

Fatigue and recovery at long and short muscle lengths after eccentric training

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ABSTRACT

WILLEMS, M. E. T., and W. T. STAUBER. Fatigue and recovery at long and short muscle lengths after eccentric training. *Med. Sci. Sports Exerc.*, Vol. 34, No. 11, pp. 1738–1743, 2002. **Purpose:** To determine the effects of high-speed eccentric training of rat plantar flexor muscles on: 1) maximum (120 Hz) force at 90° ankle position; 2) fatigue (40 concentric muscle actions, ROM 50°) and recovery (6 concentric muscle actions) tested at short or long muscle lengths; and 3) low-frequency fatigue. **Methods:** Training consisted of eccentric muscle actions from ankle positions of 140° to 40° (velocity $\sim 400^\circ\text{s}^{-1}$) followed by unresisted concentric muscle actions (5×10 repetitions, $5 \text{ d}\cdot\text{wk}^{-1}$ for 6 wk). Fatigue was induced by concentric muscle actions with a rest of 12.5 s between muscle actions, and recovery consisted of equivalent concentric muscle actions performed every 5 min for 30 min. Low-frequency fatigue was measured 35 min after testing at 90° ankle position by using the ratio of isometric force produced by 20- and 100-Hz stimulation frequencies. **Results:** Eccentric training increased maximal isometric force per muscle weight by 22% whereas muscle weights were unchanged. In control muscles (C), isometric force immediately preceding each concentric muscle action decreased more at long lengths than at short lengths during the fatigue protocol; this length-dependent difference disappeared after 30 min of recovery. At short lengths, isometric force decreased less in trained muscles (T) (C: $78.4 \pm 3.6\%$; T: $59.6 \pm 4.4\%$) and recovered more during the following 30-min period (C: $84.7 \pm 2.5\%$; T: $95.4 \pm 2.8\%$ of initial values). Changes in F20/F100 were smaller for trained muscles (C: $35.4 \pm 2.0\%$; T: $22.0 \pm 1.4\%$). **Conclusions:** High-speed eccentric training ($5 \text{ d}\cdot\text{wk}^{-1}$ for 6 wk) reduced fatigability and enhanced recovery mainly at long muscle lengths. It also reduced low-frequency fatigue, which may be attributed to alterations in intracellular calcium handling. **Key Words:** SKELETAL MUSCLE, MUSCLE LENGTH, ISOMETRIC FORCE, RESISTANCE TRAINING, LOW-FREQUENCY FATIGUE

Repeated high-intensity isometric actions of skeletal muscles can produce a loss of force with time (i.e., muscle fatigue) (15,26). Numerous studies have examined mechanisms of fatigue (i.e., central and peripheral) (for a review, see 6) and adaptations in fatigability with training (5,10,18,19,24). Only a few studies recognized the importance of muscle length on fatigability, but contrasting observations were reported. For example, in toad sartorius muscle (1) and human tibialis anterior muscle (25), isometric muscle actions at short muscle lengths led to larger force losses than at long muscle lengths. In contrast, smaller declines in force were observed at short muscle lengths for ankle dorsiflexor (8), ankle plantar flexor (15), and elbow flexor muscles in humans (20) than at long muscle lengths. In general, knowledge of the length-specific adaptability to fatigue of skeletal muscles could be useful for the treatment of sport-specific muscle imbalances.

When exercise training does not result in muscle length changes but improves fatigue resistance, one can expect

fatigue resistance to be reduced at all muscle lengths. Training with eccentric and concentric muscle actions occurs without muscle and fiber length changes (14) and is known to reduce fatigue (28). Such training provides a useful intervention to study adaptations of muscle length-related fatigue and recovery.

After fatigue induced by repeated high-intensity isometric muscle actions, recovery has been demonstrated to be faster at high compared with low stimulation frequencies (i.e., low-frequency fatigue) (e.g., 13). Low-frequency fatigue was caused by decreased release of calcium from the sarcoplasmic reticulum (3,7). Because high-intensity training enhanced the peak in release of calcium from the sarcoplasmic reticulum (22), a reduction in low-frequency fatigue may result from high-intensity training; such training adaptation has not been examined.

Two hypotheses were tested in the present study. First, high-speed eccentric training would reduce fatigue and improve recovery of isometric force both at short and long muscle lengths. Second, eccentric training would reduce low-frequency fatigue.

METHODS

Approach to the problem and experimental design. This study was primarily designed to examine muscle performance at two different joint positions after training. A research design using high-speed eccentric training of one muscle group as the independent variable and production of

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muscle force as the dependent variable was used. The control group consisted of caged rats.

After the training period, trained and control rats were each randomly divided in two groups (group 1: short muscle length, and group 2: long muscle length). By using direct nerve stimulation, the changes in isometric force production with intermittent muscle actions were recorded and assessed an indicator for fatigue and recovery. Experimental tests included also the assessment of training adaptations in low-frequency fatigue.

Animal care and high-speed eccentric training.

Female Sprague Dawley rats (4–5 months, $N = 20$) were used. Rats were provided standard rat chow and water *ad libitum*, and kept in animal facilities maintained at 21°C with a 12:12-h light-dark cycle. The present study complied with Animal Welfare Act P.L. 91–579 and DHHS Guidelines governing the care and use of laboratory animals. All procedures were approved by and followed the guidelines of the West Virginia University Animal Care and Use Committee (WVU-ACUC no. 9809–02) and were conducted in accordance with the principles of the American College of Sports Medicine.

Procedures for high-speed eccentric training of rat plantar flexor muscles have been described before (28). In brief, training was performed on muscles of rats given atropine (0.08 mg·kg⁻¹ s.c.) and anesthetized with ether. Electrodes for electrical stimulation were inserted subcutaneously and positioned bilaterally along the surface of the plantar flexor muscles of the lower left hindlimb (29). Parameters for electrical stimulation (pulse duration: 0.2 ms, stimulation frequency: 70 Hz, voltage: 40 V) provided near maximal activation. The left foot of the rat, lying on its back, was held between thumb and index finger at an ankle position of 140°. After onset of stimulation, the ankle was dorsiflexed to 40° by pushing at the sole of the foot (i.e., forced eccentric muscle action, angular velocity about 400°·s⁻¹) and returned to the starting position with (i.e., concentric muscle action) with little resistance. Training consisted of five bouts of 10 repetitions (time needed to turn on and off stimulation and perform 10 repetitions was about 5 s) with 30-s rest intervals between bouts, performed 5 d·wk⁻¹ for 6 wk. Training involved a fairly high angular velocity and will be referred to as high-speed eccentric training. Muscles of rats exposed to high-speed eccentric training will be referred to as trained muscles. Control rats were also exposed daily to ether.

Fatigue and recovery of skeletal muscles using concentric muscle actions imposed on isometric muscle actions. Experiments to induce fatigue and recovery from fatigue were performed on nerve-stimulated plantar flexor muscles of the left hindlimb of rats anesthetized with sodium pentobarbital (75 mg·kg⁻¹ i.p.). Details on the dissection procedure for nerve cuff placement, animal positioning, dynamometer, and force recording are described elsewhere (4,27). Briefly, the foot of the rat was positioned on an aluminum plate, which was connected to a dynamometer. The dynamometer consists of a DC permanent magnet servomotor (Model 1410C) and a Unidex 1

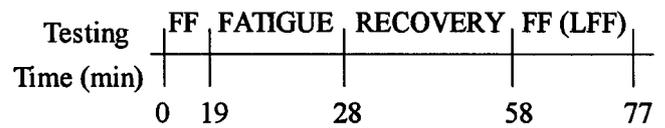


FIGURE 1—Time sequence for testing of rat plantar flexor muscles. FF, force-frequency; LFF, low-frequency fatigue.

single-axis motion controller (Aerotech Inc., Pittsburgh, PA). Below the aluminum plate is a Z-11/5-kg load cell (HBM Inc., Marlboro, MA). Force of the plantar flexor muscles by stimulation via the tibial nerve was recorded as a reaction force under the sole of the foot. Electrical stimulation of the tibial nerve with stimulus parameters (200- μ s pulse duration, 80 Hz, 5.8 ± 0.4 V, mean \pm SE) provided near maximal activation. Pulse duration and voltage of the stimulus parameters were kept constant for the force-frequency measurements (see below).

The time sequence for force-frequency measurements and fatigue/recovery testing is presented in Figure 1. Fatigue was tested using 40 concentric muscle actions (velocity 50°·s⁻¹) immediately after isometric muscle actions (duration 1.9 s, rest period 12.5 s) (28). For fatigue and recovery testing, each group of eccentric-trained and control rats was randomly subdivided into two groups (long and short muscle lengths) with differing starting position. The long muscle length group ($N = 5$) was exposed to concentric muscle actions from an ankle position of 40–90°. The short muscle length group ($N = 5$) was exposed to concentric muscle actions from an ankle position of 70–120° (short muscle lengths, $N = 5$). The ankle position of 40° lies at one end of the range of motion used during high-speed eccentric training. The ankle position of 70° is near the optimum length of the plantar flexor muscles (27). In both testing conditions, the rat's ankle was rotated to the starting ankle position (from 90° to 40° or from 120° to 70°) with a velocity of 50°·s⁻¹ with relaxed muscles. After a 100-ms pause, the plantar flexors were activated (i.e., isometric muscle action), and 600 ms later the ankle was rotated for the concentric muscle action. Figure 2A shows a typical force-time pattern of a muscle action used at short muscle lengths, illustrating the isometric and concentric phase. Concentric work was similar for the groups tested at short and long muscle lengths (Fig. 2B). Recovery was monitored using equivalent muscle actions every 5 min for 30 min. In a previous study, 30 min resulted in almost full recovery of maximal force production (28). All muscle actions (fatigue and recovery) were preceded by one movement of the same magnitude but with no muscle activation.

Low-frequency fatigue using isometric muscle actions. Force-frequency measurements were obtained before fatigue testing and 35 min thereafter with stimulation frequencies between 5 and 120 Hz. Force-frequency measurements were performed at an ankle position of 90° using isometric muscle actions. Force traces of isometric muscle actions with stimulation frequencies of 20 Hz (stimulation time 1500 ms) and 100 Hz (stimulation time 600 ms), used to calculate low-frequency fatigue, are illustrated in Figure

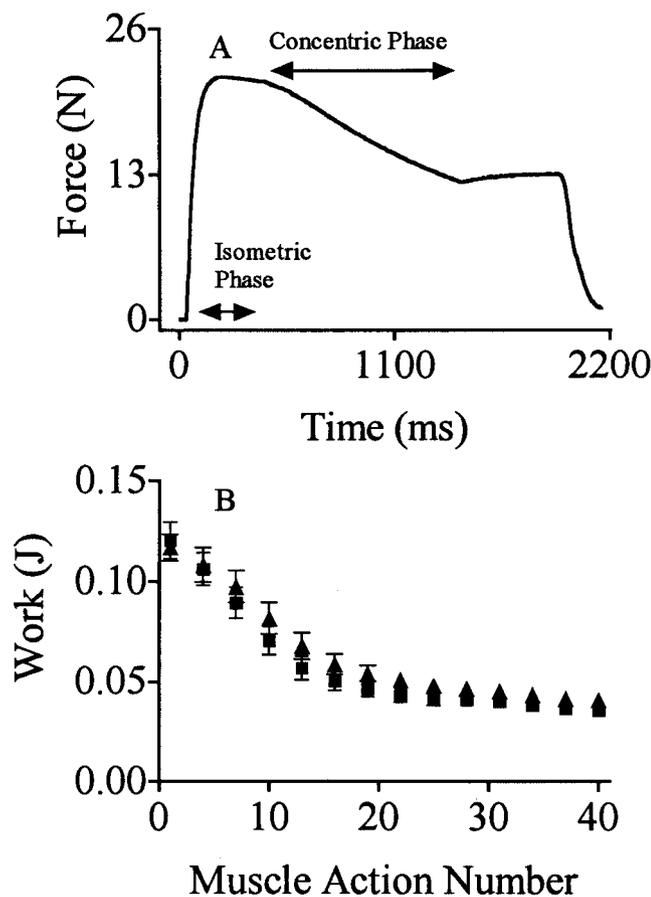


FIGURE 2—(A) Example of the force-time trace for the first muscle action during fatigue testing with the isometric and concentric phases indicated. (B) Concentric work as a function of muscle action number for control and eccentric-trained muscles tested at long muscle lengths. ■, control muscles; ▲, eccentric-trained muscles.

3. With a stimulation frequency of 100 Hz, isometric forces of over 95% of the maximal isometric force (at 120 Hz) are produced (unpublished observations).

Data collection and analysis. Isometric forces during fatigue and recovery testing were calculated by subtracting the average force (100 ms) before stimulation from the average total force (between 500 and 600 ms) during stimulation (i.e., on the tetanic plateau during the isometric phase) for each muscle action. The relative decline in isometric force during fatigue and recovery testing was calculated as the isometric force decline index (IFDI) by $(F_1 - F_x)/F_1 \times 100$, where F_1 is the isometric force of the first muscle action during fatigue testing and F_x the isometric force for each muscle action.

Isometric forces at stimulation frequencies of 20 Hz and 100 Hz were calculated by subtracting the average force (100 ms) before stimulation from the highest total force during stimulation. Before and 35 min after fatigue testing, the ratio of force at 20 Hz to the force at 100 Hz (F_{20}/F_{100}) was calculated. Low-frequency fatigue was quantified by the change in the ratio F_{20}/F_{100} .

Plantar flexor muscles (i.e., soleus, plantaris and gastrocnemius muscles) of right and left hindlimb were dissected, trimmed of external fat, and wet weights were measured. In

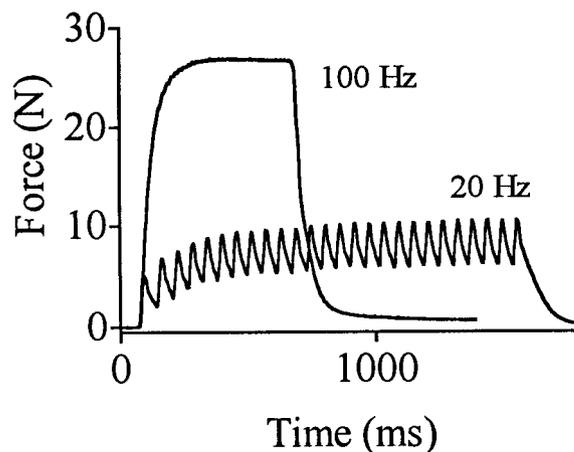


FIGURE 3—Examples of force recordings for rat plantar flexor muscles activated with a stimulation frequency of 20 Hz and 100 Hz. Forces were measured with the knee at 90°.

each group, total wet weights of left and right adrenal glands were taken.

Statistics. Student *t*-tests were used to test for differences between eccentric-trained and control rats for 1) body weight, 2) weights of the plantar flexor muscles of the right and left hindlimbs, 3) weight of the adrenal glands, 4) isometric force with a stimulation frequency of 120 Hz, 5) changes in isometric forces (IFDI) at the end of fatigue and recovery testing, and 6) change in the ratio F_{20}/F_{100} . Two-way analysis of variance (ANOVA) with Bonferroni *post hoc* testing (GraphPad Prism v3.0 for Windows, GraphPad Software, San Diego, CA) was used to test for differences between eccentric-trained rats and control rats for the decline in IFDI throughout fatigue (8.9 min) and recovery (30 min) testing. Significance was accepted at $P < 0.05$.

RESULTS

During high-speed eccentric training for 6 wk, body weights increased similarly for eccentric-trained and control rats (data not shown). Adrenal glands of eccentric-trained rats were 14% larger than that of control rats (Table 1). In eccentric-trained rats, weights of the plantar flexor muscles in the left (i.e., eccentric-trained muscles) and right hindlimb were similar to each other and to the respective muscles from control rats (Table 1). The maximal isometric force of eccentric-trained muscles was 22% larger than that of control muscles (Table 1).

Decline in isometric force during fatigue and recovery at different muscle lengths. Changes in isometric force (IFDI) at short muscle lengths (Fig. 4A) and long muscle lengths (Fig. 4B) were used as indexes of isometric fatigue and recovery for control and eccentric-trained muscles. The isometric force decreased exponentially during repeated muscle actions (i.e., 40 in 8.9 min) and increased exponentially during recovery testing (i.e., 6 muscle actions in 30 min) for all rats and conditions (Fig. 4, A and B). At the end of 40 muscle actions in control rats, the IFDI was less at short muscle lengths ($67.5 \pm 2.7\%$) than at

TABLE 1. Measured variables in control and high-speed eccentric-trained rats.

Group	Control		Training	
Body weight (g)	265 ± 3		269 ± 5	
Adrenal weight (mg)	63.8 ± 2.1		72.6 ± 3.4 (9)*	
Plantar-flexors weight (mg)	Right hindlimb	Left hindlimb	Right hindlimb	Left hindlimb
Isometric force (120 Hz) (N·g ⁻¹)	2174 ± 37	2187 ± 55	2186 ± 72 (9)	2041 ± 72 (8)
	ND	10.9 ± 0.6	ND	13.3 ± 0.9 (8)*

Values are presented as mean ± SE; N = 10 if otherwise indicated between brackets.

* Significant difference between control and eccentric-trained rats (Student's t-test, $P < 0.05$). ND, not determined.

long muscle lengths (78.4 ± 3.6), indicating that more fatigue occurred at the long muscle lengths. For rats tested at short muscles lengths, the IFDI of eccentric-trained and control muscles was not different during fatigue and were smaller for eccentric-trained muscles for the first 10 min only during recovery testing ($F[1,48] = 54.8$, two-way ANOVA) (Fig. 4A). In contrast, for rats tested at long muscle lengths, the IFDI was significantly smaller for eccentric-trained muscles after 2.1 min (i.e., after 11 muscle actions) during the fatigue test (i.e., reduced fatigability, Fig. 4B) ($F[1,320] = 453.4$, two-way ANOVA) and was smaller for eccentric-trained muscles throughout recovery testing for 30 min ($F[1,48] = 18.67$) (Fig. 4B). After 30 min of recovery, there were no differences for the IFDI among control muscles tested at either short ($19.7 \pm 1.9\%$) or long

lengths ($15.3 \pm 2.5\%$) and eccentric-trained muscles at short lengths ($20.5 \pm 2.8\%$), but in eccentric-trained muscles the IFDI was smaller only at the long lengths ($4.6 \pm 2.8\%$).

Low-frequency fatigue. In each group (i.e., control and eccentric-trained muscles) tested at short and long lengths, the decrease in the ratio F20/F100 was not different, and, therefore, data were averaged for each group. Control and eccentric-trained muscles had decreased ratios of F20/F100 (Fig. 5), indicating the presence of low-frequency fatigue for both groups. However, eccentric-trained muscles had smaller changes in the ratio F20/F100 ($22.0 \pm 1.4\%$) than control muscles ($35.4 \pm 2.0\%$) ($P < 0.0001$), indicating that high-speed eccentric training reduced low-frequency fatigue of skeletal muscles.

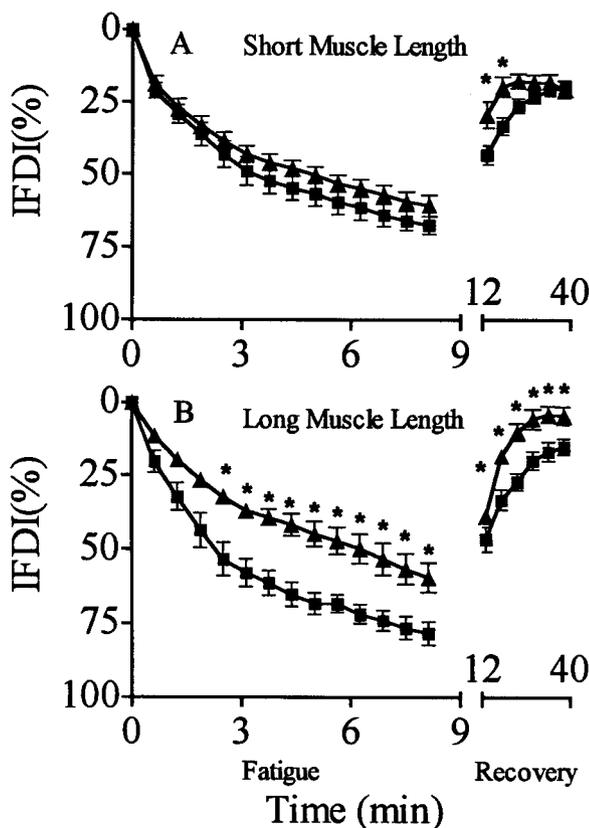


FIGURE 4—The isometric force decrement index (IFDI) of the rat plantar flexor muscles as a function of time during fatigue testing and subsequent recovery for control (■) and eccentric-trained muscles (▲) at short (A) and long lengths (B). Data are presented as mean ± SE for five animals. For illustrative purposes, only force data of every third muscle action during fatigue testing are plotted. * Significant difference between control and eccentric-trained muscles, $P < 0.05$.

DISCUSSION

After a vigorous 6-wk high-speed eccentric training program of rat plantar flexor muscles, adaptations in muscle fatigue were present at long muscle lengths and not at short muscle lengths. Eccentric-trained muscles had improved recovery at long muscle lengths throughout the recovery period of 30 min but, at short muscle lengths, only for the first 10 min. Plantar flexor muscles were more fatigable at long muscle lengths in comparison with short muscle length in untrained, control rats.

Fatigue has been shown to be greater at long muscle lengths than at short muscle lengths during repetitive maximal voluntary muscle actions of plantar flexor muscles (15)

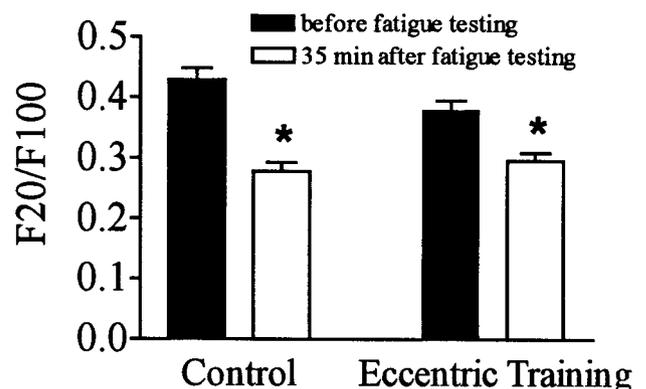


FIGURE 5—Ratio of force at 20 Hz to force at 100 Hz (F20/F100) before and 35 min after a fatigue test with high-intensity muscle actions. * Significant difference between the ratio F20/F100 before and 35 min after a fatigue test in either control and eccentric-trained muscles, $P < 0.05$.

and elbow flexor muscles (20) in humans. For voluntary muscle actions at specific joint positions (e.g., knee fully extended or flexed at 90°), the length-specificity of fatigue could be explained by differential changes in activation between muscles that are predominantly composed of either fast-twitch (i.e., m. gastrocnemius) or slow-twitch fibers (i.e., m. soleus) as well as the contribution of each of the muscles to the joint torque (15,16). Activation in our study was not a limiting factor because of the use of electrical nerve stimulation, which results in activation of all muscle fibers. Our use of electrical stimulation guaranteed full activation of all muscle fibers at all joint positions and over-rides any neural influences on fatigue and recovery during voluntary activation.

Comparison with other studies that reported more fatigue at short muscle lengths (1,8,13,25) is complicated because of substantial differences in experimental approach [e.g., the intensity, type, and duration of the exercise (for a review of muscle fatigue, see (9))]. For example, Sacco et al. (25) fatigued ischemic tibialis anterior muscles with electrical stimulation (at 30 Hz) using six 15-s tetani with a 5-s rest interval between isometric muscle actions at joint positions with substantial differences in muscle length. In that study, ischemia, associated with a modest decline in muscle oxygenation could have caused part of the fatigue (21). These differences in length-dependent fatigue remained poorly defined.

In untrained, control rat plantar flexor muscles, length-dependent fatigue could result from differences in the amount of active cross-bridges (8). The 6-wk eccentric training reduced fatigability only at long muscle lengths. Such specific-length adaptation in fatigue would not be expected if muscle length changes occurred due to the training protocol. However, muscle length changes due to the eccentric training program would seem unlikely because 12 wk of only eccentric muscle actions (50 repetitions, 2 d·wk⁻¹) did not lead to increases in sarcomere number (17). Any long-term training or treatment of skeletal muscle that did result in anatomical length changes of the muscle could influence the outcome of muscle fatigue testing if examined at constant joint positions.

Throughout the 30-min recovery period, eccentric-trained skeletal muscles improved force production at long length:

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at short length, however, improved force production was present only for the first 10 min of recovery (Fig. 4). Because training adaptations at the end of the 30-min recovery period were not equal at long and short muscle lengths, force losses during recovery were not expected to have a common metabolic or ionic basis (2). At the long muscle length, eccentric training could have resulted in an improved force transmission. An improved force transmission might be due to an adaptation of the muscle's connective tissue. Connective tissue has been shown to adapt to high loading conditions. Adaptations of the connective tissue could influence force production at particular muscle lengths because its configuration changes with muscle length (23).

Low-frequency fatigue (LFF) of skeletal muscles is a loss of force at low stimulation frequencies (e.g., 20 Hz), which exceeds the loss of force at high stimulation frequencies (e.g., 100 Hz) (11). The LFF reported in single muscle fibers of mouse provides support for some intracellular mechanism for LFF (3,26), such as a failure of excitation-contraction coupling, probably resulting from reduced calcium release from the sarcoplasmic reticulum (SR) (26). Reduced LFF after eccentric training could result from an adaptation of excitation-contraction coupling leading to an increased calcium release by the SR. The SR has been reported to respond to exercise training. In elderly women, resistance training increased calcium uptake by the SR, which was depressed with aging (12), and high-intensity sprint training for 5 wk increased the volume of the SR in healthy men (22).

In summary, high-speed eccentric training of rat plantar flexor muscles (5 d·wk⁻¹ for 6 wk) reduced fatigue by high-intensity muscle actions and improved recovery mainly at long muscle lengths. High-speed eccentric training reduced low-frequency fatigue, suggesting an adaptation of intracellular calcium handling.

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