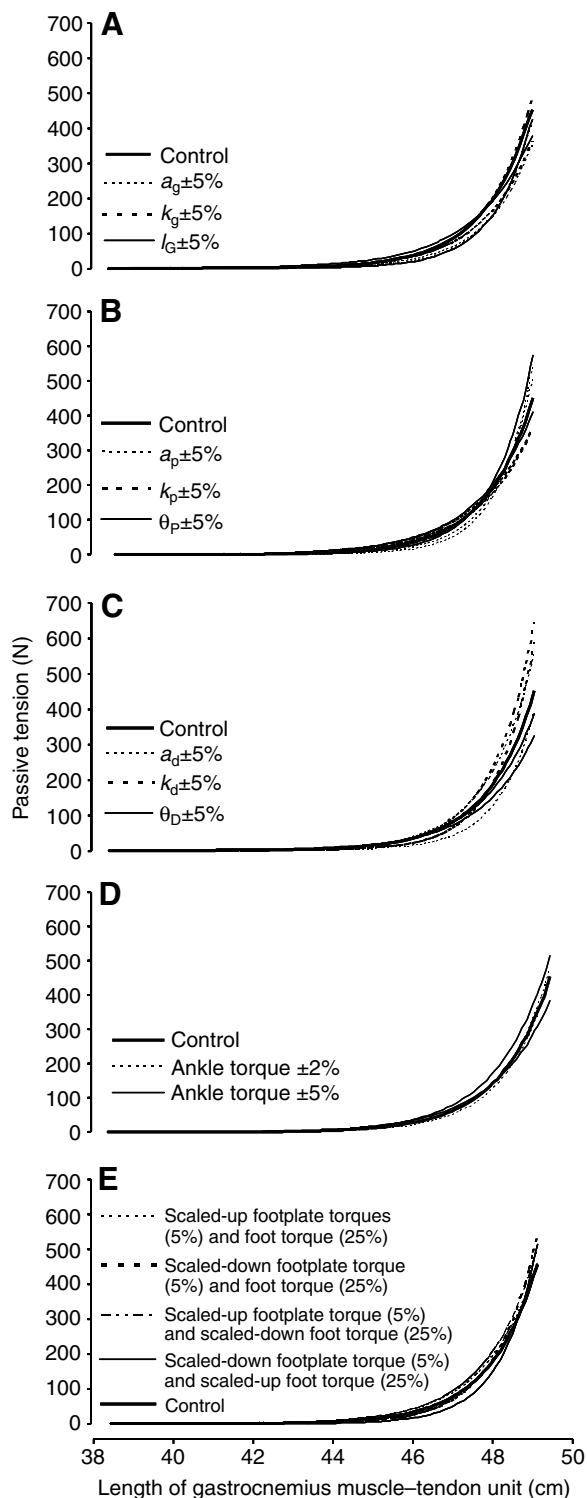
Fig. 6. Changes in length–tension curves from one subject associated with errors in estimation of model parameters, experimentally recorded ankle passive torques and other torque calculations. (A–C) Changes in the passive length tension curve due to 5% errors of each parameter. (D) Changes in the passive length–tension curve after scaling up or down by 2% and 5% the initial experimentally recorded passive ankle torque. (E) Changes in the length–tension curve after adding biases to the footplate torques (of 5%) and the foot torque (of 25%). See List of symbols for definitions of parameters.

all changes (absolute deviations from the control values) were 2%, 9% and 3% for muscle–tendon unit, muscle fascicles and tendon, respectively. This is well within one standard deviation of the means from six subjects (Table 2). These data are presented fully in Table 3. Table 4 also gives a summary of the nine parameters fit from each subject.

Discussion

In this study, ultrasonography was used in combination with a newly developed method for measuring passive length–tension properties of human gastrocnemius muscle–tendon units (Hoang et al., 2005). This made it possible to quantify *in vivo* length–tension properties and strains of fascicles and tendons of the relaxed human gastrocnemius.

We found that the gastrocnemius fell slack close to the shortest length at which we could obtain measurements. However, the shortest length of the gastrocnemius measured in this experiment was not necessarily the true shortest physiological length *in vivo* because it was not possible to obtain ultrasound images with the knee in a fully flexed position. The range of knee angles used in this study was between 0° and 100°. Given that the physiological range of movement of the knee joint is ~0–135°, it was estimated that the 'true' shortest physiological length of the gastrocnemius is ~1 cm shorter than the shortest length of the gastrocnemius measured in this study. This means that although the slack length of the gastrocnemius muscle–tendon unit in three subjects was shorter (by a mean of ~0.4 cm) than the shortest measured length of the muscle, the slack lengths in these subjects were probably just within the 'true' physiological range of lengths. On average, the muscle–tendon unit was slack for about one-quarter of its total excursion.

Our estimate of mean slack length appears to be shorter than the estimate provided by Muraoka and colleagues (Muraoka et al., 2005). They fixed the ankle in a dorsiflexed position (10° more dorsiflexed than the position in which the sole of the foot is at right angles to the leg) and then measured the length of the gastrocnemius muscle fascicles with ultrasound while passively extending the knee from a flexed position. The slack length of the gastrocnemius muscle fascicles was defined as the length at which the ankle torque first increased above baseline values, and they found this occurred when the knee was 43° short of full knee extension. Some simple calculations show that this implies that the gastrocnemius is slack over more than half of its physiological range. Our data suggest that the gastrocnemius is slack over about one-quarter of its range. The differences may reflect differences in the subjects, or they may reflect the different methodological approaches.

The muscle–tendon unit underwent strains of about 16% when passively stretched to its longest physiological length. Tendons experienced much smaller strains (9%) than muscle fascicles (86%). However, because the tendon of the gastrocnemius is more than 11 times as long as the muscle fascicles, the tendons contributed a slightly greater part of the total change in muscle–tendon length. This is broadly consistent with the findings of our earlier studies on animal (Herbert and Crosbie, 1997) and human muscles (Herbert et al., 2002; De Monte et al., 2006). The results from the present study extend the earlier observations by providing measures of the length–tension properties of the muscle fascicles and tendons.

Table 3. *Results of an analysis of sensitivity of length–tension curves to errors in parameters*

(A) Effects of parameter errors on length–tension curves and maximal strains of MTU, muscle fascicles and tendon

	$a_g \times 1.05$	$a_g \times 0.95$	$k_g \times 1.05$	$k_g \times 0.95$	$l_G \times 1.05$	$l_G \times 0.95$
Changes in the length–tension curves*	6.1	4.5	1.2	4.6	4.8	2.3
Changes in strains of the muscle–tendon unit, fascicles and tendon, respectively[†]	–2, 9, –3	–4, 10, –4	n/a	n/a	–6, 2, –6	n/a
	$a_p \times 1.05$	$a_p \times 0.95$	$k_p \times 1.05$	$k_p \times 0.95$	$\theta_P \times 1.05$	$\theta_P \times 0.95$
Changes in the length–tension curves*	3.4	4.6	3.2	3.6	3.9	2.4
Changes in strains of muscle–tendon unit, fascicles and tendon, respectively[†]	–2, 9, –2	n/a	2, –15, 2	1, –8, 1	4, –30, 4	n/a
	$a_d \times 1.05$	$a_d \times 0.95$	$k_d \times 1.05$	$k_d \times 0.95$	$\theta_D \times 1.05$	$\theta_D \times 0.95$
Changes in the length–tension curves*	6.4	5.3	5.4	8.9	2.8	6.0
Changes in strains of the muscle–tendon unit, fascicles and tendon, respectively[†]	–2, 9, –2	–2, 8, –2	–3, 10, –3	n/a	–1, 7, –1	0, 0, 0

(B) Effects of biases in measured passive ankle torques

	Raw torque increased 2%	Raw torque decreased 2%	Raw torque increased 5%	Raw torque decreased 5%
Changes in the length–tension curve*	0.9	1.7	4.2	2.9
Changes in strains of the muscle–tendon unit, fascicles and tendon, respectively[†]	n/a	0, 0, 0	3, –24, 3	–1, 5, –1

(C) Effects of biases in measured footplate torques and calculating foot torques

	Footplate torque increased 5%; foot torque increased 25%	Footplate torque decreased 5%; foot torque increased 25%;	Footplate torque increased 5% foot torque increased 25%	Footplate torque increased 5%; foot torque increased 25%
Changes in the length–tension curve*	1.4	3.4	3.0	3.4
Changes in strains of the muscle–tendon unit, fascicles and tendon, respectively[†]	n/a	n/a	3, –3, 3	2, –20, 2

Sensitivity was tested by adding errors to the passive length–tension curve of one randomly selected subject. Errors were added to each of the nine estimated model parameters (±5%), raw passive ankle torque data (±2% and 5%) and the weight torques due to the footplate (±5%) and the foot (±25%).

*Changes in length–tension curves were calculated by root-mean-square estimates of the curves and expressed as a percentage of maximal control passive tension.

[†]Changes in strains of the muscle–tendon unit, muscle fascicles and tendon are expressed as deviations from the control values of strain calculated for this randomly chosen subject, which are 21%, 82% and 14% for the muscle–tendon unit, muscle fascicles and tendon, respectively. Minus and plus signs indicate that the new strain values are lower or higher than control values, respectively. n/a indicates that the new values of slack length of the muscle–tendon unit are shorter than the shortest length; therefore, it was not possible to use Eqn 3 to calculate slack length of the fascicles.

The tendon strain reported in this study includes strain of both intramuscular (aponeurosis) and extramuscular (free tendon) parts of the tendon. The design of the study did not allow us to differentiate the passive properties of the two parts. The question as to whether the stiffness of the aponeurosis is similar to the stiffness of the free tendon is controversial. Some studies on animal muscles show that the stiffness of aponeurosis and the free tendon is similar (Rack and Westbury, 1984; Scott and Loeb, 1995; Trestik and Lieber, 1993) while other studies on animal muscles find differences (Ettema and Huijing, 1989; Lieber et al., 2000; Lieber et al., 1991). Ultrasonographic studies of human muscles also give discordant results. Some authors report that the strain of the aponeurosis and free tendon of the human gastrocnemius are similar (Arampatzis et al., 2005; Muramatsu et al., 2001) whereas others have concluded that the strain of the aponeurosis is different from that of the free tendon (Maganaris and Paul, 2000; Magnusson et al., 2003). All of

these observations have been made on contracting muscles and, because it is possible that the aponeurosis changes its intrinsic properties when the muscle contracts (Ettema and Huijing, 1989; Lieber et al., 2000), they may not apply to passive muscle.

Our methods rely on estimates of moment arms obtained from cadavers. In an earlier paper, we argued that these estimates are likely to be accurate on average, but we showed that when individuals' moment arms departed substantially from average values, length–tension curves could be substantially in error (Hoang et al., 2005). The estimation of nine non-linear parameters also presents a potential difficulty. However, we consistently obtain estimates that are plausible, as demonstrated, for example, by values of muscle–tendon slack length that are close to the shortest *in vivo* length. To assess the sensitivity of parameter estimates to errors in estimation of other parameters, we conducted an analysis in which we first obtained parameter estimates in the usual way and then we fixed the value

Table 4. *Median values and quartiles of nine estimated model parameters obtained via quasi-Newton optimization using Eqn 1*

	a_p	k_p	θ_P	a_d	k_d	θ_D	a_g	k_g	l_G (cm)
Median	−11.617	−0.727	−72.234	2.540	0.008	243.680	0.053	92.428	41.381
1st quartile	−24.551	−28.619	−213.139	1.207	0.005	142.779	0.008	81.776	40.994
3rd quartile	1.153	−0.111	66.866	4.509	0.019	438.225	0.274	128.868	42.570

See List of symbols for definitions of parameters.

of a single parameter at 5% above or below its estimated value before re-estimating the remaining eight parameters. The analysis showed that, while errors of 5% produced small to moderate changes in length–tension curves, there was no evidence of an excessive sensitivity of length–tension curves to errors in the estimates of individual parameters (the largest change was 9% of the initial maximal passive tension). In addition, to assess the sensitivity of parameter estimates to biases in the measured ankle torques, we systematically increased or decreased the final torques used for data analysis by 2% and 5%, and then re-estimated the nine parameters (see Materials and methods). This analysis showed that errors of 2% or 5% in the measurement of ankle torques resulted in approximately proportional changes in the length–tension curve but there was not an excessive sensitivity to the errors in ankle torque. It also showed that, for the subject randomly chosen for the sensitivity analysis, adding 5% errors to the parameters and biases to the ankle torque and weight torques produced only small changes in the maximum strains of the muscle–tendon unit, the fascicles and the tendon (Table 3).

Huijing and colleagues have conducted a series of studies on rat muscles *in situ* in which they demonstrated length-dependent differences between forces measured at the distal and proximal insertions of the muscle (Yucesoy et al., 2003). This suggests there is some transmission of force to adjacent structures, presumably by extramuscular connective tissue (Maas et al., 2005). The presence of inter-muscular myofascial force transmission would violate the assumption, made in our analysis, that passive tension in the gastrocnemius depends only on the knee and ankle angles. However, one observation strongly suggests that force transmission *via* extramuscular connective tissue has negligible effects on passive properties of the human gastrocnemius muscles *in vivo*: in all subjects we observed the same relationship between ultrasonographically measured changes in muscle fascicle length and the length of the muscle–tendon unit at different knee angles (Fig. 4). That is, regardless of whether the lengthening occurred by changing ankle or knee position, we observed the same relationship between muscle fascicle length and the length of the muscle–tendon unit. In addition, a recent study (Lichtwark et al., 2007) shows that the medial gastrocnemius muscle fascicles act in a similar way along the length of the muscle belly (distal, midbelly and proximal) during both walking and running and that muscle fascicle lengths are similar along the length of the muscle belly throughout the gait cycle (a difference of ~4 mm between distal and proximal fascicles). Our observations and those of Lichtwark and colleagues (Lichtwark et al., 2007) suggest there are not functionally important extramuscular myofascial connections between the human gastrocnemius and adjacent tissues.

Care needs to be taken with the interpretation of the length–tension curves in Fig. 5. Tension is not distributed uniformly in the extramuscular and intramuscular parts of the tendon, nor is it distributed uniformly in muscle fascicles and intramuscular tendon (Epstein et al., 2006). Thus, the length–tension curves do not show the relationship between the length of each element (muscle fascicles or tendons) and the tension in that element. Instead, they show the relationship between the length of each element and the tension at the origin and insertion of the muscle–tendon unit. Consequently, comparison between our length–tension curves and those derived from isolated muscle or tendon tissue is not straightforward. Nonetheless, the data do have a pragmatic interpretation: they indicate how much each element lengthens, and how much each element contributes to the total change in muscle–tendon length, when tension is applied to the muscle–tendon unit.

In conclusion, we have shown that it is possible to quantify length–tension properties of the muscle fascicles and tendons of a relaxed human muscle *in vivo*. The human gastrocnemius muscle–tendon unit falls slack over about one-quarter of its *in vivo* length. The muscle fascicle strains are much greater than the tendon strains but, because the tendons are much longer than the muscle fascicles, the tendons contribute more than half of the total passive compliance of the muscle–tendon unit.

List of symbols

a_g, k_g constants determining stiffness of the length–tension curve of gastrocnemius (estimated with non-linear regression using Eqn 1)

a_p, k_p, a_d, k_d constants determining the stiffness of single-joint structures that cross the plantar and dorsal aspects of the ankle (estimated with non-linear regression using Eqn 1)

b, c, d parameters of the regression of muscle fascicle length against muscle–tendon unit length (estimated with linear regression using Eqn 3)

F tension in the gastrocnemius (calculated with Eqn 2)

l_f length of muscle fascicles (measured)

l_F slack length of muscle fascicles (calculated with Eqn 3)

l_g instantaneous length of gastrocnemius [calculated from anthropometric data and θ_a, θ_k using equations of (Grieve et al., 1978)]

l_G slack length of gastrocnemius (estimated with non-linear regression using Eqn 1)

l_T slack length of the tendon, calculated by subtracting the slack longitudinal displacement of the muscle fascicles from the slack length of gastrocnemius

m_g moment arm of the gastrocnemius at the ankle
         (calculated by differentiation of l_g with respect to
         θ_a)
α, α_s,   fascicle pennation, fascicle pennation at slack
α_{max} length and fascicle pennation at maximum
         length, respectively (measured)
τ_{ankle} passive ankle torque (measured)
θ_a, θ_k ankle and knee angles, respectively (measured)
θ_P, θ_D ankle angles at which single-joint structures acting
         across the plantar and dorsal aspects of the ankle,
         respectively, fall slack (estimated with non-linear
         regression using Eqn 1)

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