Repetitive contractions alter the geometry of human skeletal muscle

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Maganaris, Constantinos N., Vasilios Baltzopoulos, and Anthony J. Sargeant. Repeated contractions alter the geometry of human skeletal muscle. J Appl Physiol 93: 2089–2094, 2002.—The aim of this study was to investigate the effect of repeated contractions on the geometry of human skeletal muscle. Six men performed two sets (sets A and B) of 10 repeated isometric plantarflexion contractions at 80% of MVC with a rest interval of 15 min between sets. By use of ultrasound, the geometry of the medial gastrocnemius (MG) muscle was measured in the contractions of set A and the displacement of the MG tendon origin in the myotendinous junction was measured in the contractions of set B. In the transition from the 1st to the 10th contractions, the fascicular length at 80% of MVC decreased from 34.0 ± 4.0 (mean ± SD) to 30.3 ± 3.0 mm (P < 0.001), the pennation angle increased from 35.3 ± 3.2 to 42.3 ± 3° (P < 0.001), the myotendinous junction displacement increased from 5.3 ± 0.3 to 10.3 ± 3.0 mm (P < 0.001), and the average fascicular curvature remained constant (P > 0.05) at 0.00004 m⁻¹. No changes (P > 0.05) were found in fascicular length, pennation angle, and myotendinous junction displacement after the fifth contraction. Electrogoniometry showed that the ankle rotated by ~6.5° during contraction, but no differences (P > 0.05) were obtained between contractions. The present results show that repeated contractions induce tendon creep, which substantially affects the geometry of the in-series contracting muscles, thus altering their potential for force and joint moment generation.

ultrasound; in vivo; fascicular length; pennation angle; curvature

THE FASCICULAR GEOMETRY IN a muscle is a major determinant of the muscle’s functional capabilities. For identical muscular compositions and volumes, the longer the fascicles the higher the excursion and velocity of contraction, and the higher the fascicular insertion angle to the in-series tendon (pennation angle), the higher the contractile force potential (3, 18). The magnitude of these changes in a single static contraction is determined by the force elicited in the muscle and the compliance of the in-series tendon. The higher the contractile force and the more compliant the tendon, the higher the fascicular shortening and pennation angle increase with respect to rest (5, 12, 14). If, however, the same muscle were called on to contract repeatedly, its fascicular geometry during contraction could also be affected by the tendon’s time-dependent properties. Numerous experiments show that tendons exhibit creep (i.e., they elongate over time) when loaded in an oscillating pattern (for review, see Refs. 1, 21), which suggests that repeated contractions might result in greater fascicular shortening and pennation angle increase compared with a single contraction, thus altering the muscle’s potential for force and joint moment production. Evidence for this hypothesis was sought in the present experiment. We studied the fascicular geometry of the in vivo human medial gastrocnemius (MG) muscle.

METHODS

Experimental protocol. Six healthy male volunteers (age: 24 ± 4 yr, height: 172 ± 5 cm, body mass: 72 ± 6 kg; mean ± SD) gave their consent to participate in this study. The experimental procedures involved were approved by the institutional ethics committee. The subjects lay prone on the couch of an isokinetic dynamometer (Cybex Norm) set in the isometric ankle plantarflexion mode. Measurements were taken in the left leg, with the knee fully extended and the ankle fixed at its neutral position (the sole of the foot at right angles to the tibial axis) on the dynamometer footplate with straps. The effectiveness of this fixation method in preventing ankle rotation was assessed during the experiments by using an electrogoniometer (Biometrics) with its ends attached 7 cm above and 3 cm below the lateral malleolus (Fig. 1). The recordings of the goniometer were collected with a Biopac MP100 system (Biopac Systems) at a sampling frequency of 500 Hz.

Each subject performed 10 successive isometric plantarflexion voluntary contractions (set A), all at an absolute

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moment corresponding to 80% of the moment generated during plantar flexion maximal voluntary contraction (MVC). We considered that a constancy in the absolute measured plantar flexion moment between repeated contractions would correspond to a respective constancy in the force generated by the MG muscle alone. We will return to this point in the Discussion. Each contraction was elicited by requesting the subject to increase the plantar flexion moment gradually over a 3-s period until reaching the absolute moment targeted. The subject was then asked to maintain that moment for 1 s before relaxing the contracting muscles. After 1 s of rest, the next contraction was elicited. Audiospatial feedback of the plantar flexion moment generated and time elapsed was provided. The dynamometer signals were collected (with the acquisition system used for collecting the electrogoniometry data) at 500 Hz.

Measurements of the MG muscle fascicular geometry were taken in the contractions of set A by B-mode ultrasonography (5, 9, 10, 12, 14, 19). The accuracy of this method for resting-state measurements has been confirmed by direct measurements on cadaveric muscles (9, 12), but further validation is required for measurements under dynamic conditions. The reproducibility of the method has also been confirmed previously (12, 14, 19). Sagittal-plane scans were taken with a 7.5-MHz linear ultrasound probe (AU5 Esaote Biomedica; axial and lateral resolutions of 0.2 and 0.3 mm, respectively) placed on the skin at the midlength and midwidth of the MG muscle. The fascicular geometry in this region has been shown to represent that along and across the MG muscle belly (10, 12, 14, 19). In the muscle scans produced, fascicular, interfascicular, and aponeurotic echoes were identified. The probe was then oriented in the plane over which the fascicles lay, where it was fixed with adhesive tape. The ultrasound, dynamometer, and electrogoniometer recordings were synchronized, and the 10 contractions were then elicited. In the scans recorded, the fascicular length was assumed to be the length of the curved fascicular path between the two aponeuroses, and the pennation angle was assumed to be the angle between the fascicular path and the deep aponeurosis (Fig. 2). The results of this measurement approach depend not only on the positions of the fascicular insertion and origin in the aponeuroses, but also on the fascicular curvature. Fascicular curvature values were therefore estimated. The approach we followed for deriving these estimates assumed that the fascicular path is an arc of a circle (Fig. 3), as recently described by Muramata et al. (19).

An additional set of 10 contractions (set B) was performed at the absolute moment reached in the contractions of set A. Each subject executed set B in the same way as set A, 15 min after completing set A. This rest period is much longer than that required to resume the properties of tendon after loading (~5 min; Ref. 21); therefore, we considered that set B would yield results independent of the loading applied in set A. In set B, the scanning probe used before was shifted toward the distal myotendinous junction of the muscle, keeping the probe on the axis and plane over which muscle scans were previously taken. At the myotendinous junction level, an echoabsorptive marker was glued on the skin underneath the probe. The probe was then taped on the skin; the ultrasound, dynamometer, and electrogoniometer recordings were synchronized, and the 10 contractions were elicited. In the scans recorded, the displacement of the echo generated by the end point of the MG tendon origin in the myotendinous junction relative to the position of the echo generated by the external marker was measured along the MG tendon. Similar protocols to the one described above have recently shown that ultrasonography provides reproducible measurements of tendinous displacement during contraction (11, 15–17).

Data analysis. The scans recorded when the plantarflexion moment measured was maintained at 80% of the MVC moment were identified. For each subject and contraction number in either set, we selected for analysis three scans with the best available quality in the structures seen. In each scan, each geometrical characteristic studied was quantified from measurements in one to three different regions where the fascicular orientation could be best seen. All morphometric measurements were carried out by digitization by the same investigator in a randomized order for contraction number. For each subject and contraction number, the measurements of each individual geometrical characteristic were averaged and used for further analysis. One-way ANOVA was used to test 1) differences in fascicular geometry between contractions (set A) and 2) differences in myotendinous displacement between contractions (set B). Two-way ANOVA was used to test differences within and between sets A and B in the ankle joint rotations corresponding to the scans examined. Tukey’s tests were used for post hoc analysis where appropriate. Statistical significance was set at $P < 0.05$. Values are reported as means ± SD.

RESULTS

The absolute value of plantarflexion moment to which all the following data refer is 105 ± 6 N·m. In the transition from the 1st to the 10th contractions in set A, the fascicular length of the MG muscle decreased from 34 ± 4 to 30 ± 3 mm ($P < 0.001$), and its pennation angle increased from 35 ± 3 to 42 ± 3° ($P < 0.001$). No changes ($P > 0.05$) were obtained in fascicular length and pennation angle after the fifth contraction (Fig. 4, A and B). The average fascicular curvature was ~4.3 m⁻¹, with no differences ($P > 0.05$) obtained between contractions (Fig. 4C), which indicates lack of artifactual changes in fascicular length and pennation angle. In the transition from the 1st to the 10th contractions in set B, the displacement of the MG myotendinous junction increased from 5 ± 3 to 10 ± 3 mm.
(P < 0.001). No displacement changes (P > 0.05) were obtained after the fifth contraction (Fig. 4D). The ankle joint rotated in the plantarflexion direction in all the contractions because of inevitable imperfect fixation of the foot on the dynamometer. The average rotation corresponding to the scans examined was ~6.5°, with no differences (P > 0.05) obtained either within or between sets A and B (Fig. 5).

DISCUSSION

The present study was conducted to investigate the effect of repeated contractions on the fascicular geometry of the human MG muscle. Our results show that the fascicular behavior during contraction is time dependent.

The use of optic fibers has recently enabled the quantification of in vivo human tendon forces during muscle contraction (2). However, this technique cannot measure the contractile forces generated by different muscles ending in one tendon (e.g., the three muscles comprising the triceps surae complex). Here, we have assumed that the MG muscle would produce a given force in different contractions generating the same net plantarflexion moment. (Note that conventional electromyogram recordings could be misleading in verifying this assumption because they do not relate to all motor units being active during a submaximal contraction; hence, we did not record such data.) However, it may be argued that the MG muscle force could decrease as a function of contraction number due to
fatigue, with the net moment measured remaining at the constant level required by recruiting more fibers from fiber type I-predominant and therefore more fatigue-resistant plantarflexors, e.g., the soleus muscle (8). Therefore, if the metabolic state of the MG muscle could be preserved, 1) more pronounced fascicular geometry changes might be seen, and 2) more contractions might be required to generate a steady fascicular behavior. On the other hand, muscle potentiation would produce the opposite effect of fatigue. However, it is unlikely that potentiation occurred to a substantial extent in our experiments because the high contractile forces elicited would not be affected by increases in either Ca\(^{2+}\) sensitivity or myoplasmic Ca\(^{2+}\) concentration (e.g., Ref. 13).

The simultaneous changes in fascicular length and pennation angle found indicate that these phenomena originated from creep in soft tissue mediating contractile force transmission from the fascicles to the dynamometer footplate. The plantarflexion rotations measured were similar in all contractions, which suggests that any creep in extraskeletal soft tissue had no measurable effect on the geometry of the MG muscle in our tests. However, the MG tendon did exhibit creep as indicated by the increase in the myotendinous junction displacement. In fact, the MG tendon and the fascicles exhibited very similar time-dependent behaviors over the same number of contractions (see Fig. 4, A and D), indicating a cause-and-effect relation between the two phenomena. Another structure that could have exhibited tensile creep in our experiment is the aponeurosis. In an attempt to assess whether aponeurotic creep occurred to an extent sufficient to cause a measurable change in muscular geometry, we calculated the distance traveled by the fascicular insertion in the aponeurosis in the first five contractions (i.e., the contractions in which a time-dependent behavior was seen).

Fig. 3. Graphical representation of the fascicular geometry measurements taken. The scan window in the figure encloses the structures seen in the muscle scans shown in Fig. 2. The length of the curved fascicular path AB is the fascicular length; \( \theta \) is the pennation angle formed between the straight line \( e_2 \) (passing through B and D) and the deep aponeurosis; \( \alpha \) is the angle formed between the straight line \( e_1 \) (passing through A and C) and the superficial aponeurosis; and \( T \) is the distance between the 2 aponeuroses. \( T \) and \( \alpha \) were used to calculate the fascicular curvature, by assuming that the fascicular length AB is an arc of a circle with radius \( R \). This assumption has been validated by Muramatsu et al. (19), who calculated that the fascicular curvature \( R^{-1} = (\cos 2\alpha - \cos 2\theta) \cdot (2T \cdot (\cos \alpha + \cos \theta))^{-1} \). The fascicular curvature values in the present study were derived from the above equation.

Fig. 4. Summarized results (means ± SD; \( n = 6 \)) of fascicular length (A), pennation angle (B), fascicular curvature (C), and myotendinous junction displacement (D). The resting-state values of fascicular length and pennation angle before the 1st contraction are also given. In A, B, and D, \( P < 0.05 \) between the 1st and 2nd, 2nd and 3rd, 3rd and 4th, and 4th and 5th contractions, and \( P > 0.05 \) between the 5th, 6th, 7th, 8th, 9th and 10th contractions. In C, \( P > 0.05 \) between the contractions.
As shown in Fig. 6, the estimates obtained are similar to the respective measured differences in the myotendinous junction displacements, which suggests that the fascicular changes observed were not affected substantially by creep development in the aponeurotic part lying between the tendon origin and the fascicular insertion.

The present results are consistent with some of the results reported recently by Kubo et al. (11) from experiments on the distal tendon-aponeurosis and pennation angle of the human vastus lateralis muscle before and immediately after several repeated-contraction protocols. In accordance with the present findings, the repeated loading applied by the above authors increased the pennation angle of the muscle. Surprisingly, however, this effect was not always related to an increased tendon-aponeurosis elongation. The reasons for the above dissociation were neither discussed nor are readily apparent. It may be the case that certain loading conditions in some muscles induce tensile creep mainly in the proximal tendon aponeurosis. Irrespective, however, of the "contributions" made by the proximal and distal tendinous components in changing muscular geometry under different loading circumstances, the finding of a time-dependent fascicular behavior has important biological implications. The fascicular shortening after repeated loading would correspond to a reduction in the average operating length of the sarcomeres. In the MG muscle, which operates in the ascending limb of the force-length relation (6), the shortening induced would shift the average operating sarcomeric length away from that corresponding to optimal myofilament overlap, thus reducing the contractile force generated on activation.

For an average number of 17,600 in-series sarcomeres in the MG muscle (7), it follows from our fascicular length measurements that repeated loading would reduce the length of the average sarcomere from ~1.9 to 1.7 μm, which according to the theoretical force-length relation obtained by applying the cross-bridge model of contraction (4) to human myofilament lengths (22) might reduce the force-generating potential by ~10%. The increased pennation angle in the muscle would further reduce both the effective vectorial component of contractile force transmitted along the Achilles tendon and the resultant moment generated about the ankle. Hence, a reduction in the moment generated in a series of maximal plantarflexion contractions should not be ascribed to neuromuscular fatigue only. In addition to changes in force- and moment-generating capabilities, the present findings could also have implications for proprioceptive control. If fascicular shortenings of the order obtained in the present study can be "seen" by the muscle spindles, excitatory and inhibitory reflexes could be triggered through alterations in the firing of Ia afferents, introducing potential errors in positional control due to changes in the activity balance between agonist and antagonist muscles (e.g., Ref. 20). This would be of no functional relevance in an experiment.

Fig. 5. Summarized results (means ± SD; n = 6) of ankle plantarflexion rotation compared with rest at the time points corresponding to 80% of MVC moment in sets A (A) and B (B). *P < 0.05 within and between sets.

As shown in Fig. 6, the estimates obtained are similar to the respective measured differences in the myotendinous junction displacements, which suggests that the fascicular changes observed were not affected substantially by creep development in the aponeurotic part lying between the tendon origin and the fascicular insertion.

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Fig. 6. Triangle ABC represents the effect of creep in the distal tendon-aponeurosis of the MG muscle on the geometry of a fascicle. A is the origin of a fascicle, B and C are the insertions of the fascicle in 2 consecutive contractions, and α and ϕ are the corresponding pennation angles. From the law of sines, it follows that \( \frac{BC}{AC} = \frac{\sin \alpha}{\sin \phi}, \) where \( \theta = 360 - \alpha - 180 + \phi. \) Application of the above equation in the first 5 contractions of set A gave the average lengths illustrated as black bars in the graph at the bottom. The white bars shown represent the respective average differences in the myotendinous junction displacement in the first 5 contractions of set B. The numbers 1–2 to 4–5 in the horizontal axis refer to transitions from a given contraction number to the next contraction number.

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involving isometric contractions, but it could complicate the control of movement generated by physiologically repeated contractions of high intensity, such as those elicited when running.

REFERENCES