Neuromuscular fatigue after maximal stretch-shortening cycle exercise

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Strojnik, V., and P. V. Komi. Neuromuscular fatigue after maximal stretch-shortening cycle exercise. J. Appl. Physiol. 84(1): 344–350, 1998.—To examine some possible sites of fatigue during short-lasting maximally intensive stretch-shortening cycle exercise, drop jumps on an inclined sledge apparatus were analyzed. Twelve healthy volunteers performed jumps until they were unable to maintain jumping height >90% of their maximum. After the workout, the increases in the blood lactate concentration and serum creatine kinase activation were statistically significant (P < 0.001 and P < 0.05, respectively) but rather small in physiological terms. The major changes after the workout were as follows: the single twitch was characterized by smaller peak torque (P < 0.05) and shorter time to peak (P < 0.05) and half-relaxation time (P < 0.01). The double-twitch torque remained at the same level (P > 0.05), but with a steeper maximal slope of torque rise (P < 0.05); during 20- and 100-Hz stimulation the torque declined (both P < 0.01) and with the maximal voluntary torque changed nonsignificantly but with a smaller maximal slope of torque rise (P < 0.01) and a higher activation level (P < 0.05), accompanied by an increased electromyogram amplitude. These findings indicate that the muscle response after the short-lasting consecutive maximum jumps on the sledge apparatus may involve two distinct mechanisms acting in opposite directions: 1) The contractile mechanism seems to be potentiated through a transient and faster cross-bridge cycling, as implied by twitch changes. 2) High-frequency action potential propagation shows an impairment, which is suggested as the possible dominant reason for fatigue in exercise of this type.

fatigue sites; maximal intensity; short duration; electrical stimulation

FATIGUE IS A VERY COMPLEX phenomenon, and it may be described as a loss of force-generating capability (4) or an inability to sustain further exercise at the required level (7). During sustained isometric maximum voluntary contraction (MVC), force declines progressively. Fatigue processes can develop in many places during the activation-contraction chain (2). They can be found in an insufficient central neural drive, i.e., central fatigue, or in events beyond the neuromuscular junction, i.e., peripheral fatigue. After the activation-contraction chain, peripheral fatigue can be further divided into high- and low-frequency fatigue (7). High-frequency fatigue occurs as a result of an impairment in action potential propagation over the sarcolemma; low-frequency fatigue denotes an impairment in excitation-contraction coupling.

Stretch-shortening cycle (SSC) is defined as a stretching of an active muscle immediately followed by concentric contraction (17). Fatigue during submaximal SSC is characterized by reduced movement efficiency (11) as well as a dramatic decline in maximal isometric force (15). High peak lactate values also appear after this type of exercise. The peak of serum creatine kinase (CK) accumulation is delayed, occurring on the 2nd day after exercise (22). The fatigue during an SSC exercise may be even more complex, since neural control, besides central activation, depends on reflexively induced activation. Reduced muscle activation in the eccentric phase (10) and a smaller monosynaptic response to a sudden stretch of the relaxed soleus (Sol) muscle (23) have been obtained in submaximal SSC fatigue exercise.

Most fatigue studies in SSC exercise have concentrated on submaximal workout intensity levels (17, 18, 22). However, the fatigue mechanisms in maximum SSC exercise may differ from the mechanisms at the submaximal level, since exercise at higher intensity involves greater reaction forces, greater muscle activation, and shorter exercise duration. Because of these factors, more muscle stress and lower blood lactate may be expected at maximal-intensity exercise. According to our previous comparison of maximal and submaximal concentric workouts (25), a shift from low- to high-frequency fatigue may be expected as well. The aim of the present study was to examine some possible fatigue events during short-lasting maximally intensive SSC exercise. Contractile characteristics of the muscle, i.e., force during low- and high-frequency stimulation, activation level, and blood analysis, were measured and used in an attempt to clarify further the possible fatigue mechanisms.

METHODS

Subjects. Twelve healthy men (physical education students) volunteered for the study (age = 28.1 ± 5.8 yr, height = 179.8 ± 5.3 cm, body mass = 78.9 ± 12.3 kg). They were not involved in intensive sport training. Subjects were well informed about possible risks associated with the experiment and gave their informed consent before the experiment. The study was approved by the University Ethical Committee.

Experimental design. Subjects performed a warm-up, which consisted of 6 min of stepping on a 20-cm-high bench with a frequency of 0.5 Hz, with a leg exchange each minute. After the warm-up, tests for the assessment of the initial status were performed in the following sequence: blood sample, response of the relaxed vastus lateralis (VL) muscle to single electrical impulse (twitch), response of the relaxed quadriceps femoris muscle to double electrical impulse (double twitch), response of the VL muscle to electrical stimulation (ES) at 20 and 100 Hz, explosive isometric maximum voluntary knee extension, and steady maximum voluntary extension with superimposed double twitch. All these measurements were performed at predefined times after the end of the warm-up. Then, the maximum jumping height was determined on the sledge ergometer, which was used for the fatigue exercise. The same test sequence was used after fatigue; the last test ended 4 min after the workout. Additionally, blood was...
collected 5 min, 2 h, and 2 days (at the same time of day and after the same warm-up) after fatigue was induced. Surface electromyogram (EMG) activity during some pre- and postfatigue tests was recorded from the tibialis anterior (TA), Sol, gastrocnemius medialis, VL, and vastus medialis (VM) muscles by bipolar silver chloride miniature skin electrodes (Beckman) with an interelectrode distance of 20 mm and transmitted telemetrically (model 2000, Glonner Biomes). The electrodes were placed longitudinally on the belly of the observed muscles. Care was taken to ensure that the interelectrode resistance did not exceed 5 kΩ. All signals were digitized with a sampling frequency of 1 kHz and fed to a computer for further processing. They were also stored simultaneously on a magnetic tape recorder (Racal).

Fatigue workout. The fatigue workout was performed on a special sledge gliding on a track inclined at 23° from the horizontal. The apparatus has been described in more detail elsewhere (18). The maximum jumping height was measured by releasing the sledge from 80 cm above the position in which subjects’ legs were maximally extended (zero position). Once the maximum jumping height was established, 90% of the distance between the zero position and the maximum height was marked as the limit for the fatigue workout termination. Subjects were asked to perform consecutive maximum jumps (in an “all-out” manner) without pause, until told to stop. When they were no longer able to jump to >90% of their preset maximum height, the workout was terminated. During jumping, the subjects maintained a 90° knee angle in the lowest sledge position. Oral feedback was provided to secure correct angular position. To prevent trunk movements, the subjects were secured to the sledge. Their arms were placed on the seat sides next to the thighs and were not moved during jumping. Verbal encouragement was used to motivate subjects for maximum output throughout the workout. The mean duration of the fatigue workout was 62.4 ± 24.8 s, during which the subjects were able to execute 36.5 ± 16 rebound jumps.

Electrical stimulation. In all measurements with ES and during explosive voluntary knee extension, the subjects sat in an isometric knee extension-measuring device (adapted model 200, David) and were fixed to the apparatus at the pelvis and over the distal part of the thigh to prevent trunk and thigh movements. The distal part of the shank was fixed to the force transducer, which had a constant lever arm to the knee joint axis. The knee joint angle was fixed at 45°. Self-adhering neurostimulation electrodes (5 × 5 cm; Axelgaard, Fallbrook, CA) were placed over the VL, VM, and rectus femoris muscles. Distal electrodes were placed over the distal part of the muscle belly, and proximal electrodes were placed over the middle part of the muscle belly. Each pair of electrodes was galvanically separated from the other pairs. On all occasions, constant-current square biphasic impulses of 0.3-ms duration were employed, and a custom-made computer-controlled electrical stimulator was used.

Stretch reflex test. The stretch reflex was measured with a special ankle dynamometer (23), which could induce different angular displacements at constant angular velocities around the ankle joint. The subject sat relaxed in the chair; his right foot was placed and fixed to the footplate with the ankle angle at 90°. Thus the rotational axis of the platform and the ankle joint were aligned. The knee was fixed at 60° to prevent knee and shank movements. Eight consecutive dorsiflexions (amplitude = 6°, velocity = 160°/s) were applied. The interval between two flexions was 5 s. EMG activity from the Sol, gastrocnemius medialis, and TA muscles and the positional data from the ankle ergometer were collected. Only those EMG records without TA activation and no EMG signal in the Sol before the stretch were analyzed. EMG records were high-pass filtered (cutoff frequency = 10 Hz), rectified, and averaged. The latency, duration, and area of EMG responses were examined. EMG cross talk was minimal. A method described earlier (23) was employed for evaluation.

Single twitch test. Three supramaximal stimuli were delivered consecutively with 1-s delay to the relaxed VL muscle. The torque signals from the twitch responses were smoothed (moving average, \( n = 5 \)) and averaged. Maximum twitch torque (\( T_{TW} \)), electromechanical delay (EMD), contraction time (CT), half relaxation time (RTH), and maximum rate of torque development (\( MTR_{TW} \)) were obtained.

Double twitch test. Two consecutive supramaximal stimuli with 10-ms delay were delivered to the relaxed quadriceps femoris muscle via all three electrode pairs simultaneously. The torque signal of the double-twitch response was smoothed (moving average, \( n = 5 \)) and analyzed for maximum torque (\( T_{DTW} \)) and maximum torque development (\( MTR_{DTW} \)).

Low- and high-frequency torque tests. The relaxed VL muscle was stimulated with two consecutive trains of impulses with a frequency of 20 Hz (1-s duration) and 100 Hz (0.8-s duration; Fig. 2). Stimulation amplitude was set to three times that of the motor threshold amplitude (30–54 mA) and was kept the same for both frequencies. The mean torque during the last 50 ms of stimulation for each frequency (\( F_{20} \) and \( F_{100} \)) was obtained.

Voluntary explosive knee extension test. Each subject was placed in turn on the same chair under the same conditions as
for the ES measurements. On command, the subjects tried to achieve their maximum isometric knee extension torque as quickly as possible. They started from a relaxed position, without preparatory movements, and maintained the maximum activation for 2 s. The force signal was smoothed (moving average, \( n = 5 \)) and analyzed for maximum torque \((T_{\text{MVC}})\) and maximum rate of torque development \((\text{MTR}_{\text{MVC}}})\).

Activation level. The activation level \((\text{AL})\) was assessed by a superimposed double-twitch technique derived from the twitch interpolation method described by Merton (19) \(\text{(Fig. 3)}\). \(T_{\text{DTW}}\) was compared with the torque rise during superimposed double twitch over maximum voluntary knee extension. At the command signal, the subjects started to exert force. Two seconds after the start of voluntary contraction, when the maximum torque \((T_{\text{max}})\) was attained, the subjects received two stimuli in the same way as in the double-twitch test. The difference \((D)\) between the torque level just before the double twitch \((T_{\text{b}})\) and the maximum torque during the double twitch was compared with \(T_{\text{DTW}}\) as follows

\[
\text{AL} = 100 - D \times \frac{T_{\text{b}}}{T_{\text{max}}} / T_{\text{DTW}} \times 100
\]

A correction of \(D\) was included in the original equation, since the double twitch was not always applied during maximum torque level, but also later when the torque was already slightly declining. Because \(D\) tends to grow at torques lower than maximal and because this relationship was shown to be linear \((19)\), the expression \(T_{\text{b}} / T_{\text{max}}\) can be used to correct \(D\).

EMG activity during isometric MVC. Both EMG signals were rectified and integrated. Time was normalized \((\text{EMG}_{\text{VL}}\) and \(\text{EMG}_{\text{VM}})\) for the steady part of the maximum knee extension at the activation level measurement, appearing before the superimposed double twitch during a 0.5-s interval. The EMG signal was also normalized to a mean torque established for the same interval \((\text{nEMG}_{\text{VL}}\) and \(\text{nEMG}_{\text{VM}})\), respectively.

Blood analysis. Blood samples for blood lactate concentration analysis \((20\, \mu\text{l})\) were drawn from the fingertip, whereas the blood samples used to determine serum CK activation were taken from the antecubital vein of the right arm. Both samples were analyzed with a spectrophotometer \((\text{model U-2000, Hitachi})\) and reagents from Boehringer \((\text{Mannheim, Germany})\).

Statistics. The t-test for paired samples was used to calculate the statistical significance of differences between the initial measurement and the state after workout. Additionally, Pearson correlation coefficients were calculated between relative changes in parameters after workout according to the initial state. Statistical significance was accepted at \( P < 0.05 \) \(\text{(2-tailed)}\).

RESULTS

Responses to single and double supramaximal stimulus had some common features \(\text{(Fig. 4)}\). In the single-twitch test the mean maximum torque dropped from an initial \(12.7 \pm 4.4\) to \(11.6 \pm 4.6\) \((\text{SD})\) \(\text{N} \cdot \text{m}\) after the fatigue test \((P < 0.05)\). EMD showed no statistically significant change, whereas CT as well as RT, became shorter: from \(68.7 \pm 10.5\) to \(60.1 \pm 8.4\) \((\text{ms})\) \((P < 0.05)\) and from \(67.8 \pm 7.0\) to \(56.1 \pm 12.9\) \((\text{ms})\) \((P < 0.01)\), respectively. In contrast, the mean double-twitch maximum torque did not change significantly \((55.5 \pm 10.6\) to \(57.5 \pm 13.2\) \((\text{N} \cdot \text{m})\)), although the mean peak rate of torque development was greater after the exercise \((1,470 \pm 300\) to \(1,672 \pm 412\) \((\text{N} \cdot \text{m} \cdot \text{s}^{-1})\), \(P < 0.05\). The peak rate of torque development increased also in the single twitch \((6.7 \pm 10.8\%), \text{although not significantly}\). When it was normalized to \(T_{\text{TW}}\), it became significantly greater \((19.5 \pm 12.1\%, P < 0.001)\).

In the low- to high-frequency stimulation test, both torques \((F_{20} \text{ and } F_{100})\) were significantly reduced: from \(15.3 \pm 6.3\) to \(12.8 \pm 6.4\) \((\text{N} \cdot \text{m})\) \((P < 0.01)\) and from \(26.0 \pm 12.3\) to \(19.9 \pm 9.6\) \((\text{N} \cdot \text{m})\) \((P < 0.01)\), respectively. The correlation analysis between the blood lactate change and the \(F_{20}\) change revealed a significant positive correlation \(\left( r = 0.75, P < 0.01 \right)\); the subjects with the smallest lactate change exhibited a greater \(F_{20}\) reduction after exercise.

In the isometric explosive MVC knee extension, the subjects demonstrated a significantly lower mean rate of torque development \((2,163 \pm 724\) to \(1,735 \pm 576\) \((\text{N} \cdot \text{m} \cdot \text{s}^{-1})\) \((P < 0.01)\) but no significant changes in the

Fig. 3. Data from 1 subject to show measurement of activation level. A: torque-time curve of superimposed double twitch during sustained maximal voluntary contraction \((\text{MVC})\) knee extension. Vertical line, instant of electrical stimulation \((\text{ES})\) application. Because stimulus was not delivered exactly at point when maximal torque was obtained, a corresponding index was introduced \(\text{(see Eq. 1)}\). It was assumed that fall in MVC torque just before ES can be accounted for by normal deviations seen when one is trying to maintain MVC tension, and not to fatigue. B: responses of relaxed and MVC-activated muscle to double stimulus. In MVC attempt, torque was adjusted to level at ES impulse delivery so that both responses can be presented on same scale.
maximal torque level. Comparison in maximal torque and rate of torque development between the double twitch and the explosive MVC knee extension revealed no significant change in the mean ratio of the maximal torque levels, whereas the mean ratio of $\text{MTR}_{\text{MVC}}$ to $\text{MTR}_{\text{DTW}}$ decreased by $8.5 \pm 5.4\%$ ($P < 0.001$). Relative changes in other MVC and ES parameters are presented in Fig. 5.

During the sustained isometric MVC knee extension, the mean EMG amplitudes in VL and VM muscles demonstrated no significant change (Fig. 6). The changes in the mean MVC torque during sustained contraction were related to the changes in EMG amplitude of the VL muscle ($r = 0.72$, $P < 0.01$) but not to changes in EMG amplitude of the VM muscle. When the EMG amplitudes were normalized to torque, EMG appeared to be significantly greater ($P < 0.001$) in the VL muscle after exercise.

In the stretch reflex test, no significant mean change was observed after the workout in any of the analyzed parameters. The blood sample analysis revealed a statistically significant increase in blood lactate concentration and CK ($P < 0.001$ and $P < 0.05$, respectively), with mean peak values after the workout of $5.4 \pm 1.4$ mmol/l and $359.4 \pm 287.4$ U/l, respectively, compared with initial values of $1.93 \pm 0.3$ mmol/l and $259.3 \pm 206.0$ U/l, respectively. The mean peak lactate level was observed 5 min after the workout and the mean peak CK level 2 h after the workout. These changes were much smaller than those obtained in our earlier studies (35) with longer duration of submaximal SSC exercises.

**DISCUSSION**

The main findings in this study were 1) a shorter single twitch with a smaller peak torque, 2) preserved peak torque and an even faster rate of torque development in the double twitch, 3) smaller low- and high-

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**Fig. 4.** Typical sample responses of a relaxed muscle of 1 subject as measured after warm-up and 2.5 min after end of workout. In both cases, faster contraction appeared after end of workout when subject was no longer able to jump >90% of his maximum jumping height. A: response of vastus lateralis (VL) muscle to single supramaximal stimulus. B: response of quadriceps femoris (QF) muscle to double supramaximal stimulus.

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**Fig. 5.** Relative changes in mechanical MVC and ES parameters. $T_{\text{TW}}$, single-twitch peak torque; $\text{MTR}_{\text{TW}}$, maximum rate of torque development of single twitch; CT, contraction time of single twitch; $RT_{\text{t}}$, half relaxation time of single twitch; $T_{\text{DTW}}$, double-twitch peak torque; $\text{MTR}_{\text{DTW}}$, maximum rate of torque development of double twitch; $F_{20}$, torque during 20-Hz ES; $F_{100}$, torque during 100-Hz ES; $T_{\text{MVC}}$, maximal torque during explosive isometric MVC; $\text{MTR}_{\text{MVC}}$, maximum rate of torque development during explosive isometric MVC; AL, activation level. Vertical lines, SD. *$P < 0.05$; **$P < 0.01$.

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**Fig. 6.** Relative changes in mean EMG amplitudes and EMG-to-torque ratio during sustained isometric MVC knee extension. $\text{EMG}_{\text{VL}}$, mean EMG amplitude of VL; $\text{EMG}_{\text{VM}}$, mean EMG amplitude of vastus medialis; $n\text{EMG}_{\text{VL}}$, EMG-to-torque ratio of VL; $n\text{EMG}_{\text{VM}}$, EMG-to-torque ratio of vastus medialis. ***$P < 0.001$. 

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frequency stimulation torque, 4) preserved maximal MVC torque with a slower rate of torque development, 5) no changes in the mean stretch reflex response, and 6) a significant but small increase in blood lactate concentration.

In fatigue the twitch tension decreased in human (3, 13) and frog muscles (9, 27). Recovery from twitch tension falls into two phases, the first of which is very rapid and takes ~2 min (27). In the present study the twitch was measured 2.5 min after the end of the fatigue protocol, which means that the twitch tension at the end of the workout might be lower than the twitch tension measured. Hainaut and Duchateau (13) reported 67% of the initial level after a protocol with ES, whereas after 60 s of MVC the twitch tension may decline almost to 70% (3). If a time delay is assumed, the twitch tension after the workout might well fall into that range in the present study.

Twitch times, on the contrary, showed completely different behavior. A normal response to fatigue is a prolongation of CT and RT, which may increase up to 300 and 800%, respectively (26). These changes seem to be smaller in human muscles (12–17% and 36–41%, respectively) (13). Shorter CT and RT, obtained in the present study do not seem to agree well with the fatigue response, especially when it is considered that the maximum rate of torque development increased as well. Again, the recovery effect must be considered when our data are examined, even though possible changes would probably be quantitative rather than qualitative.

An impairment in the contractile mechanism seems to be the most direct reason for fatigue. An isometric twitch has frequently been used as an indicator of muscle fatigue, providing information about the number of active cross bridges. In the present study the peak torque response to a single stimulus declined after exercise, which is in accordance with other fatigue studies (9, 27). The reduced torque could be associated with a reduced Ca$^{2+}$ release from the sarcoplasmic reticulum and/or reduced capability of cross bridges to form strong binding (20). Shorter CT and RT, suggest that the reduced T_{TW} may have resulted from a shorter Ca$^{2+}$ transient. This view can be further supported by T_{DTW}, which remained unchanged after the exercise. Because of two consecutive stimuli, the Ca$^{2+}$ transient was longer, thus making T_{DTW} less sensitive to changes in the Ca$^{2+}$ transient. The small change in blood lactate concentration may indicate that the decline in T_{TW} was not accompanied by significant changes in H$^{+}$ and/or PO$_4$$. Such an occurrence was also observed by Vøllestad et al. (28), although after different exercise. In addition, the peak rate in torque development in single- and double-twitch conditions increased, suggesting a higher rate of cross-bridge binding, as observed by Metzger and Moss (20). If a low pH inhibits the rate of cross-bridge binding (21), the increased slope of torque rise would suggest no physiologically significant change in pH. However, shorter CT and RT, may also be due to increased muscle temperature because of exercise. The temperature effect on muscle contractile characteris-
study. Despite the generally low lactate levels, it was possible to observe that the relative lactate change significantly discriminates the response in $F_{20}$ (Fig. 7). The relationship is in the direction opposite that expected, since low-frequency exercise normally develops during submaximal exercise. Such a differential response would additionally support the suggestion that a shorter Ca$^{2+}$ transient and faster cross-bridge cycling as well as an impairment of high-frequency action potential propagation, which could be the dominant reason for fatigue.

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