Behavior of human muscle fascicles during shortening and lengthening contractions in vivo

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Reeves, Neil D., and Marco V. Narici. Behavior of human muscle fascicles during shortening and lengthening contractions in vivo. J Appl Physiol 95: 1090–1096, 2003.—The aim of the present study was to investigate the behavior of human muscle fascicles during dynamic contractions. Eight subjects performed maximal isometric dorsiflexion contractions at six ankle joint angles and maximal isokinetic concentric and eccentric contractions at five angular velocities. Tibialis anterior muscle architecture was measured in vivo by use of B-mode ultrasonography. During maximal isometric contraction, fascicle length was shorter and pennation angle larger compared with values at rest (P < 0.01). During isokinetic concentric contractions from 0 to 4.36 rad/s, fascicle length measured at a constant ankle joint angle increased curvilinearly from 49.5 to 69.7 mm (41%; P < 0.01), whereas pennation angle decreased curvilinearly from 14.8 to 9.8° (34%; P < 0.01). During eccentric muscle actions, fascicles contracted quasi-isometrically, independent of angular velocity. The behavior of muscle fascicles during shortening contractions was believed to reflect the degree of stretch applied to the series elastic component, which decreases with increasing contraction velocity. The quasi-isometric behavior of fascicles during eccentric muscle actions suggests that the series elastic component acts as a mechanical buffer during active lengthening:

isokinetic dynamometry; muscle contraction; muscle architecture; ultrasonography

The architecture of a skeletal muscle is an important determinant of its functional characteristics (13). Human muscle architecture may be studied noninvasively in vivo both at rest and during muscle contraction, by using real-time ultrasonography (15, 20, 22). Indeed, several investigators (9, 24, 27) have demonstrated that during isometric contractions muscle architecture undergoes remarkable changes. However, very few studies (10, 17) have explored the changes in muscle architecture occurring in dynamic contractions. This is despite the fact that most contractions performed in daily living are dynamic. In humans, the fascicles of the gastrocnemius muscle have been observed to contract quasi-isometrically during the support phase of walking, whereas the muscle-tendon complex lengthens (10). During the eccentric phase of walking in the cat, while the muscle-tendon complex lengthens, the fibers actually shorten, suggesting that the length change is almost entirely accounted for by the compliance of the tendon (14).

Wickiewicz et al. (31) used the architectural features obtained from cadavers in an earlier study (32) to estimate the in vivo maximum shortening velocity of muscle fibers from contractions performed by healthy subjects. However, because of the changes occurring in muscle tissue during the fixation process, measurements obtained from cadavers should not be used to predict the behavior of muscle fibers in vivo. The dynamic behavior of muscle has been studied in vivo by using sinusoidal oscillations during submaximal contractions (3) and has been shown to fit well to the force-velocity relationship predicted by Hill’s hyperbola (28). The first study that investigated changes in human muscle architecture measured in vivo during shortening contractions was performed by Ichinose et al. (17). It was found that the degree of shortening of muscle fascicles decreased as contraction velocity increased. However, the above study presents two limitations. The first was that of having investigated only a limited range of shortening velocities (30 and 150°/s), with a peak velocity that represents only 20% of the estimated maximal shortening velocity for this muscle group, knee extensors (see Ref. 31). The second limitation was that of having investigated changes in muscle architecture only in shortening contractions but not in lengthening contractions. Hence the purpose of the present study was to extend these measurements also to lengthening contractions, investigating changes in fascicle lengths and pennation angles over a greater range of shortening and lengthening angular velocities with the aim of comparing the behavior of fascicles during both shortening and lengthening contractions. The hypothesis of the present study was that changes in fascicle length would reflect the degree of stretch of the series elastic component (SEC), which comprises the intra- and extramuscular tendon tissue as well as that residing within the cross bridges, and that this would be dependent on the velocity of contraction.
METHODS

Subjects. Eight subjects (4 men and 4 women, mean ± SD age, height, and body mass of 25.1 ± 2.6 yr, 175 ± 7.4 cm, and 70.3 ± 9.5 kg, respectively) gave their written, informed consent to participate in this study, after the ethics committee of the Centre for Biophysical and Clinical Research into Human Movement at the Manchester Metropolitan University had approved the procedures involved. This sample size was selected on the basis of a power analysis performed previously with repeated measures of fascicle length, pennation angle, and isokinetic torque. All procedures complied with the Declaration of Helsinki.

Torque measurements. The force-velocity features of the dorsiflexor muscle group [tibialis anterior (TA) muscle] were investigated by measuring the torque developed during maximal voluntary contraction (MVC) performed on an isokinetic dynamometer (Cybex NORM, Ronkonkoma, NY). Subjects lay in the supine position on the bench with the right knee joint securely fixed at an angle of 1.57 rad (90°) to prevent movement of the tibia with respect to the center of rotation of the talocrural joint. The right foot was tightly strapped to a footplate; all measurements were performed on the right leg. Subjects had previously attended the laboratory on at least one occasion to become familiarized with the procedures of the investigation. The anatomical zero of the foot was defined as a 1.57-rad angle between the coronal plane of the tibia and the footplate. The range of motion was from full plantarflexion to full dorsiflexion. Maximal isometric dorsiflexion torque was measured at ankle joint angles of +0.52, +0.35, +0.17, 0, −0.17, and −0.35 rad (+30, +20, +10, 0, −10, and −20°, respectively). Two maximal contractions were performed at each joint angle, separated by 60 s of rest between contractions. Contractions were held until the experimenter observed a plateau in torque, displayed on the screen of a computer (Apple Macintosh, G4, Cupertino, CA) interfaced with an acquisition system (Acknowledge, Biopac Systems, Santa Barbara, CA) used for analog-to-digital conversion. This time period was ~3–5 s. Maximal isokinetic concentric and eccentric dorsiflexion contractions were performed at angular velocities of 0.87 (50), 1.75 (100), 2.62 (150), 3.49 (200), and 4.36 rad/s (250°/s). A set of five concentric and five eccentric maximal contractions was performed at each angular velocity. Contractions were performed in cycles, with a concentric contraction being immediately preceded by an eccentric contraction. An isometric phase lasting ~100 ms preceded each eccentric contraction, ensuring that the muscle underwent a period of isometric preloading, thereby maintaining a constant preactivation level. Pilot work indicated that this phase of isometric contraction, preceded by maximal concentric contraction, was sufficient to produce an isometric fascicle length before the eccentric action. A rest period of 180 s separated each set of contractions. During all contractions, torque, ankle joint angle, TA muscle electromyographic (EMG) activity, and angular velocity were sampled simultaneously by the acquisition system at a frequency of 2,000 Hz and were saved for subsequent analysis.

Isokinetic torque was analyzed at a position corresponding to an ankle joint angle of 0.14 rad (8°) for both concentric and eccentric contractions. The rationale for this procedure was justified by the observation that the isovelcity phase of the contraction decreased and occupied a narrower portion, toward the midrange of joint motion with increasing angular velocity. The ankle joint angle of 0.14 rad was selected as a position to read torque, because it fell within the isovelocity phase of both concentric and eccentric contractions for all angular velocities. If this specific angle did not lie within the isovelocity phase for a certain subject, the closest angle corresponding to an isovelocity phase was selected; in any case this angle did not deviate more than ±0.02 rad from the ankle joint angle of 0.14 rad. The highest isovelocity torque from each of the five concentric and eccentric contractions at each angular velocity was selected.

The TA moment arm was assumed to represent the common moment arm of the dorsiflexors, and this was estimated at 0.14 rad of ankle joint angle from the data of Rugg et al. (29). Rugg et al. measured the TA moment arm during contraction, from sagittal-plane magnetic resonance imaging scans. Force (N) of the dorsiflexor muscle group was calculated from the following equation

\[ F_d = T/MA \]

where \( F_d \) is the force generated by the dorsiflexor muscle group, \( T \) is the joint torque, and \( MA \) is the TA moment arm at 0.14 rad of ankle joint angle (29). The peak of the two isometric contractions at each ankle joint angle was selected. The isometric force at 0.14 rad was estimated from the torque-ankle joint angle data by fitting the experimental points with a line of best fit.

Ultrasoundography. The architectural features of the TA muscle: pennation angle, fascicle length, and the distance between aponeuroses (Fig. 1) were assessed from images obtained using real-time B-mode ultrasonography (ATL-HDI 3000, Bothwell, WA). After identification and marking of the proximal and distal insertions of the muscle, a 7.5-MHz linear-array probe with a 38-mm scanning length was positioned perpendicular to the dermal surface along the mid sagittal plane of the TA muscle at the site corresponding to the thickest portion of the muscle, identified by ultrasound. This site was clearly marked to provide a standardized measurement site and ensure that measurements at all velocities were taken from the same external site. The probe was coated with a water-soluble transmission gel to provide acoustic contact without depressing the dermal surface. Accuracy of the ultrasound method in measuring muscle architectural features has been previously demonstrated to show good agreement with direct anatomical measurement on a cadaver (27).

Images were obtained at rest and during maximal isometric contraction at ankle joint angles of +0.52 to −0.35 rad in 0.17-rad increments. Images were obtained during maximal isokinetic concentric and eccentric contractions at 0.87, 1.75, 2.62, 3.49, and 4.36 rad/s. Images were recorded onto videotape at 50 Hz for subsequent analysis. At rest and during contraction, the probe was firmly held in place at the measurement site by the experimenter. Ultrasound images were
taken with adjusted depth and focus to optimize image quality and sampling frequency. Sampling frequency was maintained at or above 28 Hz. Acquired isometric images were analyzed at the time point at which peak torque was generated. Acquired isokinetic concentric and eccentric contraction images were analyzed at the time point corresponding to 0.14 rad of ankle joint angle. The image corresponding to the highest concentric and eccentric force at 0.14 rad of ankle joint angle for each angular velocity was analyzed. An external voltage (10-V) trigger was used to synchronize the ultrasound with the acquisition system. The delta time was measured from the point of application of the external trigger to the desired torque or ankle joint angle displayed on the acquisition system. To locate the corresponding ultrasound image, this time period was then applied to the ultrasound sequence, starting from the point of application of the external trigger.

Measurements of fascicle length, pennation angle, and distance between aponeuroses were performed by using digitizing software (NIH Image, version 1.61, National Institutes of Health, Bethesda, MD). Pennation angle was defined as the angle made between the echogenic fascicle by axial-plane ultrasound insertion into the aponeurosis. This was measured at the superficial and central aponeuroses, and the two values were then averaged. Measurements of ″t″, defined as the distance between the superficial and central aponeuroses, were made on either side of the image and then averaged (Fig. 1). One end of the fascicle generally extended off the acquired ultrasound image. The visible part of the fascicle was measured by using digitizing software and, by assuming a linear continuation, trigonometry was used to estimate the part of the fascicle that was not visible. To estimate the order of error associated with this method of determining fascicle length, additional measurements were taken in a subsample of subjects (n = 6). A maximal isometric contraction was performed and maintained for 4–5 s, during which the ultrasound probe was moved along the midsagittal plane of the muscle, over a series of external markers fixed on the skin with surgical tape. The ultrasound image was reconstructed and the entire length of fascicles identified. The actual fascicle length was measured and compared with the estimated fascicle length determined when using the available scan window of 38 mm. These measurements indicated that the order of error associated with estimating fascicle length was 2.4%. In the event of fascicles inserting curvilinearly into the aponeurosis, pennation angle was measured by using an approach previously applied for the triceps surae muscle group (24). Muscle architecture was analyzed from the superficial half of the bicipitate TA only, on the basis of reports that the architectural features are not significantly different between the two parts of the muscle at rest in any joint position or during isometric contraction (23).

**Measurement of electromyographic activity.** Electromyographic activity was assessed from the TA muscle. Two self-adhesive Ag-AgCl electrodes 10 mm in diameter (Neuroline, Medicotest, Rugmarken, Denmark) were placed in a bipolar configuration with a constant interelectrode distance of 20 mm at a site corresponding to the proximal third of the muscle (34), with the reference electrode placed on the lateral tibial condyle. In an attempt to minimize cross-talk from adjacent muscles, electrodes were placed along the midsagittal plane of the muscle, guided by axial-plane ultrasound scanning. To reduce skin impedance below 5,000 ″Ω″, electrode placement was preceded by shaving, skin abrasion, and cleansing with an alcohol-based solution. Sampled at 2,000 Hz by the acquisition system, the raw EMG signal was preamplified and filtered by using high- and low-pass filters set at 10 and 500 Hz, respectively. The EMG activity was measured over a 30-ms time period corresponding to 0.14 rad of ankle joint angle for both concentric and eccentric contractions. During an isometric contraction performed at 0.17 rad, the EMG activity was measured over a 30-ms time period corresponding to maximal torque. Measurements were performed taking into account the electromechanical delay, and the raw signal was then rectified, integrated, and normalized for a 1-s time period.

**Statistical analysis.** Repeated-measures 2 × 6 factorial analysis of variance (ANOVA) was used to test for any differences in pennation angle, fascicle length, distance between aponeuroses of the TA muscle as a result of changes in ankle joint angle (+0.52 to −0.35 rad), and contraction state (rest; isometric MVC). Repeated-measures 2 × 6 factorial ANOVA was used to test for any differences in pennation angle, fascicle length, distance between aponeuroses of the TA muscle as a result of changes in angular velocity (0 to 4.36 rad/s), and contraction type (concentric or eccentric). Repeated-measures 2 × 6 factorial ANOVA was applied to test for any differences in the integrated EMG activity of the TA muscle as a result of changes in angular velocity (0 to 4.36 rad/s) and contraction type (concentric or eccentric). Where necessary, post hoc analysis was performed by using Scheffé’s procedure. Significance was accepted at P < 0.05, and values presented are means ± SD.

**RESULTS**

**Effect of ankle joint angle and isometric contraction on fascicle length, pennation angle, and distance between aponeuroses.** Fascicle length (mean of resting and contracted fascicle length) at +0.52 rad of ankle joint angle (80.4 ± 2.4 mm) was significantly greater than fascicle length at every other ankle joint angle, with the exception of +0.35 rad (P < 0.01). Fascicle length averaged across all ankle joint angles during maximal isometric contraction (53.8 ± 2.9 mm) was significantly shorter compared with that at rest (71.9 ± 1.9 mm; P < 0.01; Fig. 2A).

Pennation angles (mean of resting and contracted pennation angles) at +0.52 rad of ankle joint angle (8.5 ± 0.5°) were significantly smaller compared with pennation angles at every other ankle joint angle, except +0.35 rad (P < 0.01). Pennation angles (mean across all ankle joint angles) were significantly greater during maximal isometric contraction (13.9 ± 0.7°) compared with those in the relaxed state (9.6 ± 0.5°; P < 0.01). A significant interaction indicated that pennation angle at every given ankle joint angle, with the exception of +0.52 rad, was significantly greater during isometric contraction compared with that at rest (P < 0.01; Fig. 2B).

Changes in ankle joint angle from +0.52 to −0.35° and the transition from rest to isometric MVC did not result in significant changes in muscle thickness.

**Effect of angular velocity and contraction type on fascicle length, pennation angle, and distance between aponeuroses.** Fascicle length at a constant ankle joint angle (0.14 rad) was significantly greater during concentric contraction at angular velocities of 3.49 (68.2 ± 5.9 mm, P < 0.01) and 4.36 rad/s (69.7 ± 5.1 mm, P < 0.01) compared with that during isometric contraction (0 rad/s; 49.5 ± 3 mm). Furthermore, fascicle length
during concentric contraction at 0.87 rad/s (54.1 ± 3.7 mm) was significantly shorter compared with that at 4.36 rad/s (Fig. 3A). Fascicle length measured at a constant joint angle during eccentric contraction was independent of angular velocity and was not significantly different from fascicle length during isometric contraction (Fig. 3A).

At a constant ankle joint position, pennation angles during isometric contraction (0 rad/s; 14.8 ± 0.8°) were significantly greater compared with pennation angles during concentric contractions at 1.75 (11.8 ± 0.8°; P < 0.01), 3.49 (10.2 ± 0.6°; P < 0.01), and 4.36 rad/s (9.8 ± 0.9°; P < 0.01). Pennation angles during eccentric contraction at all angular velocities except 4.36 rad/s (11.8 ± 0.6°) were significantly smaller compared with those during isometric contraction (0 rad/s). Pennation angles did not change significantly as a function of angular velocity during eccentric contraction; however, during concentric contraction pennation angles at 3.49 and 4.36 rad/s were significantly less than those at 0.87 rad/s (13.3 ± 0.8°; Fig. 3B).

Averaged over all angular velocities, eccentric contractions resulted in a significantly greater distance between superficial and central aponeuroses (12.7 ± 0.3 mm) compared with during concentric contraction (12.2 ± 0.4 mm) at a constant ankle joint angle. The distance between aponeuroses did not change significantly as a function of angular velocity.

Force-velocity features of the dorsiflexor muscle group. Force-velocity characteristics of the dorsiflexor muscle group are displayed in Fig. 4. The peak isovelocity force of the dorsiflexors produced during eccentric contractions (1,548.3 ± 384 N) was 1.27 times greater than the force produced during isometric contraction (1,218.5 ± 293.1 N). Because the highest tested angular velocity was 4.36 rad/s, which corresponds to ~54% of the maximum shortening velocity of the dorsiflexor muscle group (31), the data points were deliberately not fitted with a predicted curve such as Hill's equation, because this would have required the measurement of force-velocity values up to zero load. Nevertheless, the data points at the highest two velocities (3.49 and 4.36 rad/s) seem clearly above the force values that would be expected from a hyperbolic data distribution passing through all the positive force-velocity data points. Possible reasons for this phenome-
non are suggested in the DISCUSSION. There were no significant differences in the integrated EMG activity of the TA muscle over the tested angular velocities during either concentric (ranging from \(2.24^{-01} \pm 2.38^{-02}\) to \(2.64^{-01} \pm 5.78^{-02}\) mV·s; \(P > 0.05\)) or eccentric (ranging from \(2.58^{-01} \pm 3.66^{-02}\) to \(2.88^{-01} \pm 3.19^{-02}\) mV·s; \(P > 0.05\)) contractions. There were also no significant differences in the integrated EMG activity between concentric and eccentric contractions at any angular velocity (\(P > 0.05\)).

**DISCUSSION**

The main findings of the present study were 1) at a constant ankle joint angle, fascicle length and pennation angle changed significantly as a function of shortening velocity; 2) fascicle length was greater at the higher compared with the lower shortening velocity; and 3) during eccentric muscle actions, fascicles behaved quasi-isometrically. Each of these findings will be discussed in detail in the sections below.

**TA muscle architecture at rest and during isometric contraction.** Fascicle length at rest was found to be dependent on ankle joint angle, decreasing by 38% with passive movement from full plantarflexion to full dorsiflexion (Fig. 2A), accompanied by a 64% increase in pennation angle (Fig. 2B). Fascicle length was shorter and pennation angle greater during maximal isometric contraction compared with that at rest. This has been observed previously (9, 24, 27) in other muscles and is due to the fascicles shortening at the expense of the SEC (19). Pennation angle of the TA muscle during isometric contraction was greater than at rest at every joint angle except +0.52 rad (Fig. 2B). The magnitude of the difference between rest and isometric contraction was greater closer to full dorsiflexion (−0.35 rad). A similar pattern has been observed in the vastus lateralis muscle (9) and is likely due to the low passive tension of the slack muscle-tendon complex. This concept is supported by the 166% increase in pennation angle of the slack-fibered bra-

chialis muscle in the transition from rest to maximal isometric contraction (16). In agreement with findings in the gastrocnemius medialis (GM) muscle (27), the transition from rest to maximal isometric contraction, in conjunction with changes in joint angle, had no effect on the distance between the superficial and central aponeuroses in the TA muscle.

**Force-velocity features of the dorsiflexors.** Concentric force at the faster angular velocities appeared to be higher than might be expected and seems to deviate from the typical hyperbolic relation. A possible explanation is that the concentric contractions may have been potentiated by the immediately preceding eccentric contraction, via the storage and subsequent release of elastic energy (e.g., Ref. 2). Indeed, this has been demonstrated to occur in the knee extensors, where the performance of a prior eccentric contraction enhanced the subsequent concentric torque beyond that using a prior isometric contraction (8). Dorsiflexion force is produced by the combined effects of four muscles: TA, extensor digitorum longus, extensor hallucis longus, and peroneus tertius (30). The TA muscle was considered to be the major contributor to dorsiflexion torque because of its relative physiological cross-sectional area composing −60% of the entire dorsiflexor volume (11, 12).

It has not yet been possible to directly measure in vivo the force exerted by one of these synergist muscles, and a number of assumptions must be made when calculating the force exerted by this muscle group. The generated joint moment was divided by the moment arm at 0.14 rad of ankle joint angle, taken from the data of Rugg et al. (29) during contraction, to provide an estimate of the combined dorsiflexor muscle group force. This is assuming that the TA moment arm represents the common moment arm for the entire dorsiflexor muscle group. The force presented is assuming no coactivation of plantarflexors, which would subtract from the gross force produced by the dorsiflexor muscle group. Antagonist integrated electromyographic (iEMG) activity of the soleus muscle during maximal isometric dorsiflexion was identified to be <3% of the iEMG activity produced during maximal isometric plantarflexion (26). By assuming a linear iEMG-MVC relationship, it was estimated the antagonist soleus iEMG signal would result in an opposing moment of 1–6 Nm during maximal isometric dorsiflexion.

**Changes in muscle architecture during shortening contractions.** At a constant ankle joint angle, TA muscle fascicle length increased curvilinearly (from 49.5 to 69.7 mm) during concentric contractions of increasing angular velocity from 0 to 4.36 rad/s (Fig. 3A). These results agree with findings in the vastus lateralis muscle, showing that during concentric contraction the extent of fascicle shortening is greater at a lower compared with a higher angular velocity (17). In the present study, fascicles were shorter by 41% during contraction at 0 rad/s compared with those during concentric contraction at 4.36 rad/s. An equivalent increase in angular velocity during concentric contraction resulted in a concomitant 34% decrease in pennation angle (Fig. 3B).
The mechanism responsible for the observed changes in fascicle length and pennation angle as a function of shortening velocity is most likely due to the compliance of the SEC. The SEC can only be stretched by applying a force, either passive (changes observed at rest as a function of ankle joint angle) or active, and the greater the force, the greater the extension (33). During isometric contraction, the force is greater compared with during any concentric contraction; therefore shortening of fascicles, stretching of the SEC, and pennation angles are all at their greatest. As the angular velocity increases during concentric contraction, the muscle produces less force, which results in a reduced shortening of the contractile element. As fascicle shortening becomes less pronounced, a smaller proportion of the central aponeurosis is pulled proximally, which leads to smaller pennation angles during faster shortening velocities. Evidence in support of this concept comes from ramp isometric contractions in which greater proximal displacement of the central aponeurosis (25), greater fascicle shortening, and increasing pennation angles (24, 27) occur with increments in force from rest up to isometric MVC. The decreasing pennation angles during concentric contraction of increasing angular velocity observed in the present study are advantageous for reducing the loss of force transmission to the tendon. Torque is often read at a constant joint angle during concentric contraction of increasing angular velocities, creating an elongated muscle. Elastic deformation of a constant volume can only occur if more than one contraction is preceded by a maximal concentric contraction but more importantly by an isometric phase, which ensured that the preactivation level was maximal and furthermore that it remained constant across angular velocities. The finding that both force and iEMG activity of the TA muscle remained relatively constant across eccentric angular velocities adds further support to this point.

Changes in muscle architecture during lengthening contractions. During eccentric muscle actions, the TA muscle fascicles contracted quasi-isometrically. Pennation angles during eccentric contractions were reduced compared with those during isometric contraction. Both fascicle length and pennation angle were independent of angular velocity during eccentric contractions (Fig. 3, A and B, respectively). The quasi-isometric behavior of fascicles during eccentric muscle actions reveals an important role for the SEC in acting as a mechanical buffer during this type of contraction. This may be an important factor for preventing injury to muscle fibers during rapid, high-force eccentric contractions. Because most of the elongation appears to occur at the expense of the tendon, this has important implications for energy saving during locomotion. During ground impact, energy is stored in lengthening tendons as strain energy, which is then released during the subsequent tendon recoil, permitting metabolic energy saving (2). In agreement with the findings of the present study, fascicles of the GM muscle have been identified to contract quasi-isometrically during the eccentric support phase of walking (10). It has been shown by Kawakami et al. (21) that, during the eccentric phase of a countermovement jump, the GM muscle fascicles contracted isometrically, whereas the tendon is suggested to have lengthened, thus storing elastic energy that resulted in a force enhancement on plantarflexion above that found in the same action performed with no countermovement. Cat muscle fibers have been identified to actually shorten as the muscle-tendon unit continues to lengthen during the eccentric phase of gait (14). In contrast to the findings of the present study, vastus lateralis muscle fascicles have been reported to initially contract isometrically, but then to lengthen during the subsequent phase of an eccentric muscle action (18). These contrasting findings, however, might represent differences between the muscles and joint systems studied. The biochemical fiber type composition of the TA muscle is thought to be relatively unimportant in explaining the results of the present study, given that mathematical modeling has revealed a dominance of architectural over fiber-type effects in determining muscle function (1). Changing the level of preactivation in eccentric contractions has been shown to affect not only the force produced but also the length of fascicles (18). In vitro studies on isolated fibers suggest that the development of an isometric tension is necessary before any change in length, to ensure full preactivation (4–6). It is clear, therefore, that the preactivation status of the muscle is an important factor influencing both force and the behavior of fascicles during the subsequent eccentric contraction. In the present study, the eccentric contraction was preceded by a maximal concentric contraction but more importantly by an isometric phase, which ensured that the preactivation level was maximal and furthermore that it remained constant across angular velocities. The finding that both force and iEMG activity of the TA muscle remained relatively constant across eccentric angular velocities adds further support to this point.

Changes in muscle thickness with shortening and lengthening contractions. The distance between aponeuroses (averaged over all angular velocities) at a constant ankle joint angle was significantly greater during eccentric compared with during concentric contraction. The smaller distance between aponeuroses during concentric contractions may be a consequence of the smaller pennation angles and greater fascicle lengths at higher angular velocities, creating an elongated muscle. Elastic deformation of a constant volume can only occur if more than one side is elastic (7); therefore, if the muscle becomes longer it also becomes thinner. Greater muscle length and a reduced muscle thickness at the same ankle joint angle during concentric contractions of increasing angular velocity may therefore explain the smaller distance between the aponeuroses compared with during eccentric contractions. Because the TA muscle does not act solely in a sagittal plane, this may result in scanning the muscle from a slightly different orientation, resulting in the appearance of an increased distance between aponeuro-
ses. However, great care was taken to scan the muscle along the sagittal plane of the fascicles so that in each image the entire visible length of the fascicles could be tracked.

In conclusion, the present study has demonstrated that at a constant ankle joint position fascicle length of the TA muscle increases curvilinearly during concentric contractions of increasing angular velocity, with a concomitant curvilinear decrease in pennation angle. These architectural features appear to be modified during shortening contractions, according to the force being applied to extend the SEC. The TA muscle fascicles were observed to contract quasi-isometrically during eccentric muscle actions, independent of angular velocity. Pennation angles during eccentric contractions were smaller compared with those during isometric contraction but were independent of angular velocity. The present study shows that inferences regarding fascicle length during dynamic contractions of different angular velocities cannot be assumed solely from joint angle.

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DISCLOSURES

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