In vivo human gastrocnemius architecture with changing joint angle at rest and during graded isometric contraction

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1. Human gastrocnemius medialis architecture was analysed *in vivo*, by ultrasonography, as a function of joint angle at rest and during voluntary isometric contractions up to the maximum force (MVC).

2. At rest, as ankle joint angle increased from 90 to 150 deg, pennation increased from 15·8 to 27·7 deg, fibre length decreased from 57·0 to 34·0 mm and the physiological cross-sectional area (PCSA) increased from 42·1 to 63·5 cm^2.

3. From rest to MVC, at a fixed ankle joint angle of 110 deg, pennation angle increased from 15·5 to 33·6 deg and fibre length decreased from 50·8 to 32·9 mm, with no significant change in the distance between the aponeuroses. As a result of these changes the PCSA increased by 34·8%.

4. Measurements of pennation angle, fibre length and distance between the aponeuroses of the gastrocnemius medialis were also performed by ultrasound on a cadaver leg and found to be in good agreement with direct anatomical measurements.

5. It is concluded that human gastrocnemius medialis architecture is significantly affected both by changes of joint angle at rest and by isometric contraction intensity. The remarkable shortening observed during isometric contraction suggests that, at rest, the gastrocnemius muscle and tendon are considerably slack. The extrapolation of muscle architectural data obtained from cadavers to *in vivo* conditions should be made only for matching muscle lengths.

The architecture of human pennate muscles has been described mainly with the muscle at rest and using data obtained in preserved cadavers as reference values of fibre length and pennation angle. These values have then been commonly used to describe the mechanical properties of active muscles in the course of isometric tetani on the assumption that upon contraction, the change in length of the muscle and its tendons was small enough not to affect the results. This approach now seems to be questionable for three reasons. First of all, it is well known that preserved muscle fibres undergo shrinking during the fixing process (Yamaguchi, Sawa, Moran, Fessler & Winters, 1990). Secondly, the length of muscle fibres at rest is several millimetres shorter than that of dead fibres (Rack & Westbury, 1969) and this finding should be taken into account when considering the length–tension relation of a muscle. Thirdly, pennation angle and fibre length change both as a function of muscle length at rest (Muhl, 1982; Huijing & Woittiez, 1985), the human brachialis muscle perhaps representing an exception (Herbert & Gandevia, 1995), and as a function of isometric contraction intensity (Muhl, 1982; Huijing & Woittiez, 1985). Drastic changes in muscle architecture have indeed been shown to occur during contraction as fibres shorten, swing across their insertion point increasing their pennation angle, and pull the aponeuroses towards each other (Gans & Bock, 1965). Knowledge of these quantitative morphological changes is essential for understanding the mechanics of isometric processes of pennate muscles and the energetics thereof. This approach has been followed by Muhl (1982) on the rabbit digastric muscle by taking photographs of the rabbit digastric muscle at rest and during isometric contractions at different muscle lengths, and by Griffiths (1991) using ultrasound techniques on the cat medial gastrocnemius at rest and during isometric and lengthening contractions. Until recently, however, studies of the architecture of human muscle *in vivo* were scanty. Since the introduction of non-invasive techniques, such as magnetic resonance

imaging (MRI) and ultrasonography (US), it has become possible to describe human muscle architecture *in vivo* both at rest (Narici, Landoni & Minetti, 1992; Rutherford & Jones 1992; Henrikkson-Larsen, Wretling, Lorentzon & Öberg 1992) and in the contracted state (Narici, Binzoni, Hiltbrand, Fasel & Apicella, 1994; Herbert & Gandevia, 1995; Kuno & Fukunaga, 1995; Fukashiro, Itoh, Ichinose, Kawakami & Fukunaga, 1995). In a brief report of a study using ultrasonography, the architecture of the human gastrocnemius was described for the first time *in vivo* both at rest and in the contracted state (Narici *et al.* 1994). The present study, representing an expansion of this earlier work, was designed to answer the following questions. (1) Does human gastrocnemius architecture change with varying ankle joint angles at rest? (2) What are the changes of human gastrocnemius muscle architecture during isometric contractions of increasing intensity up to the fully contracted state? (3) How does the ultrasound technique compare with direct anatomical inspection in evaluating muscle architectural features?

METHODS

Subjects

The present investigation was conducted on the gastrocnemius medialis (GM) muscle of six healthy males (age, 38·0 ± 8 years; height, 1·76 ± 0·05 m; mass, 67·8 ± 6·5 kg) whose muscle architectural features were studied both at rest and during isometric plantar flexions of increasing intensity up to the maximum voluntary contraction (MVC). The subjects gave their written informed consent to participate in this study and the protocols were approved by the Ethical Committee of the Istituto di Tecnologie Biomediche Avanzate, Consiglio Nazionale delle Ricerche.

Determination of muscle volume and muscle length

This was done from a series of eighty contiguous MRI axial images, 5 mm thick, obtained at rest with a whole body 1·5 T scanner (Picker International, Highland Heights, OH, USA). During the scanning, the subject lay supine with the base of the foot resting on a polystyrene block to maintain an angle of 90 deg to the tibia. A 3-D, fast feed echo sequence with an echo time of 15 ms and repetition time of 35 ms was used. The central slice was placed at the mid-belly of the gastrocnemii. Before each scanning session the MRI signal was checked for space calibration using water-filled phantoms. For each of the eighty axial images the anatomical cross-sectional area (ACSA) of the gastrocnemius medialis (GM) was calculated.

For GM muscle volume calculation all slices were fitted with a spline algorithm in order to interpolate for the missing slices. The total volume was then calculated by adding up the individual ACSA of each image and multiplying the sum by the slice thickness (5 mm). The error of muscle volume estimation from MRI images has previously been shown to be within ±3% (Narici *et al.* 1992) and the repeatability of PCSA determination by MRI, tested with a test–retest analysis, was characterized by an r^2 value of 0·98.

Muscle length was measured as the distance between the most proximal and most distal images in which the GM was identifiable.

Force measurements

The subjects sat on a couch with the back supported and the lower limbs fully extended. All measurements were carried out on the right leg, dominant in all the subjects, with the foot positioned at 90 deg relative to a footplate. A previous MRI sagittal examination of the ankle showed that with the foot set in this position the corresponding ankle joint angle was 112 deg. The force exerted by the plantar flexors was measured by connecting the footplate to a force transducer (FN 3030; FGP Instrumentation, Les Clayes-sous-Bois, France) with a steel cable 3 mm in diameter. From the footplate, the steel cable ran parallel to the limb of the subject to the force transducer, which was attached to the frame of the couch just laterally to the waist of the subject. Care was taken to maintain the cable normal to footplate and force transducer. The compliance of this measuring system was 0·003 mm N^{-1}, which implies that, at MVC, the maximum extension of the system was about 2 mm. The output of the force transducer was fed into an amplifier (portable indicator PR2500; Leane International, Monticelli, Parma, Italy), with a liquid crystal display visible both to the subject and to the operator, and was displayed on paper on a chart

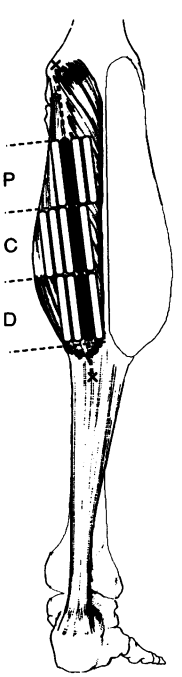

Figure 1. Posterior view of the gastrocnemius medialis showing the proximal (P), central (C) and distal (D) regions investigated by ultrasound
The filled regions indicate the measurements performed along the mid-sagittal axis (indicated by the dashed line running between the two crosses) in all subjects. The open regions indicate the additional measurements performed medially and laterally to the mid-sagittal axis in two subjects.

recorder (Servogor 420; ABB Metrawatt, Nürnberg, Germany). Each subject was asked to perform eight to ten isometric plantar flexions, 4 s in duration at 30 s intervals, from rest to 100% of the MVC, and to hold each contraction steady for at least 2 s. The exact force developed during the steady state of each contraction was recorded.

Pennation angle, fibre length and distance between aponeuroses

These architectural features of the GM were assessed from images obtained with a real time computerized sonograph (Acuson 128XP, Mountain View, CA, USA) using a 7·5 MHz probe 4 cm long and 1 cm thick. During the scanning, the subjects sat on a couch with the back supported at a right angle to the legs by a rigid structure. The lower limbs were fully extended over the couch and the right ankle rested on a footplate. A gap of about 50 cm was allowed in the couch under the right leg to give free access to the calf muscle with the US probe. The probe was positioned normal to the surface of the right GM and oriented along the median longitudinal axis of the muscle (Fig. 1). This axis was determined by marking the distal end of the muscle belly and the proximal tendon, which can be localized at the level of the knee joint, and by joining the two marked sites. Along this axis, three adjacent regions, each 4 cm in length, were investigated, a proximal (P), a central (C) and a distal one (D) with reference to the distal end of the GM. For each US image of regions P, C and D, pennation angle (θ) was measured at the fibre insertions into the superficial and deep aponeuroses, and the two values were then averaged (θ_{mean}). Fibre length (L_f) was measured as the distance between the insertions of the fibre into the superficial and deep aponeuroses. The distance (t) between aponeuroses was measured on either side of each image and then averaged. Measurements of L_f, θ and t were performed on-line using a dedicated piece of software. These measurements were performed both at rest and during isometric plantar flexions of increasing intensity up to MVC. During the steady state of each contraction an US image was acquired, digitalized and stored in the memory of a hard disk of a Macintosh LC-II computer connected on-line. Typical US images obtained at rest and at MVC, respectively, are shown, for region C, in Fig. 2*A* and *B*.

The repeatability of the measurements of pennation angle, fibre length and aponeurosis distance was tested by performing seven separate US scans of region C in one subject. Altogether, sixty-six angles of pennation, thirty-three fibre lengths and fourteen aponeurosis distances were analysed in this subject.

Physiological cross-sectional area estimation

From the architectural features of the GM, the reduced physiological cross-sectional area (PCSA) was calculated according to the equation:

$$\text{PCSA} = \left(\frac{m}{\rho L_f}\right)\cos\theta,$$

which simplifies to:

$$\text{PCSA} = (V/L_f)\cos\theta,$$

where m is muscle mass, ρ is muscle density (1·050 g cm^{-3}), V is muscle volume, θ is the angle of pennation and L_f is fibre length.

Effect of joint angle on GM architecture at rest

To investigate the effect of changing muscle length on GM architecture at rest, US measurements were repeated when changing the ankle joint angle from 90 to 150 deg, in steps of 5 deg. The ankle joint angle was measured with an electronic goniometer (Penny and Giles, angle display unit ADU201, Biometrics Ltd, Blackwood, Gwent, UK) with a liquid crystal display visible to the operator.

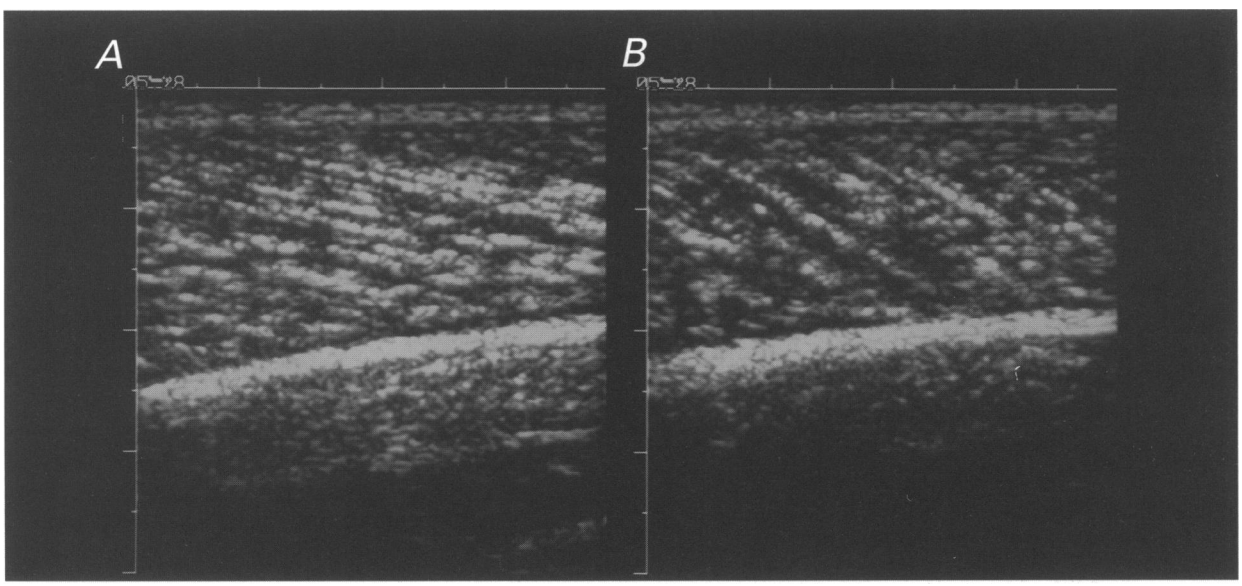

Figure 2. Sonograph of the gastrocnemius medialis muscle

A, sagittal image obtained at rest, at an ankle joint angle of 110 deg. *B*, sagittal image obtained during an isometric MVC at an ankle joint angle of 110 deg. In the images the pennation of the fibre fascicles is identifiable as the diagonal striations running across the muscle from the deep to the superficial aponeuroses. In each image the large ticks on the horizontal and vertical scales correspond to 1 cm.

Analysis of GM architecture across and along the muscle belly

In addition to the US images obtained along the median longitudinal axis of the GM, a series of pennation angles and fibre lengths were also measured on two subjects, at rest and at the MVC, at four or five adjacent sites positioned laterally and medially to the mid-sagittal axis running along the GM belly (Fig. 1). Each US image allowed ten to twelve measurements of pennation angle, five or six measurements of fibre length and two measurements of the distance between the aponeuroses. These measurements were repeated in regions P, C and D, for a total of eleven to thirteen investigated sites, to compare resting values of fibre length and pennation angle both along and across the muscle belly. Additional aims of this set of experiments were to find out: (1) whether the data obtained at rest for the three regions along the mid-sagittal axis were comparable to those found in the medial and lateral portions of the muscle; and (2) whether the changes in pennation and fibre length observed at the fully contracted state were homogeneous across the mediolateral axis or were affected by a possible fibre rotation.

Comparison of ultrasound-determined muscle architecture with direct anatomical measurements

In order to check the accuracy of the US technique, the architectural parameters of the GM of a human cadaver were assessed both by US and by direct measurement. The anatomical specimen used in this study was from a 62-year-old male who placed *expressis verbis*, by his last will, his body at the disposal of the medical sciences. The *corpus* had been fixed according to routine embalming procedures. The leg was positioned and investigated by US as for the aforementioned *in vivo* measurements. The longitudinal axis and the three regions investigated by US were marked on the skin of the specimen. Following the US investigation the corresponding planes were demonstrated anatomically by vertical incisions through all layers of the calf along the marked longitudinal axis (Fig. 3). *In situ* inspection of the slice surface corresponding to the median longitudinal plane was performed by retraction of the adjacent lateral part of the muscle, thus maintaining the medial half in an unaltered position and length. On the exposed slice surface, the parameters (superior and inferior pennation angles, fibre length, distance between the superficial and deep aponeuroses) were measured *in situ*. The slices were then resected, maintained at the same length, rested on a wax plate and re-measured. Finally, the resected slices were photographed and once again the parameters were measured. These three measurements were compared with the US findings.

The medial head of the gastrocnemius medialis, when considered as an individual muscle, can be conceived as unipennate in the sagittal plane. The fasciculi pass obliquely between the proximal superficial and the distal deep aponeuroses (Strasser, 1917). With regard to the

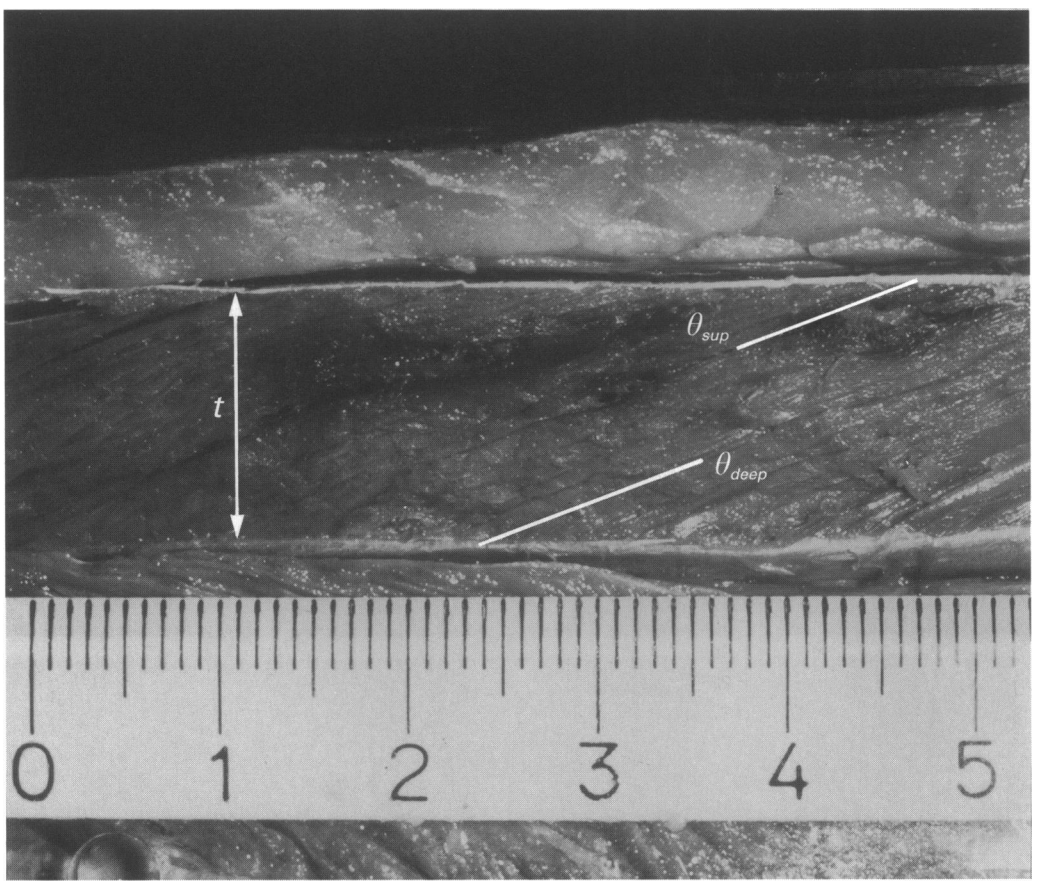

Figure 3. Mid-sagittal section, lateral view of the right gastrocnemius medialis of the investigated cadaver

Deep and superficial pennation angles of muscle fibre fascicles are indicated by θ_{deep} and θ_{sup}, respectively. t is the distance between the deep and superficial aponeuroses. In the scale 4 cm (the length of the probe) corresponds to the length of each region investigated by ultrasound.

longitudinal axis of the muscle, the fasciculi take essentially a parallel course in the distal part of the muscle belly. As one moves towards the proximal region of the muscle, fibres increasingly converge in the direction of the proximal tendon, which is attached to the region over the medial femoral condyle. In the longitudinal axis itself, the fasciculi remain parallel also in the proximal portion of the muscle. In the present study the muscle was examined along this axis taking its course from the distal end of the muscle belly to the proximal tendon. By this procedure it could be assumed that with the US procedure the fasciculi were investigated along their longitudinal axis.

Statistics

Data are reported as mean values ± S.D. Significance of differences was analysed by means of Student's paired t test for rest and MVC measurements. One-way analysis of variance (ANOVA) was used for comparison of t, θ and L_f in the various sections of regions P, C and D. In the event of significant values of F in the ANOVA, the Scheffé test of critical differences was used to locate significance between means. Level of significance was set for P values of less than 0·05. Linear regressions were used to describe the relation between fibre length and force, and between pennation angle and force. Non-linear equations were used to describe the relation at rest between pennation angle, fibre length and joint angle and between fibre length and pennation angle.

RESULTS

Muscle volume and muscle length

Out of the eighty contiguous MRI axial images, the GM extended over a total number of images ranging from forty-eight to fifty-seven. Summation of the volumes between contiguous MRI slices gave a total GM muscle volume of 245·9 ± 36·7 cm^3. GM muscle length measured between the most proximal and most distal MRI axial images was 27·0 ± 1·6 cm.

Effect of joint angle on GM architecture at rest

At rest, pennation angle and fibre length were found to be closely dependent on ankle joint angle (Fig. 4*A*). The data of the relations of θ and L_f *versus* joint angle (α) were fitted (least-squares method) with variable power functions, $\theta = 0{\cdot}0022(\alpha^2 - 0{\cdot}339)(\alpha + 28{\cdot}489)$ ($r^2 = 0{\cdot}997$, $P < 0{\cdot}001$), and $L_f = -0{\cdot}0026(\alpha^2 - 0{\cdot}260)(\alpha + 53{\cdot}825)$ ($r^2 = 0{\cdot}995$, $P < 0{\cdot}001$). It can be observed from Fig. 4*A* that, as joint angle increased, pennation angle significantly increased from 15·8 ± 2·0 to 27·7 ± 2·3 deg ($r^2 = 0{\cdot}995$, $P < 0{\cdot}001$). This was accompanied by a decrease in L_f from 57·0 ± 3·0 to 34·0 ± 1·5 mm ($r^2 = 0{\cdot}997$, $P < 0{\cdot}001$). Using the above functions, when pennation angle is plotted against fibre length, it can be observed that the increase in pennation angle is tightly accommodated by the concomitant decrease in fibre length (Fig. 4*B*). When PCSA is calculated using the L_f and θ of Fig. 4*B*, it can be seen that, as joint angle α increases from 90 to 150 deg, PCSA increases by 51 %, from 42·1 to 63·5 cm^2 (Fig. 4*C*).

Fibre pennation, fibre length, distance between aponeuroses and PCSA

The muscle fibres' pennation angle, fibre length and distance between the aponeuroses as a function of force at 110 deg of joint angle, are shown from rest to MVC for regions P, C and D in Fig. 5. A linear increase in pennation angle ($P < 0{\cdot}001$) with force was observed for all three regions (Fig. 5*A*). This effect was accompanied by a linear decrease in fibre length ($P < 0{\cdot}001$, Fig. 5*C*). Measurements of L_f were limited to region C because they were particularly time consuming. No significant change in distance between aponeuroses was observed during muscle contractions from rest to MVC for regions P, C and D (Fig. 5*B*). A comparison of the mean values of θ_{mean}, L_f (region C only), t, and the resulting PCSA, at rest and at MVC are presented for regions P, C, and D in Table 1. As shown in this table, in the transition from rest to MVC, pennation angle increases on average from 15·5 to 33·6 deg ($P < 0{\cdot}001$); fibre length decreases by 35·2% from 50·8 to 32·9 mm ($P < 0{\cdot}001$). There was no significant change in distance between aponeuroses from rest to MVC. The PCSA increased by 34·8 ± 20·1 %, from 46·5 ± 5·7 to 62·5 ± 10·8 cm^2 ($P < 0{\cdot}01$).

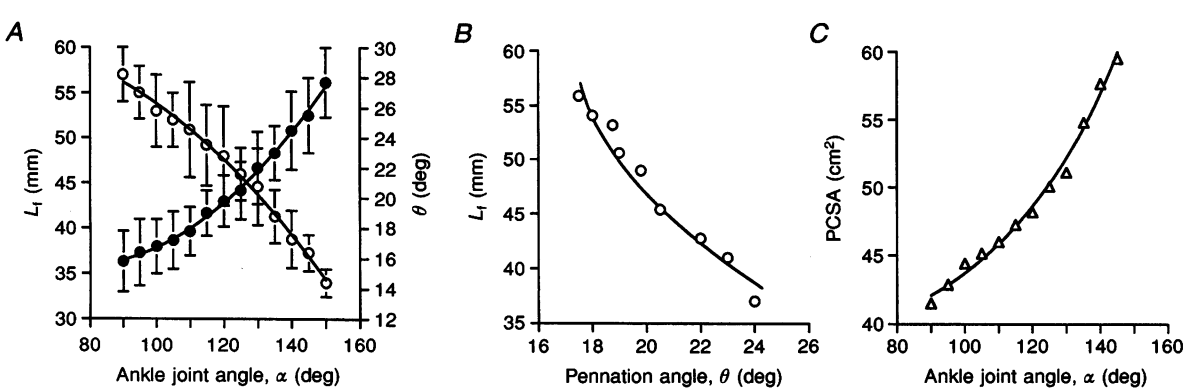

Figure 4. Gastrocnemius medialis architecture as a function of ankle joint angle, at rest

A, fibre length (L_f, ○) and pennation angle (θ, ●) as a function of ankle joint angle (α) at rest (values are means ± S.D.). *B*, the relation between fibre length and pennation angle at rest. *C*, the relation between physiological cross-sectional area (PCSA) and ankle joint angle, at rest.

Table 1. Pennation angle (θ), fibre length (L_f), distance between aponeuroses (t) and physiological cross-sectional area (PCSA) at rest and at the MVC in GM regions P, C and D

	θ_{mean} (deg)	L_f (mm)	t (mm)	PCSA* (cm^2)
P				
Rest	16·2 ± 5·9	—	21·1 ± 3·4	—
MVC	35·0 ± 7·8†	—	18·2 ± 2·6 (n.s.)	—
C				
Rest	17·3 ± 2·6	50·8 ± 3·6	19·8 ± 2·3	46·5 ± 5·7
MVC	35·3 ± 4·1†	32·9 ± 2·6†	18·5 ± 3·1 (n.s.)	62·5 ± 10·8‡
D				
Rest	13·0 ± 2·3	—	17·2 ± 3·2	—
MVC	30·4 ± 5·8†	—	16·5 ± 2·5 (n.s.)	—

Values are means ± S.D. * PCSA = $(V/L_f)\cos\theta$. † $P < 0{\cdot}001$, ‡ $P < 0{\cdot}01$.

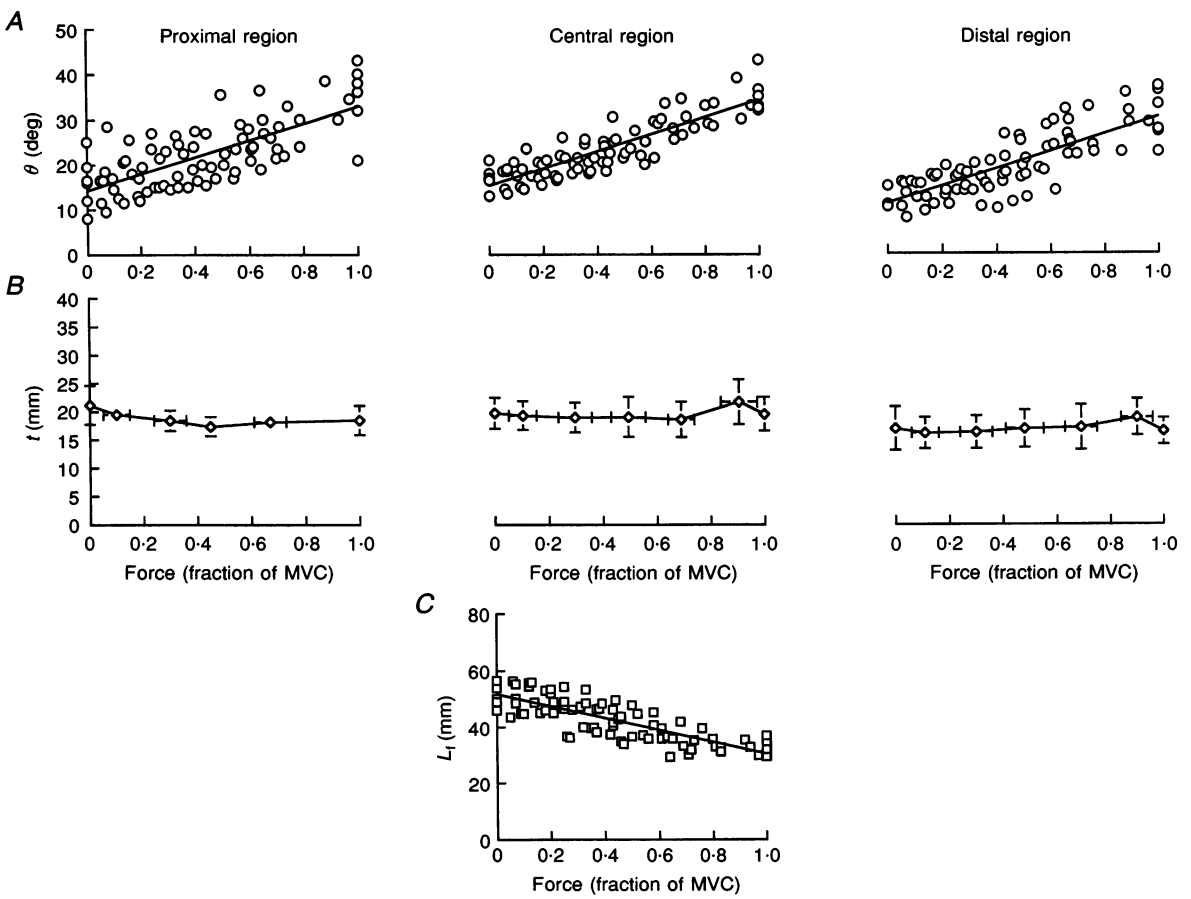

Figure 5. Gastrocnemius medialis architecture as a function of isometric contraction intensity (fraction of MVC) in the proximal, central and distal regions of the muscle

A, pennation angle (θ). *B*, distance between aponeuroses (t). *C*, fibre length (L_f). Fibre length measurements were limited to the central region.

Table 2. Analysis of GM muscle architecture in two subjects in regions P, C and D

	θ (deg)	L_f (mm)	t (mm)
Rest			
P	22·3 ± 3·7 (18·7–27·0)	49·2 ± 4·7 (42·5–52·5)	18·6 ± 1·9 (18·7–27·0)
C	20·9 ± 4·8 (14·6–25·2)	53·0 ± 7·7 (45·2–60·5)	19·5 ± 0·9 (15·5–20·2)
D	17·2 ± 1·6 (15·3–19·3)	59·0 ± 7·4 (51·0–69·0)	16·9 ± 1·9 (14·5–18·8)
MVC			
P	37·1 ± 6·9 (28·2–45·0)	31·3 ± 3·0 (27·0–33·9)	18·0 ± 2·3 (16·5–20·2)
C	34·1 ± 3·7 (29·5–38·4)	34·4 ± 4·8 (30·4–41·7)	19·1 ± 1·1 (17·7–20·3)
D	29·1 ± 2·2 (27·0–32·3)	36·2 ± 1·5 (34·3–37·7)	17·8 ± 1·9 (16·6–20·7)

Values shown are means ± S.D. (range).

Analysis of GM architecture across and along the muscle belly

The data obtained in the two subjects in whom measurements of θ, L_f and t were repeated on sites across the lateral to medial axis of regions P, C and D of the GM at rest and at MVC are shown in Table 2. No significant differences were found, either at rest or at the MVC, between the values of t, θ and L_f across the lateral to medial sites of each of the regions P, C and D. Similarly, along the proximal to distal regions, the values of t, θ and L_f did not differ significantly between P, C and D, although a tendency, albeit non-significant, for a decrease in θ and an increase in L_f was observed from regions P to D. At the MVC, changes in t were non-significant and both absolute and percentage changes in θ and L_f did not differ significantly between regions P, C and D. Therefore, it was concluded that the measurements performed along the mid-sagittal axis were representative of the GM architecture both at rest and in the contracted state.

Maximum voluntary contraction force of plantar flexors

The maximum isometric MVC of the plantar flexors, measured at a footplate angle of 90 deg, was 755·3 ± 23·8 N. In order to calculate the tendon component, the MVC was divided by 0·308 ± 0·02, the mechanical advantage of this lever system. This was given by the ratio between the moment arm of the Achilles' tendon, 4·7 ± 0·1 cm, measured on a MRI image at a footplate angle of 90 deg (with respect to the tibia) and the moment arm of the external force, 15·2 ± 1·0 cm. Both moment arms were measured as the distance from the centre of rotation of the ankle as reference point. The resulting tendon force component was 2489 ± 200 N.

GM architecture obtained by the US technique and by direct measurement on the anatomical specimen

In Table 3 the architectural data evaluated in the proximal, central and distal region of the human cadaver leg by US and by direct measurement on the anatomical specimen are presented. As can be observed from this table, good agreement exists between the two techniques in terms of pennation angles, fibre length and distance between the aponeuroses.

Repeatability of the US measurements performed at rest

From the analysis of the seven separate US scans obtained in one subject, it was found that the coefficient of variation (S.D./mean) of repeated measurements was 4·8% for t (< 2 mm), 9·8% for θ (< 2 deg), and 5·9% for L_f (< 4 mm).

DISCUSSION

This study describes, for the first time, the architecture of the human gastrocnemius muscle *in vivo*, both at rest and during isometric plantar flexions up to the fully contracted state. At variance with previous studies, the reliability of the ultrasound technique for the measurement of muscle architectural parameters was tested by direct comparison on a human cadaver limb and found to be in good agreement. The present values of pennation angle and fibre length obtained at rest, *in vivo*, are in line with the values of 18 deg and 52 mm, respectively, reported by Huijing (1985), although the PCSA of the present study is 48% greater than that found by Huijing. This difference is probably accounted for by muscle volume being 35% smaller (160 cm^3) in the study of Huijing (1985), compared with our study (246 cm^3). In the study of Huijing (1985) muscle volume was measured on preserved cadavers, whose muscle fibres were presumably shrunk by the fixation process, whereas in the present study it was measured *in vivo*.

The results obtained *in vivo* indicate that human gastrocnemius muscle architecture drastically changes both as a function of ankle joint angle at rest and as a function of the force developed during isometric contractions at a fixed joint angle. At rest, when changing the ankle joint angle from 90 to 150 deg, GM pennation angle increased from

Table 3. Deep and superficial pennation angles (θ), fibre lengths (L_f) and distance between aponeuroses (t) measured by ultrasonography (US) and by direct anatomical inspection (AI) in regions P, C and D of the cadaver GM muscle

Image	θ_{deep} (deg)	θ_{sup} (deg)	L_f (mm)	t (mm)
P				
AI	21·0 ± 4·0	16·0 ± 1·7	39·9 ± 2·5	14·0
US	20·0 ± 1·6	14·0 ± 1·9	39·6 ± 1·9	13·3
C				
AI	20·7 ± 2·0	20·3 ± 1·5	36·6 ± 1·5	12·3
US	19·0 ± 1·0	19·0 ± 1·6	35·4 ± 1·7	10·4
D				
AI	18·7 ± 3·2	15·7 ± 2·9	35·8 ± 2·1	8·0
US	17·0 ± 2·1	13·0 ± 2·8	31·2 ± 3·9	8·3

Values are means ± S.D.

15·8 to 27·7 deg, fibre length decreased from 57·0 to 34·0 mm and, as a consequence, PCSA increased by 51%. These results indicate that fibre length and pennation angle of the human gastrocnemius cannot be assumed to remain constant with changing muscle length. This finding is in line with the observations of Huijing & Woittiez (1985) on the rat gastrocnemius and of Muhl (1982) on the rabbit digastric muscles, but is in contrast to recent findings of Herbert & Gandevia (1995) on the human brachialis muscle. A plausible explanation offered by Herbert & Gandevia (1995) to account for the lack of changes in pennation with elbow angle is the considerable slack of the brachialis muscle and of the tendon at rest. A greater slack of the brachialis compared with the gastrocnemius should be reflected in their respective active length–force (L–F) relation, since that of the brachialis should be narrower than that of the gastrocnemius. According to Woittiez, Huijing, Boom & Rozendal (1984), however, the active L–F relation should be narrower for muscles with a large pennation angle compared with those with small pennation angles. Then, since the mean pennation of the brachialis reported by Herbert & Gandevia (1995) is 9·0 deg and the present mean value for the gastrocnemius is 15·5 deg, one would expect the L–F relation of the gastrocnemius to be narrower than that of the brachialis. Therefore, it would be interesting if future ultrasound investigations were directed to the study of the L–F relation of human muscles of notably different pennation.

The decrease in fibre length and increase in pennation angle with increasing muscle length may be ascribed to the taking up of the slack characterizing these structures (Huijing & Woittiez, 1985). Using ultrasound, Ichinose, Kawakami & Fukunaga (1995) have recently shown on the human vastus lateralis that the slack of muscle fibres, at rest, is a function of knee joint angle. These authors observed that when the knee is fully extended, muscle fibres are remarkably slack, for they decrease by about 35% in length when contracting only by 10% of the MVC. Instead, when the knee is at 110 deg from full extension, muscle fibres are probably stretched and their length decreases by about 8% when contracting by 10% of the MVC. In the present study, the decrease in fibre length from 57 to 34 mm occurring from 90 to 150 deg of passive plantar flexion also suggests that muscle fibres became progressively slack with increasing ankle joint angles. Fibre length and pennation angle measured in cadavers would also refer to a specific muscle length and thus the extrapolation of such data to *in vivo* conditions may be made only for matching muscle lengths. A particularly noteworthy observation was that, at rest, the decrease in fibre length and increase in pennation angle resulted in an increase in PCSA of 51% as joint angle increased from 90 to 150 deg. This implies that calculations of muscle specific tension made without using the PCSA relating to the joint angle at which the force was measured may be considerably wrong.

The present study showed that from rest to MVC, pennation angle increased from 15·7 to 33·7 deg, whereas fibre length decreased from 50·8 to 32·9 mm, with no significant change in the distance between the aponeuroses. This finding agrees with the predictions of Gans & Bock (1965) according to whom, 'the thickening of pinnately arranged fibres is compensated for by the change in fibre angle during contraction; thus surfaces of origin and insertion remain parallel and equidistant'.

The 35% decrease in fibre length observed in the present study appears much greater than that expected from compliance values of isolated animal muscles, which range from 2 to 4% (Wilkie, 1956; Bobbert, Brand, de Haan, Huijing, Van Ingen Schenau & Woittiez, 1986) to 10%

(Bahler, 1967). However, the present findings are consistent with recent observations of R. C. Woledge (personal communication) on the human gastrocnemius medialis and of Ichinose *et al.* (1995) on the human vastus lateralis muscles. Moreover, a shortening of muscle fibres comparable to that found in the present study has been reported by Griffiths (1991) on the cat medial gastrocnemius muscle, whose fibres shorten by 28% during a maximal isometric contraction at optimal muscle length. These observations suggest that the human gastrocnemius aponeurosis and tendon are considerably compliant and add support to the view of Griffiths (1991) that these structures act as mechanical buffers, protecting the muscle from damage during high-intensity contractions, such as occur in eccentric conditions. The observed shortening of fibre length from 50·8 to 32·9 mm, in a muscle of resting length 270 mm, with a concomitant increase in pennation from 15·5 to 33·6 deg, results in an actual decrease in muscle length of 21 mm, equal to 8% of resting muscle length ((cos 15·5 deg × 50·8 mm − cos 33·6 deg × 32·9 mm)/270 mm). Since the change in muscle length due to the compliance of the force transducing apparatus was 2 mm, the effective change in muscle length in the presence of a perfectly rigid structure should have been 7·1%. This value is indeed in line with the range of muscle shortening reported for isolated animal muscles (Bahler, 1967).

From the data of Fukunaga *et al.* (1992), it may be calculated that the GM PCSA is about 18% of the total PCSA of the main plantar flexors (gastrocnemius medialis and lateralis, soleus, tibialis posterior and peroneus longus). Therefore, at MVC, the force developed by the GM should be 18% of the total force developed by the plantar flexors (2489 N), i.e. 448 N. Assuming that the stiffness of the elastic structures, 24·5 N mm^{-1}, described by Cavagna (1970) reflects the Achilles' tendon stiffness, then the expected decrease in muscle length due to stretching of the tendon and of the aponeurosis should be 18 mm (448 N/24·5 N mm^{-1}), which is not far from the observed decrease of 21 mm. Interestingly, the stiffness of the elastic structures reported by Cavagna (1970) matches that found in the Achilles' tendon of the wallaby by Griffiths (1989); however, this similarity may be purely coincidental, since the method used by Cavagna (1970) relied on the determination of the frequency of natural oscillations while that used by Griffiths (1989) referred to direct measurements on isolated free tendon.

Provided 448 N is a correct estimate of the GM contribution to the total force of the plantar flexors, the specific tension of this muscle should then be given by 448 N/46 cm^2, i.e. 9·7 N cm^{-2}. This figure seems rather low compared with the values of 38·3 and 25 N cm^{-2}, respectively, reported by Haxton (1944) in the same muscle group and by Narici *et al.* (1992) in the human quadriceps, but is in line with the value of 10·8 N cm^{-2} recently obtained by Fukunaga, Roy, Shellock, Hodgson & Edgerton (1996) in the gastrocnemius. The divergence between the values of specific tension in the present study and that of Fukunaga *et al.* (1996) from that of Haxton (1944) could be due to the fact that, in the first two studies, PCSA calculation was based on muscle volume measured *in vivo*, whereas in the latter study it was measured on preserved cadaver legs. The cadaveric muscles of Haxton's (1944) study were probably shrunk by the fixation process and were possibly atrophic because of old age, as indicated by their 48% smaller ACSA compared with the control living subjects of that study. Part of the difference between the present value of specific tension of 9·7 N cm^{-2} and the 25 N cm^{-2} estimated in the human knee extensors (Narici *et al.* 1992) may be explained by the fact that, in the present study, MVC was measured at a footplate angle of 90 deg. At this angle the force of the plantar flexors is 73% of that exerted at 110 deg, which is the optimal angle for maximum plantar flexion force (Sale, Quinlan, Marsh, McComas & Belanger, 1982). Correcting for the difference in the force at these footplate angles, the resulting specific tension of the GM should be 13·3 N cm^{-2} (9·7 N cm^{-2} × 1·37), which still leaves a considerable gap from the specific tension of the knee extensors. This finding supports the view of Fukunaga *et al.* (1996) that there may not be a common value of specific tension for all human muscles. According to these authors, the variance in specific tension among different human muscle groups may reflect an imperfect transmission of the force by any given muscle fibre to the tendon, since much of the tension may be transmitted to the tendon via the interfibre matrix of a muscle. However, it cannot be excluded that when strength testing involves several muscles acting at a joint, activation at a specific joint angle may not be maximal for all of them. In human arm muscles, van Zuylen, Gielen & van der Gon (1988) have indeed observed that the relative activation of the muscles varies with elbow angle. Changing joint angle affected the mechanical advantage of the elbow flexor and extensor muscles differently; those muscles with the greater mechanical advantage at a specific angle received the larger neural input. A similar mechanism could also exist for the human plantar flexors. Finally, this study has shown that at rest, PCSA considerably increases with joint angle. Therefore, a potential overestimation of specific tension may arise if the joint angles of PCSA and force measurements do not coincide.

The present study has shown that, in the fully contracted state, the increase in pennation angle and decrease in fibre length, assuming changes in muscle volume to be negligible (Baskin & Paolini, 1967), result in a 34·8% increase in PCSA. This, however, will have no consequence on the force per unit area of the GM muscle, since the force per half-sarcomere will still be the same.

The changes in muscle architecture observed from rest to MVC agreed fairly well with those predicted by a simple planar muscle model. Indeed, using a planar model for region C, the value of L_f, predicted at the MVC by a θ of 35·3 deg and a constant value of t of 19·8 mm, would be $\sin^{-1}$ 35·3 deg × 19·8 mm, equal to 34·2 mm. Thus the L_f

predicted by the simple planar model is only 3·9% greater than the observed value of 32·9 mm. Although a tendency, albeit non-significant, was observed for a greater absolute change in L_f of the distal fibres compared with the proximal ones (23 *versus* 18 mm), no differences were found between the relative shortening of muscle fibres of regions P, C and D. Therefore, the use of simple planar models in the gastrocnemius muscle seems to predict reliably the observed changes in architecture occurring with the contraction. This observation is consistent with the findings of Otten (1988), but is in contrast to those on the human brachialis by Herbert & Gandevia (1995), who raised doubts about the applicability of simple planar models of muscle architecture. The latter authors, however, reached this conclusion without measuring fibre length but measuring only pennation. The divergence between the present data on the gastrocnemius and those on the brachialis by Herbert & Gandevia (1995) may also suggest that the applicability of planar models depends on the individual muscle architecture. Van Leeuwen & Spoor (1992) developed a very comprehensive planar model of pennate muscle and found it to describe the architecture of embalmed human gastrocnemius muscle reliably. Their model took into account fibre curvature, which they observed on the dissected specimen. In the present study, however, in which architectural parameters were measured in the muscle *in situ*, no fibre curvature could be observed; the use of a simple planar model was thus considered suitable for the present conditions.

Finally, in most previous human studies, the fibre force component was calculated by multiplying the tendon force component by the cosine^{-1} of the angle of pennation measured in cadavers. The present results and those of Herbert & Gandevia (1995) demonstrate instead that pennation angle drastically increases upon contraction and makes the use of cadaver pennation data for the estimation of the fibre force component *in vivo* quite questionable.

In conclusion, this study has shown that good agreement exists between human gastrocnemius architecture obtained by ultrasound and by direct anatomical inspection. Pennation angle, fibre length and PCSA were significantly affected by changes of both joint angle at rest, and of contraction intensity, despite the imposed isometric conditions. The extrapolation of muscle architectural data obtained from cadavers to *in vivo* conditions should be made only for matching muscle lengths.

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