Abstract  The aim of the present study was to quantify changes in human skeletal muscle pennation angle ($F_\theta$) values during growth and adult life. The human gastrocnemius medialis muscle of 162 subjects (96 males and 66 females) in the age range 0–70 years was scanned with ultrasonography. The subjects were laying prone, at rest, with the ankle maintained at 90° with all muscles relaxed. $F_\theta$ increased monotonically starting from birth (0 years) and reached a stable value after the adolescent growth spurt. There was a significant (p<0.05) linear relationship between $F_\theta$ and muscle thickness ($TK$). $F_\theta = 0.84 \pm 0.09 \times TK + 3.15 \pm 1.13$. Human gastrocnemius medialis $F_\theta$ and TK data found in the literature seem to fit the $F_\theta$-TK plot in a coherent manner, independent of the physiological or anatomical characteristics of the subject. The present findings indicate that $F_\theta$ is not a constant parameter but evolves, as is the case for bone length and height, as a function of age. J Physiol Anthropol 20 (5): 293-298, 2001 http://www.jstage.jst.go.jp/en/

Keywords: human, skeletal muscle, pennation angle

Introduction

Human skeletal muscle architecture, i.e. the macroscopic arrangement of the muscle fibres, closely correlates with its function. The most important architectural parameters are pennation angle ($F_\theta$), muscle physiological cross sectional area and muscle fibre length (Lieber and Fridén, 2000). $F_\theta$ and muscle physiological cross sectional area are important determinants of the maximum force of contraction. Muscle fibre length is positively related to the speed of contraction. The first quantitative studies on muscle architecture have been pioneered by Gans & Bock (1965) and Gans & De Vree (1987). Until recent years, studies on humans have been performed on cadavers (Lieber and Fridén, 2000). With the introduction of sonography, non invasive studies of the human muscle architecture have become possible (Henriksson-Larsen et al., 1992; Rutherford & Jones, 1992) and, in particular, studies of muscular dynamics (Narici et al., 1994; Herbert & Gandevia, 1995; Kuno & Fukunaga, 1995). It has been demonstrated in humans that $F_\theta$, physiological cross sectional area and fibre length may vary as a function of joint position and force of muscle contraction (Narici et al., 1996; Herbert & Gandevia, 1995, Kawakami et al., 1998; Maganaris et al., 1998 Maganaris & Baltzopoulos, 1999), of the type of physical training (Kawakami et al., 1993; Abe et al., 2000; Kearns et al., 2000; Kumagai et al., 2000) and of gender (Chow et al., 2000).

The above observations highlight the fact that muscle architecture is subjected to a certain degree of plasticity. From a general point of view, in mammals, environmental pressure also seems to have contributed to architectural phylogenic adaptations. For example, the monkey Cynomolgus has the capacity to develop a considerable isometric force in its upper limbs (Roy, 1984), therewith facilitating the evolution in its natural environment. It happens that the Cynomolgus has a pennated biceps brachii while humans have not (Roy, 1984). Architectural differences of muscle may also be found within the same species. The Lemur catta and the Lemur fulvus show a different structure of their biceps femoris (Ward & Sussman, 1979), the latter having a higher $F_\theta$ value. This may be related to the fact that Lemur catta travels by ground over 65% of the time whereas the Lemur fulvus uses the upper level of the
canopy forest and is on the ground less than 2% of its time (Ward & Sussman, 1979). Pennation angle seems to increase with higher demands on muscle tasks.

We were interested in knowing whether some kind of adaptation, physiological or ancestral phylogenic change, also occur during human growth. In a newborn, one might expect to find small $F_\theta$ values in the lower limb muscles compared to an adult. Large $F_\theta$ allow to develop greater mechanical forces (Woittiez, 1984). One might speculate, that such a development is completely "useless" for a newborn who has not yet used his legs for weight bearing and locomotion. To test this hypothesis, the present study was undertaken to investigate, by ultrasonography, whether the human gastrocnemius medialis $F_\theta$ increases during subject growth.

**Methods**

**Subjects**

The present investigation was conducted on 134 subjects (87 males and 47 females) in the age range of 0–70 years. Height and weight values of each subject are reported in Figs. 1 and 2. The subjects gave their informed consent to participate in the study and the protocol was approved by the local Ethical Committee. For underaged subjects, informed consent was obtained from a parent. None had any clinical evidence of musculoskeletal disease, orthopaedic abnormality nor was involved in competitive physical activity.

**Ultrasound scanning**

Sonograms of the medial gastrocnemius muscle Images were obtained using a Sequoia (ACUSON, Mountain View, CA, USA) real time ultrasound scanner and a multifrequency (7.5–13 MHz) linear array transducer. Muscle thickness (TK) was measured on hard copy images as the distance between the superficial and the deep aponeurosis (Narici et al., 1994; Ichinose et al., 1995; Narici et al., 1996, Fukunaga et al., 1997). The angle between the fascicles echo and the superficial aponeurosis was defined as the muscle $F_\theta$ (Rutherford & Johnes, 1992; Narici et al., 1994; Ichinose et al., 1995; Narici et al., 1996, Fukunaga et al., 1997). The fibre bundle length ($F_L$) was estimated using the equation:

$$F_L = TK \cdot \sin (\pi \cdot F_\theta \cdot 180^{-1})^{-1}. \quad (1)$$

**Protocol**

For the sonographic study of the right gastrocnemius medialis the subject was laying prone on the examining table. The lower limbs were extended, muscles relaxed and the feet rested over the edge of the table at an angle of 90° to the leg. The linear array transducer was coated with transmission gel to obtain acoustic coupling and oriented along the mid-sagittal axis of the muscle. The probe was positioned on the midline of the right gastrocnemius medialis centred at the level of the maximum diameter of the transverse muscle section (Narici et al., 1994; Narici et al., 1996). Lower leg length (TL) was measured with a ruler between the medial malleolus and the upper articular surface of the tibia, spotted by palpation.

**Statistics**

Statistical comparison between two regression lines, corresponding in the present study to male and female groups, and the calculation of relatives slopes and intercepts was performed by one-way analysis of covariance. Calculated confidence bounds corresponds to nonsimultaneous bounds for a new observation. Errors on the estimated parameters are expressed as standard deviation (SD). The a priori level of statistical significance

![Fig. 1](image1.png) Subjects height as a function of age. (♂) males; (♀) females.

![Fig. 2](image2.png) Subjects weight as a function of age. (♂) males; (♀) females.
was set at $p<0.05$. Our results are compared to data reported for adults in some key papers in the literature (see RESULTS and DISCUSSION; Abe et al., 1997; Abe et al., 1998; Maganaris et al., 1998; Abe et al., 1999; Chow et al., 2000; Kearns et al., 2000; Kumagai et al., 2000).

**Results**

$F_\theta$ increases monotonically starting from birth (0 years) and reaches a stable value after the adolescent growth spurt. Fig. 3 shows the $F_\theta$ values as a function of age for males and females.

Figs. 4 and 5 report the TK and $T_L$ values as a function of age. $T_L$ follows the typical age dependent pattern reported in the literature (Hensiger, 1986).

Fig. 6 shows the $T_L$ values as a function of TK. $T_L$ is linearly related to TK ($p<0.05$): $T_L = 1.82 (\pm 0.26) \times TK + 5.92 (\pm 2.84)$. $T_L$ values for males ($p<0.05$) and females ($p<0.05$) are both linearly related to TK. The two regression lines for males and females are not statistically different.

Fig. 7 shows the $F_\theta$ values as a function of TK. $F_\theta$ is linearly related to TK ($p<0.05$): $F_\theta = 0.84 (\pm 0.09) \times TK + ...
3.15 (± 1.13). \( F_\theta \) values for males (\( p<0.05 \)) and females (\( p<0.05 \)) are both linearly related to TK. The two regression lines for males and females are not statistically different.

Fig. 8 illustrates a series of human gastrocnemius medialis \( F_\theta \) and TK values reported in the literature (Abe et al., 1997; Abe et al., 1998; Maganaris et al., 1998; Abe et al., 1999; Chow et al., 2000; Kearns et al., 2000; Kumagai et al., 2000). The values are plotted simultaneously with the regression line and confidence intervals calculated in the present study (see Fig. 3). The ultrasound probe position used for the measurements and the position of subjects were comparable to those of our work. For adult subjects, our data were similar to those reported in the literature.

Fig. 9 shows the fibre bundle length (\( F_L \)) as a function of TK. TK and \( F_\theta \) values utilized for the \( F_L \) calculation (see equation 1) were taken from the linear regression illustrated in Fig. 3. The TK and \( F_\theta \) values are also reported above in the present RESULTS section. A series of \( F_L \) and TK values obtained from the literature (Abe et al., 1998; Maganaris et al., 1998; Abe et al., 1999; Chow et al., 2000; Kearns et al., 2000; Kumagai et al., 2000; same as in Fig. 8) and calculated with equation (1), are included in the same figure. Figs. 8 and 9 report data obtained from the same experiments, with the exception of Abe et al. (1997) because the authors did not calculate \( F_L \) (data not presented in Fig 9).

**Discussion**

To our knowledge, no previous data for development of \( F_\theta \) during infancy and childhood have been published. Fig. 1 illustrates that \( F_\theta \) monotonically increases as a function of age, reaching a stable value by adolescence. There is a large spread of \( F_\theta \) values for a given age, which is probably due to physiological differences. The linear relationship between \( T_L \) and TK (Fig. 6) and between TK and \( F_\theta \) (Fig. 7) lets one think that \( F_\theta \) probably follows the same trend of growth observed for bones (Hensinger, 1986). Just as body weight increases by growth spurts, \( F_\theta \) might increase at different speeds as a function of age and reach maturity at a different chronological age in males than in females. At maturity, \( F_\theta \) values have been demonstrated to differ between males and females (Chow et al., 2000). The training status of the subjects probably also modulates \( F_\theta \) (Kawakami et al., 1993; Abe et al., 2000; Kearns et al., 2000; Kumagai et al., 2000). Considering that \( F_\theta \) is one of the determinants of muscle force, the present findings might in part explain the low values of mechanical muscle peak power observed in children compared to adults (Ferretti et al., 1994).

It appears from the above discussion, that it is extremely
Kawakami et al. (1993), Abe et al. (1999) and Kearns demonstrate that both $F_\theta$ (usually significantly correlated). However, our findings indicate that $F_\theta$ cannot be mathematically be linearly related to TK/TL, as found by Kawakami et al. (1993), Abe et al. (1999) and Kearns (2000). Probably, this apparently contradictory conclusion is due to the large range of variation of $F_\theta$, TK and $T_L$ measurements (the $T_L/T_\theta$ ratio further increases the error). In fact, the observed scattered data “fit” a linear model in both $F_\theta$-TK and $F_\theta$-(TK/TL) data representations. There is no doubt that more work is necessary to solve this problem.

The linear $F_\theta$-TK relationship holds when the subject foot is positioned at 90° to the leg. It is well known that $F_\theta$ changes as a function of ankle position and of the force issued by muscle contraction (Narici et al., 1996; Herbert & Gandevia, 1995, Kawakami et al., 1998; Maganaris et al., 1998 Maganaris & Baltzopoulos, 1999). As this aspect was not addressed in our study we cannot say how the $F_\theta$-TK relationship will change with different ankle positions or muscle contraction.

To facilitate the comparison between the present results and the data taken from the literature we summarize a series of $F_\theta$ and TK values obtained by different research groups in Fig. 8. It is interesting to notice that all the values fit into the confidence intervals. This representation depicts $F_\theta$ values in a logical way even if they seem very different one of each other. Small variations on $F_\theta$ values, related to different methods of measurement by different laboratories, must be taken into account. For the sake of completeness, Fig. 9 illustrates the $F_L$ values of our study together with the $F_L$ data calculated by the same groups depicted in Fig. 8. It shows that $F_L$ in our study is far from linearity for small TK values. These small TK values are representative of young subjects not examined by previous researchers.

It remains to be proven whether the observed age dependence of $F_\theta$ has any physiological aim e.g., in children, small $F_\theta$ values (i.e. low maximum isometric force) might protect tendons, or tendon insertions from high mechanical stress.

Conclusions

In conclusion, we demonstrated that the human gastrocnemius medialis pennation angle ($F_\theta$) value is not constant during growth but increases as a function of age from the newborn period to the adulthood. $F_\theta$ seems to reach a stable value after adolescence, as is also observed for bone length, height, etc. The plot of $F_\theta$ as a function of muscle thickness (TK) allows one to show, in a single simplified coherent way, data values that are usually influenced in a complex manner by other variables such as training status, age, sex, etc.

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References


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