Fatigue responses of human triceps surae muscles during repetitive maximal isometric contractions

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Kawakami, Yasuo, Kenji Amemiya, Hiroaki Kanehisa, Shigeki Ikegawa, and Tetsuo Fukunaga. Fatigue responses of human triceps surae muscles during repetitive maximal isometric contractions. J Appl Physiol 88: 1969–1975, 2000.—Nine healthy men (22–45 yr) completed 100 repetitive maximal isometric contractions of the ankle plantar flexor muscles in two knee positions of full extension (K0) and flexion at 90° (K90), positions that varied the contribution of the gastrocnemii. Electromyographic activity was recorded from the medial and lateral gastrocnemii and soleus muscles by using surface electrodes. Plantar flexion torque in K0 was greater and decreased more rapidly than in K90. The electromyographic amplitude decreased over time, and there were no significant differences between muscles and knee joint positions. The level of voluntary effort, assessed by a supramaximal electrical stimulation during every 10th contraction, decreased from 96 to 70% (P < 0.05) with no difference between K0 and K90. It was suggested that a decrease in plantar flexion torque was attributable to both central and peripheral fatigue and that greater fatigability in K0 than in K90 would result from a greater contribution and hence more pronounced fatigue of the gastrocnemius muscle. Further support for this possibility was provided from changes in twitch torque.

gastrocnemius and soleus muscles; plantar flexion; electrical stimulation; twitch interpolation; central and peripheral fatigue; fiber types

MUSCLE FATIGUE REFERS TO A CLASS OF ACUTE EFFECTS THAT IMPAIR PERFORMANCE (13). A DECREASE IN THE MUSCLE'S FORCE-PRODUCING CAPABILITY OVER PROLONGED (EITHER SUSTAINED OR INTERTMITTENT) CONTRACTIONS (9, 17) IS A TYPICAL MANIFESTATION OF MUSCLE FATIGUE. NUMEROUS FACTORS THAT HAVE BEEN PROPOSED TO MEDIATE MUSCLE FATIGUE ARE BASICALLY CLASSIFIED INTO TWO COMPONENTS WITH RESPECT TO THEIR LOCALITY, I.E., CENTRAL AND PERIPHERAL (13, 18). THE FORMER REFERS TO A DECREASE IN NEURAL DRIVE BY THE CENTRAL NERVOUS SYSTEM TO THE MOTOENEURON POOL, AND THE LATTER REFERS TO IMPAIRMENT IN IMPULSE TRANSMISSION AND/OR CONTRACTILE APPARATUS (31). BOTH OF THESE TWO COMPONENTS HAVE BEEN CONSIDERED TO CONTRIBUTE TO THE FATIGUE-INDUCED IMPAIRMENT OF PERFORMANCE, ALTHOUGH THEIR CONTRIBUTIONS VARY SUBSTANTIALLY, DEPENDING ON THE TASKS IMPOSED (22).

Because joint movement is achieved by contractions of multiple muscles in action, fatigue-induced impairment of joint performance depends on the differences in fatigue responses of various muscles. In addition, the forces generated by the muscles, and hence their contributions to torque, also change, depending on joint positions due to physiological and architectural factors. This could complicate fatigue-induced changes in joint performance.

The triceps surae, a principal ankle joint plantar flexor, is composed of the soleus (Sol) and gastrocnemius muscles. The gastrocnemii, with a mixed fiber composition, contain a considerably higher percentage of type II fast-twitch fibers than does the predominantly slow Sol (12, 19, 29). Because muscles with a higher percentage of fast-twitch fibers have been shown to be more fatigable (9, 10, 15, 25, 26), these two muscles should show different fatigue characteristics. In fact, previous studies have shown that, during maximal voluntary plantar flexions, the gastrocnemii demonstrate a greater decrease in activation than does the Sol (26), suggesting more susceptibility of gastrocnemius to fatigue. An additional distinction between the two muscles is that the gastrocnemius, unlike the Sol, crosses the knee joint; therefore, the length of gastrocnemius and hence its contribution to plantar flexion torque are affected by knee joint angle. Gastrocnemius generates greater torque with the knee extended than flexed (20, 28). It is conceivable, therefore, that fatigue-induced impairment of plantar flexion performance would not be identical between different knee joint positions. We hypothesized that fatigue in plantar flexion performance would be more evident with the knee extended, because in this position the gastrocnemius can contribute more torque; thus a reduction in torque would be more evident. This hypothesis was tested by comparing fatigue in the triceps surae during repetitive maximal isometric plantar flexions with the knee extended and flexed. The central and peripheral factors mediating fatigue were also tested by a combination of voluntary and electrically stimulated contractions.

METHODS

Subjects. Nine healthy men (age 22–45 yr; height 172.0 ± 4.2 cm; weight 71.1 ± 9.7 kg, mean ± SD) volunteered as...
subjects. They were physically fit but had not engaged in specific resistance training of plantar flexor muscle groups before the experiment. They gave written informed consent, and the procedures were approved by the local ethics committee.

Experimental settings and parameters measured. The right ankle joint was set at 10° of dorsiflexion, and the foot was securely strapped to a foot plate connected to the lever arm of an electrical myometer equipped with a computer for data analysis (Myorex, Asics, Tokyo, Japan). Two conditions were tested with the knee joint angles at full extension (K0) and flexion at 90° (K90). Testings in these two conditions were separated by at least 1 wk, and the order of testings was randomized among subjects. In K0, the subject lay prone on a test bench, and the waist and shoulders were secured by Velcro bands and held in position. In K90, the subject took an erect position with both knees flexed at 90°, and the trunk and thighs were secured to a wooden frame fixed vertically to the test bench.

After a warm-up procedure with submaximal contractions, the subject performed maximal isometric plantar flexions (maximal voluntary contraction (MVC)) for 3–5 s. Two separate efforts were made routinely, and a third extension was performed if more than a 5% difference existed. The highest peak torque was adopted as MVC torque.

During a voluntary contraction, evoked twitch contractions (double stimuli, with 500-µs duration for each and an interstimulus interval of 10 ms) were given by supramaximal electrical stimulations to evaluate the degree of voluntary effort. A high-voltage stimulator (SEN-3301, with a specially modified isolator (SS-1963), Nihon Koden, Tokyo, Japan) was used. The stimulation intensity was confirmed by setting the output of the stimulator to a level at which there was no imposed during and after (control twitch) contraction to determine %activation. The stimulation condition and postprocessing were identical to those of the MVC test. The duration of the contraction and the following rest period were thus somewhat longer (2–3 s) for every 10th contraction than for the other contractions without stimulation. Peak torque and time characteristics (time to peak: time taken from stimulation to peak twitch torque; and half relaxation time: time taken for the twitch torque to decay by one-half) of the control twitch were measured to study changes in the contractile properties of muscles involved. The evoked compound action potential (M wave) induced by the stimulation during control twitch was also recorded, and the peak-to-peak amplitude was determined.

The EMG amplitude of the initial four contractions was lower than that of the later contractions in most of the subjects; therefore, EMG and torque data were not used. Peak torque and iEMG were pooled for the consecutive nine contractions (except for the initial series), excluding every 10th contraction with electrical stimulation (i.e., contractions 5–9, 11–19, 21–29, . . . , 91–99). This provided 10 data points for each parameter for later analysis. This part of the experiment is hereafter referred to as a fatigue test.

Statistical analyses. Descriptive statistics are means ± SE unless otherwise stated. A two-way ANOVA with repeated measures (2 × 10, knee joint positions × time) with a Tukey post hoc test was used to analyze torque (peak voluntary torque and twitch torque) and %activation. For iEMG data, a three-way ANOVA with repeated measures (2 × 10 × 3, knee joint positions × time × muscles) was used. The changes in measured parameters after repeated contractions were correlated with others by using linear regression. In each statistical analysis, the level of significance was set at P < 0.05.

RESULTS

Maximal plantar flexion torque obtained during the MVC test was significantly greater in K0 (136.7 ± 10.6 N·m) than in K90 (85.9 ± 7.6 N·m). In both conditions, there was a significant increase in torque by electrical stimulations during MVC; hence %activation was smaller than 100% (96.0 ± 1.7 and 96.3 ± 1.5% for K0 and K90, respectively). There was no significant difference in %activation between K0 and K90.

Figure 1 shows typical recordings of plantar flexion torque in one subject. Peak torque decreased over time during the fatigue test. Changes in averaged peak torques of all subjects are illustrated in Fig. 2. The effect of knee positions was significant, i.e., torque was significantly greater in K0 than in K90, from the initial through the final contractions. The effect of time, as well as the interaction between time and knee positions, was significant. In K0, torque decreased rapidly at the beginning of contractions, as revealed by significant differences in torque between adjacent epochs. In contrast, torque decreased more slowly in K90; a statistical difference from the initial epoch (contractions 5–9) was observed only after contractions 41–49. At the final contractions, torque decreased by 38% in K0 but only by 19% in K90.

The iEMG changes, expressed relative to the initial values (contractions 5–9), are shown in Fig. 3. Only the
The effect of time was significant: changes in iEMG did not differ among the three muscles. The iEMG tended to be smaller in K0 compared with K90, but the differences were not significant in either muscle. The M-wave amplitude demonstrated no significant changes, and neither effect of muscle or time nor their interaction was significant.

The %activation significantly decreased during contractions, down to 66.7 ± 4.8 and 72.5 ± 4.3% in K0 and K90, respectively.
K90, respectively (Fig. 4). The effects of knee positions and interaction between time and knee positions were not significant.

The twitch torque every 10th contraction decreased over time in K0. After the final contraction, twitch torque was 81.2 ± 4.3% of the initial five contractions (Fig. 5). On the other hand, twitch torque remained unchanged in K90. Figure 6 shows typical recordings of twitch torque and M waves of medial and lateral gastrocnemii and Sol from one subject at the onset (10th) and final (100th) contraction.

The overall decrease in voluntary torque in the fatigue test was significantly correlated with that of the control twitch torque in K0 ($r = 0.74$). In K90, these parameters were almost, but not significantly, correlated ($r = 0.52$). Changes in %activation did not correlate with those in voluntary torque.

In K0, the time to peak of the control twitch during the fatigue test increased initially until the 30th contraction and then decreased systematically toward the 100th contraction (Fig. 7). A similar tendency was observed in K90, but the change was smaller, and the increase in time to peak was not significant. This resulted in significantly shorter time to peak in K90 than in K0 in the middle of the test. The decrease in time to peak toward the end of the fatigue test in K90, however, was significant. The twitch half relaxation time, on the other hand, was affected by neither time nor knee positions.

**DISCUSSION**

In the present study, we hypothesized that fatigue-induced changes in plantar flexion torque would be more pronounced when the knee was extended than
when flexed. This hypothesis was based on previous findings that 1) the contribution of the gastrocnemius muscle to plantar flexion torque decreases considerably as the knee is flexed (20, 28), 2) the gastrocnemius contains a higher percentage of fast-twitch fibers than does the Sol (12, 19, 29), and 3) the fast-twitch motor unit is more fatigable than the slow-twitch motor unit (8–10, 15). The results were as expected: plantar flexion torque decreased during the fatigue test more in K0 than in K90. Greater peak torque in K0 from the initial through the final contractions would indicate significantly greater contribution of the gastrocnemius that persisted throughout the fatigue test, but the initial 1.6-fold difference in torque between K0 and K90 decreased only to 1.2-fold at the end.

It should be pointed out that muscles other than the triceps surae also act as plantar flexors (16), although contributions of these muscles to plantar flexion torque have been shown to be <20% (24). However, only the length of the gastrocnemius muscle is affected by knee positions. Therefore, the observed differences in K0 and K90 would be attributable to the behavior of the gastrocnemius. In addition, because the Sol muscle has the largest physiological cross-sectional area (16), plantar flexion torque would be predominantly determined by the Sol, especially when the knee is flexed.

Ochs et al. (26) found, during repetitive maximal isometric contractions, a greater decrease in gastrocnemius EMG than in Sol, suggesting more fatigability of the gastrocnemius. Contrary to their findings, musclespecific EMG changes were not observed in the present study. iEMG decreased in all of the triceps surae muscles with no significant intermuscle difference. This suggests that muscle activation decreased in a similar manner for these muscles with the present protocol, which supports the notion that the difference between K0 and K90 occurs in the muscle at the level distal to the sarcolemma. This possibility is discussed later in detail. Another possibility might be that small changes in EMG have gone undetected in this study because of the nature of surface EMG, which is a noisy average of the neural activation of muscle. Indeed, it has been shown that EMGs show variable responses during exercise and no close relationship to fatigue (33). Furthermore, there might have been cross talks of EMGs between muscles, and in the present study we were not able to check it. But the pairs of electrodes were well separated, and it was visually confirmed by ultrasonogram that each electrode pair was placed on the midbelly (where muscle thickness was largest) of the respective muscle. Therefore, we believe that the recorded EMG signals were predominantly from respective muscles.

The inability to maximally activate plantar flexor muscles even in an unfatigued state (96% of activation both in K0 and K90 in the MVC test) is in agreement with previous studies. Belanger and McComas (4) reported that humans cannot fully activate some muscles, among which were plantar flexors. The limitation to maximally activate plantar flexors appears to be enhanced during fatigue (14). The present findings (decrease in %activation) support this notion. However, there was no difference between K0 and K90 in the changes in %activation, suggesting that greater fatigability in K0 was not due to greater central fatigue.

Twitch torque showed similar changes to those of voluntary torque. However, in contrast to the decreases in voluntary torque to 61% (K0) and 80% (K90) of initial values, decrement of twitch torque was smaller for the twitch both in K0 (79%) and K90 (93%, not significant). This would suggest, together with the decrease in %activation, that voluntary torque was attenuated by both central and peripheral fatigue. Because the M wave did not change during the fatigue test, failure in neuromuscular propagation would have been negligible (13, 27). Impairment of excitation-contraction coupling has been observed in sustained, low-intensity contractions but rarely in intermittent, high-intensity contractions (2, 3, 6, 13, 14). Therefore, the decrease in twitch torque was not due to neuromuscular block but to failure of contractile machinery. In K90, this impairment would have been small because of ineffectual contribution of fatigable gastrocnemius and greater contribution of fatigue-resistant Sol muscle.

Previous studies have argued various contributions of neural (or central) and peripheral fatigue. It has been shown that the contribution of central fatigue is greater when the intensity of the contraction is higher (21, 23), but, even during MVC, central drive sometimes remains maximal throughout the task (7). The degree of central fatigue appears to depend on imposed tasks (13). In the present study, %activation was not
significantly smaller than the initial values until contractions 51–59 in K0, whereas voluntary torque had decreased considerably. Furthermore, significant correlations existed between changes in voluntary and twitch torque but not between voluntary torque and %activation. These results would suggest that peripheral fatigue was more influential.

The increase in twitch time to peak torque in K0 in the middle of the fatigue test could be a result of contraction slowing, which is a typical observation in muscle fatigue (15). The difference in the responses of time to peak and half relaxation time suggests that the results were not due to muscle temperature rise over time (5, 11). No significant increase in twitch time to peak in K90 suggests that the gastrocnemius was not so fatigued as to cause slowing of contraction in this condition. The decrease in twitch time to peak from the middle toward the end of the fatigue test in both K0 and K90, however, was an unexpected result. A previous study also found a decrease in twitch time to peak after fatigue induced by intense exercise (30). It was suggested by the authors that shorter contraction time might be due to a shorter Ca2+ transient and/or a higher rate of cross-bridge binding, although reasons for those changes were not clear. Another study that found no increase in twitch time to peak during prolonged exercise proposed an increased proportion of functional Ca2+ pumps at the sarcoplasmic reticulum membrane as a possible candidate (34). The present change in twitch time to peak in K0 (an increase followed by a decrease) might be a result of an interaction between contractile slowing and faster Ca2+ kinetics. No significant change in the half relaxation time suggests that relaxation from twitch contraction, which is an active process regulated by SR Ca2+- and/or myosin-ATPase (3, 34), was not impaired by the present exercise. However, these possibilities are purely speculative at this moment, and from the present results it can only be said that some changes occurred at the level distal to the sarcolemma, which was different between the two conditions, possibly because of differences in fatigue-induced changes in the gastrocnemius muscle.

In conclusion, the present results suggest that the decrease in plantar flexion torque during repetitive maximal isometric contractions is attributable to both central and peripheral fatigue. Greater decrease in torque with the knee extended than flexed would be a result of much greater fatigability of the gastrocnemius than the Sol muscle.

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