Eccentric exercise increases EMG amplitude and force fluctuations during submaximal contractions of elbow flexor muscles

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Semmler JG, Tucker KJ, Allen TJ, Proske U. Eccentric exercise increases EMG amplitude and force fluctuations during submaximal contractions of elbow flexor muscles. J Appl Physiol 103: 979-989, 2007. First published June 28, 2007; doi:10.1152/japplphysiol.01310.2006.—The purpose of this study was to determine the effect of eccentric exercise on the ability to exert steady submaximal forces with muscles that cross the elbow joint. Eight subjects performed two tasks requiring isometric contraction of the right elbow flexors: a maximum voluntary contraction (MVC) and a constant-force task at four submaximal target forces (5, 20, 35, 50% MVC) while electromyography (EMG) was recorded from elbow flexor and extensor muscles. These tasks were performed before, after, and 24 h after a period of eccentric (fatigue and muscle damage) or concentric exercise (fatigue only). MVC force declined after eccentric exercise (45% decline) and remained depressed 24 h later (24%), whereas the reduced force after concentric exercise (22%) fully recovered the following day. EMG amplitude during the submaximal contractions increased in all elbow flexor muscles after eccentric exercise, with the greatest change in the biceps brachii at low forces (3–4 times larger at 5 and 20% MVC) and in the brachialis muscle at moderate forces (2 times larger at 35 and 50% MVC). Eccentric exercise resulted in a twofold increase in coactivation of the triceps brachii muscle during all submaximal contractions. Force fluctuations were larger after eccentric exercise, particularly at low forces (3–4 times larger at 5% MVC, 2 times larger at 50% MVC), with a twofold increase in physiological tremor at 8–12 Hz. These data indicate that eccentric exercise results in impaired motor control and altered neural drive to elbow flexor muscles, particularly at low forces, suggesting altered motor unit activation after eccentric exercise.

electromyography; motor control; muscle damage

IT IS WELL ESTABLISHED THAT unaccustomed eccentric exercise, which involves the active lengthening of muscle, produces muscle fiber damage that results in muscle soreness that occurs a day or so after the exercise (18). Although the exact mechanisms responsible for the muscle damage have not been clearly elucidated, the initial event is attributed to the mechanical disruption at the level of sarcomeres, leading to membrane damage that results in uncontrolled release of Ca2+ into the sarcoplasm (31) and an impairment in excitation-contraction coupling (41). These processes result in a number of changes in muscle properties, including a shift in optimum muscle length for force generation, a rise in passive muscle tension, and a decline in the maximal force generating capacity of the muscle (see Ref. 30 for a review). While these alterations in muscle properties undoubtedly influence muscle function, the consequences of eccentric exercise for the performance of low-force tasks remains unclear.

Using surface electromyogram (EMG) measurements, several studies have reported altered neural drive to muscles after eccentric exercise. For example, Weerakkody et al. (44) found that there was a more than proportional increase in biceps brachii EMG at low torque levels after eccentric but not concentric exercise. However, it is not known if all elbow flexor muscles respond in a similar manner after eccentric exercise. Using magnetic resonance imaging (MRI), Nosaka and Clarkson (25) revealed that some subjects showed increased transverse relaxation time (T2) signal intensity in the resting biceps brachii muscle after eccentric exercise, whereas others showed increased intensity in the brachialis muscle, suggesting differences between subjects in the extent of damage to different elbow flexor muscles. This differential damage to elbow flexor muscles may induce a change in the pattern of activity among the synergist muscles during task performance, depending on the location and extent of damage resulting from the eccentric exercise. A change in the pattern of activity among synergist muscles has been shown during maximal isometric contractions for the knee extensor muscles (16) but not for submaximal isometric contractions of the wrist extensor muscles (21).

Several studies have shown an impaired ability to control muscle force after eccentric exercise. For example, Saxton et al. (33) showed increased postural tremor of the forearm held horizontally against gravity when measured immediately after and 24 h after eccentric exercise of the elbow flexor muscles. Similarly, Lavender and Nosaka (20) found an increase in force fluctuations when performing constant-force contractions at moderate [30% and 50% of maximum voluntary contraction (MVC)] and high (80% MVC) forces that were performed immediately after and 1 h after eccentric exercise. Some features of motor output that could be responsible for these increased force fluctuations after eccentric exercise include changes in the extent of activation within and between muscles (12), and coactivation of agonist and antagonist muscles (2, 4), which will be examined in the present study. Furthermore, it is not known how eccentric exercise influences force fluctuations during low-force (<25% MVC) contractions, which are likely to be implicated in tremor.

The purpose of this study was to determine the effect of eccentric exercise on the ability to exert steady forces with the muscles that cross the elbow joint. Specifically, we wanted to quantify the change in EMG in all elbow flexor muscles and...
how this influenced submaximal force fluctuations, particularly at low contraction levels. We expected to find that eccentric exercise would result in altered EMG in all elbow flexor muscles (44) and increased coactivation of the antagonist muscle (21) that will result in increased force fluctuations (20) during submaximal contractions. It has been previously shown that the increase in biceps brachii EMG after eccentric exercise is greatest at low forces (44), which may reflect the recruitment of larger motor units, which would be expected to produce greater force fluctuations at low contractions levels (see Ref. 10). Because eccentric exercise is a part of everyday activities, it is important to understand the consequences of this type of exercise to neuromuscular performance, particularly in certain sports where the precision of motor control in the presence of significant fatigue is essential. Preliminary results from this study have been published in abstract form (36).

METHODS

Ten subjects were recruited for this study (7 men, 3 women; age 30.9 ± 2.6 yr). Eight subjects (6 men, age 31.2 ± 2.7 yr) performed concentric exercise, and 8 subjects (6 men, age 32.2 ± 2.7 yr) performed eccentric exercise. Six of these subjects (4 men, age 33.1 ± 2.8 yr) were common to both forms of exercise. All subjects reported no recent injury or musculoskeletal pain in their right arm or shoulder. Two subjects performed regular exercise (up to 3 times per week) not specific to the elbow flexor muscles, whereas all other subjects were not involved in any form of exercise regime. Written informed consent was obtained from all subjects before the beginning of the experiment. All experimental procedures were approved by the Human Research Ethics Committee at the University of Adelaide.

Subjects were seated comfortably in a modified chair with their right arm constrained in a device designed to measure isometric elbow flexion force. During all tasks, the forearm was positioned vertically, the elbow joint and shoulder were flexed at 90°, and flexion and extension forces were exerted in the sagittal plane. The forearm was secured in place by two wide nylon straps so that it remained in a supinated position throughout the experiment.

Surface EMG signals were recorded with bipolar electrodes (silver-silver chloride, 4-mm diameter) placed ~2 cm apart (center to center) over the belly of the biceps brachii, brachioradialis and lateral head of triceps brachii. Because of the depth of the muscle and to avoid EMG crosstalk, multiunit EMG activity of the brachialis muscle was measured with an intramuscular bipolar electrode, which was inserted ~2 cm into the muscle from the lateral aspect of the arm ~3 cm above the point of insertion of the brachialis muscle. The intramuscular electrode consisted of 2 × 100-μm stainless-steel wires insulated with Formvar (California Fine Wire, Grover Beach, CA) that were threaded through the lumen of a 25-gauge single-use hypodermic needle. A grounding strap located around the wrist served as a common reference for all EMG recordings. The EMG electrodes remained in place during the exercise (described below) and were used for all EMG measurements on the same day after exercise. At the end of the experiment, all electrodes were removed (including the intramuscular electrode) and the electrode positions were marked on the skin to ensure that the electrodes were placed in the same location for the EMG recordings obtained 24 h after exercise. The EMG signals were amplified (100–1,000×) band-pass filtered (high pass at 13 Hz, low pass at 1,000 Hz), displayed on an oscilloscope, and recorded on digital tape.

Experimental Procedures

Each subject was asked to perform two tasks requiring isometric contraction of the elbow flexor muscles: a MVC and a constant-force task while EMG was recorded from the elbow flexor and extensor muscles.

MVC force. The MVC task consisted of a ramp increase in flexion or extension force from zero to maximum over a 3-s period, and then the maximum force was sustained for a further 2–3 s. The experimenter provided the timing of the task verbally, and the subject monitored the force on an oscilloscope placed in front of them at eye level. Verbal encouragement was provided by the experimenter during the sustained MVC to facilitate maximum force production. The subject performed several MVCs in both flexion and extension directions, and the force was recorded on tape. Additional MVC trials were performed until two forces were within 5% of each other. The greater of these two forces was designated as the MVC force. Subjects were given at least 2 min of rest between contractions. To assess recovery from exercise, additional MVCs were performed at the end of the submaximal contractions after exercise performed on the first day, which was ~1 h after exercise.

Constant-force task. Subjects performed isometric contractions at target forces of 5, 20, 35, and 50% MVC that was expressed relative to the MVC obtained at each time point, either before, after, or 24 h after exercise. These target forces provided two tasks that were considered low forces (20% MVC) and two that were considered moderate forces (35, 50% MVC) for comparison with a previous study (20). The forces exerted during the tasks were detected by a force transducer (model MLP-150, Transducer Techniques, CA) that was located perpendicular to the forearm at the level of the wrist and mounted on a customized manipulandum. Output from the force transducer was recorded on a digital tape recorder and displayed on an oscilloscope. Subjects were required to exert a steady elbow flexion force for 15 s at the required target force represented by a horizontal line located on the oscilloscope screen. The horizontal target line on the oscilloscope remained in the same location for each target force by adjusting the gain on the vertical axis. Two trials were performed at each target force level with at least 1 min of rest between trials, and the four target forces were performed in random order.

All MVC tasks were performed before, immediately after, ~1 h after, and 24 h after both concentric and eccentric exercise. Because of the greater length of time required, the submaximal tasks were performed before, within 1 h after (herein referred to as after), and 24 h after exercise. The data obtained after eccentric exercise served to assess the influence of fatigue and muscle damage on EMG and force fluctuations (24, 31, 40), whereas the data obtained after concentric exercise assessed the effects of fatigue only, because there is not likely to be significant muscle damage (5, 37). The experiments were performed 24 h after eccentric exercise as an indicator of the effect of muscle damage without fatigue, because it is known that maximum force following a fatiguing task recovers within 2 h (40).

Exercise

Controlled eccentric exercise was performed in eight subjects with the elbow flexor muscles of the right arm and was used to reduce isometric MVC force by 40%. This protocol has been shown previously to produce consistent changes in relaxed elbow joint angle (increased passive tension), a shift in the optimal muscle length, and muscle soreness for several days following the exercise (28, 29). Furthermore, it offered the advantage of producing a similar force decline in all subjects, which facilitated the use of both sexes in this study. Subjects were seated at a standard preacher curl bench that consisted of an adjustable height seat and a padded support for the upper arm that was positioned 45° from the torso. The subject rested their upper arm on the support with the forearm held vertically. A load was placed in the hand by the experimenter, and subjects lowered the weight from an elbow joint angle of 45° to full extension (135° range of motion) by eccentrically contracting the elbow flexor muscles. The load was set to ~40% of the isometric MVC obtained at 90°, as performed in previous studies (28, 29). Each eccentric contraction lasted ~2 s followed by a 4-s rest, and contractions were performed in time with a metronome. During the rest period, the load was...
removed by the experimenter and the subject returned their arm to the starting position. The exercise set consisted of a series of 10 eccentric contractions followed by a 20-s rest period. This procedure continued until there were visible signs of tremor and verbal confirmation from the subject that they were having difficulty controlling the load during the eccentric contraction. At this point the subjects moved to the testing apparatus and performed brief isometric MVCs with the elbow joint at 90° to monitor the reduction in force. The contractions continued until the MVC force fell by >40%, which required from 50 to 200 contractions in all subjects. To monitor recovery from the exercise, the subjects performed an additional series of MVCs after the constant force tasks were completed on the first experimental day, which were obtained ~1 h after exercise.

Eight subjects underwent an exercise protocol that involved concentric contractions of the right arm to induce neuromuscular fatigue. Each subject performed eccentric exercise and concentric exercise for 10 contractions. This was achieved with a mean exercise load of 7.8 ± 20 N, but it was still significantly less than the MVC force by 40% with repeated eccentric contractions. The main goal of eccentric exercise was to reduce the isometric MVC force by 40% with repeated eccentric contractions. This was achieved with a mean exercise load of 7.8 ± 0.8 kg and required an average of 146 ± 17 contractions. These contractions resulted in a significant (45%) decline in MVC force from 244 ± 16 N before to 133 ± 7 N immediately after eccentric exercise (P < 0.001), and there was no recovery of force ~1 h after the exercise (48% lower compared with before exercise; Fig. 1A). MVC force partially recovered 24 h after exercise (184 ± 15 N), but it was still significantly less than the MVC before exercise (24% lower; P < 0.001). In contrast, exercise with concentric contractions was performed with a mean exercise load of 7.8 ± 0.6 kg and required an average of 170 ± 37 contractions before the load could no longer be lifted. This resulted in a significant (22%) decline in MVC force from 237 ± 27 to 184 ± 22 N after concentric exercise (P = 0.001). MVC force was still significantly reduced ~1 h after the exercise (202 ± 27 N; P < 0.01), but it had completely recovered 24 h later (238 ± 27 N).

EMG was measured in the elbow flexor muscles (biceps brachii, brachialis, and brachioradialis) during maximal isometric elbow flexion before, immediately after, ~1 h after, and 24 h after exercise (Fig. 1, B and C). There was no significant main effect in the ANOVA for exercise, indicating that the

RESULTS

For maximum contractions, maximum elbow flexor force was analyzed with a two-way ANOVA with a repeated-measures design, with one between-subject factor of exercise (concentric, eccentric) and one within-subject factor of time (before, after, 1 h after, 24 h after). Maximum EMG during the MVC tasks was analyzed with a three-way repeated-measures ANOVA with one between-subject factor (exercise), and two within-subjects factors of muscle (biceps brachii, brachialis, brachioradialis) and time (before, after, 1 h after, 24 h after). For the constant-force tasks, a three-way repeated-measures ANOVA for exercise, time (before, after, 24 h after), and force (5, 20, 35, 50% MVC) was used to compare the CV of force, whereas a four-way repeated-measures ANOVA (exercise, time, force, muscle) was used to compare average EMG. For the frequency-domain analysis of the force fluctuations, an additional frequency factor was included in the ANOVA for the relative power of the force fluctuations at 0–4, 4–8, 8–12 and 12–20 Hz. Because of their opposing functional actions, EMG data were analyzed separately for the elbow flexor (biceps brachii, brachialis, brachioradialis) and extensor (triceps brachii) muscles. Because there was no muscle factor for the triceps brachii analysis, triceps brachii EMG was analyzed with a two-way ANOVA (exercise, time) for MVCs and a three-way ANOVA (exercise, time, force) for the constant-force contractions. Significant main effects in the ANOVA were analyzed with a Scheffé’s post hoc test that performed all possible comparisons. For significant interactions, a Scheffé’s post hoc test was used to compare all possible combinations of dependent variables based on the interaction examined. To examine whether an increase in EMG in one elbow flexor muscle was associated with a similar increase in the other elbow flexor muscles within each subject, a simple linear regression analysis was performed on the change in EMG obtained for each of the elbow flexor muscles after eccentric exercise. Statistical significance was designated at P < 0.05 for all comparisons, and all values are reported as means ± SE.

Data Analysis

All recorded signals were downloaded onto a computer hard drive using a 16-bit analog-to-digital converter (model 1401, CED, Cambridge, UK) and sampled at either 200 Hz (force) or 2,000 Hz (EMG). All data were analyzed offline using customized scripts within the Spike 2 data analysis software (Cambridge, UK). The EMG from the MVC was full-wave rectified and the average EMG was obtained for 1 s at the point where maximum force was achieved. For the constant-force task, a 10-s sample of force from the middle of each trial was obtained to calculate the mean and coefficient of variation (CV) of force (SD/mean force × 100). EMG from all muscles was rectified and averaged over a user selectable window of 1 s corresponding to a stable portion of the EMG and force record, and it was normalized to the maximum EMG during MVC to facilitate comparisons between subjects and across days. The average normalized EMG and CV of force for the two trials at each target force level was used for subsequent statistical analysis.

The force signals were also analyzed in the frequency domain using power spectral analysis with a fast Fourier transform (FFT) implemented in Spike 2. Data from the same epochs used for time-domain analysis were analyzed in the frequency domain. The 10 s of force data (200-Hz sampling rate) were divided into blocks of 512 samples (block duration ~2.5 s) before processing by the FFT, yielding a frequency resolution in the force power spectrum of 0.4 Hz. Spectra from the four different blocks were averaged in the frequency domain, and the power spectrum of force for each task was divided into frequency bins of 0–4 Hz, 4–8 Hz, 8–12 Hz, and 12–20 Hz. To assess gradual shifts in power within these frequency bins, the power in each bin was expressed relative to the total power from 0 to 20 Hz.
EMG AND FORCE FLUCTUATIONS AFTER ECCENTRIC EXERCISE

maximum EMG was not different between concentric and eccentric exercise. For both exercise conditions combined, no significant difference was observed in maximum elbow flexor EMG before exercise (0.66 ± 0.07 mV) compared with immediately after (0.55 ± 0.06 mV), 1 h after (0.56 ± 0.07 mV) and 24 h after exercise (0.71 ± 0.08 mV). Furthermore, no significant exercise × time interaction was obtained in the ANOVA, indicating that the change in maximum elbow flexor EMG at the different recording times was consistent between the two exercise conditions. Following a significant muscle effect in the ANOVA (P < 0.001), post hoc analysis indicated that the maximum EMG was largest in the biceps brachii (0.92 ± 0.06 mV) and brachioradialis (0.75 ± 0.05 mV) muscles, and least for the brachialis (0.18 ± 0.02 mV) muscle, with all muscles displaying a significantly different maximum EMG from each other. No significant muscle × exercise or muscle × time interaction was observed in the ANOVA, suggesting that these EMG responses were consistent for different exercise and recording sessions. The maximum triceps brachii EMG during elbow flexion was not different between exercise conditions or at the different time points, where the triceps EMG was 0.12 ± 0.02 mV before, 0.13 ± 0.02 mV immediately after, 0.13 ± 0.02 mV 1 h after, and 0.10 ± 0.01 mV 24 h after exercise for both exercise conditions. In addition, maximum triceps brachii EMG was recorded during maximum elbow extension performed before, immediately after, and 24 h after exercise. No significant effect was observed for exercise (P = 0.9), time (P = 0.6), or the exercise × time interaction (P = 0.2) for the triceps brachii muscle.

Constant-Force Task

Figure 2 shows original data for a constant force trial at a target force of 20% MVC along with the EMG from the elbow flexor and extensor muscles performed before and after eccentric exercise in one subject. The MVC for this subject was 274 N before and 154 N after exercise, representing a remaining force of 56% of the control value. This recovered to 216 N (~80% MVC before) 24 h after the exercise. At each time point the 20% target force was normalized to the new maximum force. The standard deviation of force was measured from a 1-s epoch obtained from the middle section of each force record (bottom trace in Fig. 2). The standard deviation of force during this trial was 190 mN before exercise and 726 mN (~4 times larger) after exercise, corresponding to a CV of force of 0.4% before and 2.6% (~7 times larger) after exercise. Furthermore, despite contracting at the same force relative to the new maximum capacity of the muscle, the EMG in all elbow flexor muscles was larger after eccentric exercise. Based on a 1-s epoch in the middle of the contraction before and after exercise, the EMG was 7.1 times (7 vs. 47% of maximum EMG) larger in the biceps brachii, 2.3 times (34 vs. 78%) larger in the brachialis, 1.3 times (16 vs. 21%) larger in the brachioradialis, and 3.3 times (8 vs. 26%) larger in the triceps brachii muscle. In contrast, there were no changes in the EMG activity in this subject after concentric exercise that reduced the MVC by 22% (282 N before, 219 N after). For example, at a target force of 20% MVC, the CV of force was 0.6% before and 0.6% after concentric exercise. In addition, no change in EMG amplitude at 20% MVC was observed in any of the test muscles after concentric exercise (range of 1–1.2 times greater for all muscles).

The CV of force across a range of submaximal target forces was measured before, after, and 24 h after concentric and eccentric exercise. There was a significant main effect in the ANOVA for exercise, force, and time (all P values <0.001). The average CV of force for all subjects ranged from 1.92 ± 0.17% at the 5% force to 1.22 ± 0.13% at the 20% force (P < 0.001), with intermediate values for the 35% (1.38 ± 0.10%) and 50% (1.67 ± 0.11%) target force. Furthermore, the CV of force was significantly greater after exercise (2.14 ± 0.16%) compared with before (1.19 ± 0.06%; P < 0.001) and 24 h after (1.30 ± 0.06%; P < 0.001) exercise. A significant exercise × time interaction and subsequent post hoc analysis revealed that the CV of force was larger after eccentric exercise (3.02 ± 0.20%) compared with concentric exercise (1.25 ± 0.10%), whereas no difference was observed between the two
exercise conditions when measured before or 24 h after the exercise.

Figure 3 shows the CV of force at each target force level expressed relative to the new MVC when measured before, after, and 24 h after either concentric (A) or eccentric (B) exercise. A three-way ANOVA revealed significant main effects for exercise, force, and time (all \( P \) values <0.001) when both exercise conditions were combined. Following a significant exercise \( \times \) time interaction in the ANOVA (\( P < 0.001 \)), post hoc analysis indicated that the CV of force was significantly larger after eccentric exercise (3.02 ± 0.20%) compared with before (1.23 ± 0.09%; \( P < 0.001 \)) and 24 h after exercise (1.53 ± 0.09%; \( P < 0.001 \)). No significant difference in force fluctuations was observed 24 h after exercise compared with before exercise. Furthermore, no significant difference in the CV of force was observed at any time point after concentric exercise.

For eccentric exercise, the largest difference occurred at the 5% (3.2 times greater; \( P < 0.001 \)) and 20% (3.3 times greater; \( P < 0.001 \)) target force compared with the 35% (1.9 times greater; \( P = 0.006 \)) and 50% (1.9 times greater; \( P < 0.001 \)) target force. These data indicate that force fluctuations were larger after eccentric exercise and this effect was most pronounced at low forces, although the force fluctuations returned to baseline levels 24 h later.

EMG activity from three elbow flexor muscles (biceps brachii, brachialis, brachioradialis) and one elbow extensor muscle (triceps brachii) was quantified during the constant-force task and expressed relative to maximum EMG obtained during an elbow flexor and extensor MVC obtained at each time point. For all elbow flexor muscles combined, there was a significant main effect in the ANOVA for exercise, force, and time (all \( P \) values <0.001). Post hoc analysis revealed that the EMG was significantly greater for eccentric (31.2 ± 1.4%) compared with concentric (20.8 ± 1.0%) exercise. As expected, the average elbow flexor EMG for all subjects increased with increasing target force, ranging from 8.1 ± 0.7% at the 5% force to 47.8 ± 1.6% at the 50% target force (all force levels significantly different from each other at \( P < 0.001 \)). Furthermore, average elbow flexor EMG was greater after exercise (33.3 ± 1.7%) compared with before (21.6 ± 1.2%; \( P < 0.001 \)) and 24 h after exercise (23.2 ± 1.4%; \( P < 0.001 \)).

Figure 4 shows the elbow flexor EMG across target forces that were obtained before, after, and 24 h after concentric and
eccentric exercise. When averaged across all elbow flexor muscles, there was no difference in EMG after or 24 h after concentric exercise at any target force level (Fig. 4A). In contrast, there was enhanced EMG after eccentric exercise (Fig. 4B), where the average elbow flexor EMG was 2.4 times greater ($P < 0.001$) at the 5 and 20% target forces, 1.9 times greater at the 35% target force, and 1.6 times greater at the 50% target force compared with the same target forces before exercise (all $P$ values $< 0.001$). Elbow flexor EMG was also significantly larger after eccentric exercise compared with 24 h later at all force levels (all $P$ values $< 0.001$). No significant difference was observed in elbow flexor EMG when compared before and 24 h after eccentric exercise at any force level, indicating that the EMG had returned to baseline levels the day after eccentric exercise.

When the EMG data were expressed relative to the average EMG obtained before exercise in each subject, the increase in elbow flexor EMG obtained after eccentric exercise was largest at the 5% target force (347 ± 44%) and least for the 35% (209 ± 15%; $P = 0.01$) and 50% target force (181 ± 16%; $P = 0.001$). In contrast, the change in elbow flexor EMG after concentric exercise was less pronounced and ranged from 142 ± 16% at the 5% target force to 120 ± 9% at the 20% target force, and these values were not significantly different. When separated between each of the elbow flexor muscles (Fig. 5), the largest increase in EMG after eccentric exercise was observed in the biceps brachii muscle (279 ± 32%) with the smallest increase in the brachialis muscle (233 ± 26%; $P = 0.04$) for all contraction levels. After concentric exercise, the largest increase in EMG was observed in the biceps brachii muscle (168 ± 13%) compared with the biceps (113 ± 7%) and brachioradialis muscles (104 ± 7% increase) at all contraction levels, but these differences did not reach statistical significance. Furthermore, the largest increase in EMG after eccentric exercise was observed in the biceps muscle at the 5 and 20% target forces, whereas it occurred in the brachialis muscle at the 35% and 50% target forces. Despite these differences, no significant differences were observed between muscles at any force level. The change in EMG after concentric exercise was not influenced by target force, although a higher EMG was observed in the brachialis muscle at all contraction levels. Furthermore, when all target force levels were pooled, linear regression analysis showed a weak but significant positive correlation ($r^2 = 0.17$, $P = 0.02$) between the change in EMG in biceps brachii and brachioradialis muscles after eccentric exercise. No significant correlations were observed for the increase in EMG of the brachialis muscle compared with the other two elbow flexor muscles.

As an indicator of muscle coactivation, EMG was obtained from the triceps brachii muscle during the elbow flexion task and expressed relative to the triceps brachii EMG obtained during maximum elbow extension. Significant main effects in ANOVA were obtained for force ($P < 0.001$) and time ($P < 0.001$), indicating that the average triceps brachii EMG increased with increasing target force ($P < 0.001$), and ranged from 4.2 ± 0.6% at the 5% force to 18.7 ± 2.2% at the 50% target force (5 vs. 50%; $P < 0.001$). Furthermore, the average EMG was greater after exercise (13.4 ± 1.7%) compared with before (8.8 ± 1.8%; $P < 0.001$) and 24 h after (10.2 ± 1.4%; $P = 0.005$) exercise. More importantly, however, a significant
An exercise × time interaction (P < 0.001) was observed in the ANOVA, and this comparison is shown in Fig. 6. These data revealed that the triceps brachii EMG was significantly greater after eccentric exercise than before eccentric exercise (Fig. 6A; P = 0.003), and it was also greater than the EMG after concentric exercise (P < 0.05). The triceps brachii EMG returned to baseline levels 24 h after eccentric exercise. The increased triceps brachii EMG after eccentric exercise was consistently larger across all target force levels (Fig. 6C). When triceps brachii EMG was expressed relative to the average triceps EMG obtained before eccentric exercise, the increase in EMG ranged from 2.1 times greater at the 50% force to 2.6 times greater at the 20% target force. No change in triceps brachii EMG was observed at any force level after concentric exercise (Fig. 6B).

Along with the force fluctuations in the time domain, the force signals were also analyzed in the frequency domain using power spectral analysis. In this analysis, the frequency spectrum from 0 to 20 Hz was divided up into bins from 0 to 4 Hz, 4 to 8 Hz, 8 to 12 Hz, and 12 to 20 Hz, and the power in each of these frequency bins was expressed relative to the total power. This procedure was performed because, as expected, the increased force fluctuations after eccentric exercise resulted in increased power at all frequencies, and this analysis was more sensitive to relative shifts in power within the selected frequency bins. For all contractions, the power in the frequency spectrum of force was largely restricted to low frequencies, with 76% of the power at 0–4 Hz, 10% at 4–8 Hz, 7% at 8–12 Hz, and 7% at 12–20 Hz. The proportional power of force within each frequency bin was not influenced by exercise, force, or time. However, there was a significant exercise × frequency × time interaction (P < 0.001) in the ANOVA, and these data are shown in Fig. 7. Post hoc analysis revealed that the normalized power of force was significantly lower in the 0- to 4-Hz band after eccentric exercise compared with before exercise (Fig. 7A; P < 0.001). This effect was associated with an increase in normalized power of force in the 8- to 12-Hz frequency band after eccentric exercise compared with before exercise (Fig. 7B; P = 0.03), which equated to nearly a twofold increase in proportional power at 8–12 Hz after eccentric exercise. Furthermore, the proportional power at 8–12 Hz after eccentric exercise was significantly greater than 8–12 Hz after concentric exercise.
concentric exercise ($P = 0.006$). No significant differences were obtained at the 4- to 8-Hz or 12- to 20-Hz frequency bands after eccentric exercise. Furthermore, no significant differences in normalized power of force were observed within any of the frequency bins after concentric exercise.

**DISCUSSION**

It is well known that eccentric exercise results in damage to muscle fibers and a decline in maximal muscle force that can last for several days after the exercise. However, it is less clear whether this muscle damage alters the subsequent precision of force production during low-force contractions. We have confirmed previous reports indicating that eccentric exercise results in increased biceps brachii EMG (44) and elbow-flexor force fluctuations (20). We have extended these observations by examining the change in EMG from all the major elbow flexor muscles and force fluctuations during submaximal contractions at light to moderate contraction levels, where the precision of force production is likely to be most functionally relevant. The new findings for low-force contractions of the elbow flexor muscles after eccentric exercise include 1) increased EMG in all elbow flexor muscles, with the largest effect in the biceps brachii muscle at low forces; 2) increased coactivation of the antagonist (triceps brachii) muscle; and 3) increased force fluctuations at low contraction levels, particularly in the 8- to 12-Hz frequency range. These changes were observed after eccentric but not concentric exercise, suggesting that these effects are associated with neuromuscular adjustments as a result of muscle damage and fatigue induced by eccentric exercise.

**EMG and Force During Maximal Contractions**

The performance of concentric and eccentric exercise resulted in a significant decline in maximal force when measured after the exercise (Fig. 1). For the eccentric exercise, we used a procedure that has been shown previously to reveal substantial changes in relaxed elbow joint angle and muscle soreness (18, 24, 28, 33), along with a shift in optimal elbow joint angle for torque development to longer muscle lengths (19, 27, 29, 34). Recent evidence suggests that the shift in optimum length results from an increase in the series compliance of the muscle, which is likely to contribute to the decline in maximum force after eccentric exercise (14). Furthermore, the eccentric exercise resulted in significant declines in strength with subjective reports of muscle soreness from all participants 24 h after the exercise, which is indicative of muscle damage (24, 31, 40). In contrast, concentric exercise, which results in minimal indicators of muscle damage (5, 37), was followed by some recovery 1 h after the exercise and by complete recovery 24 h later with no reports of muscle soreness. Based on this information, we suggest that the decline in force after eccentric exercise is caused by a combination of muscle fatigue and damage (including an increase in series compliance) induced by the exercise, whereas the decline in force from concentric exercise is due largely to muscle fatigue.

Because recovery of maximal force resulting from fatigue is complete 2 h after exercise (40), and maximal voluntary activation has largely recovered 24 h after eccentric exercise (28), the deficits in force measured 24 h after eccentric exercise are likely to be caused largely by muscle damage. Although recent findings indicate that the extent of maximal voluntary activation is not related to muscle soreness (28), an effect of pain on maximal force 24 h after eccentric exercise cannot be completely excluded (43). Furthermore, these experiments involved a force loss after concentric exercise that recovered throughout the experimental session, something that did not occur after eccentric exercise, suggesting that at least some of the mechanisms that produce the force loss with both forms of exercise are not the same. In contrast, both forms of exercise resulted in declines in maximal EMG (19% for concentric, 13% for eccentric) that returned to normal after 24 h, indicating that this effect was caused by fatigue that was consistent for the two types of exercise, and was unlikely to be associated with muscle damage.

**Increased EMG After Eccentric Exercise for Submaximal Contractions**

Previous reports have indicated that damage to elbow flexor muscles with eccentric exercise results in increased biceps brachii EMG during submaximal isometric contractions (28, 44). We have obtained the first EMG recordings of the brachialis muscle after eccentric exercise using multunit recordings with intramuscular electrodes: a procedure that is necessary to access this deep muscle without interference from other adjacent synergistic muscles. With the forearm in a vertical position, we found that the increased elbow flexor EMG was primarily due to changes in the biceps brachii and brachialis muscles, with a lesser contribution from the brachioradialis muscle. In this arm position, the largest increase in EMG after eccentric exercise was observed in the biceps brachii muscle at low contraction levels (5–20% MVC), whereas in the brachialis muscle the largest increase in EMG was observed at moderate forces (35–50% MVC, Fig. 5). Similar to the wrist extensor muscles (21), these results indicate that during submaximal isometric contractions the decline in MVC force following eccentric exercise results in altered EMG activity in all major elbow flexor muscles, which includes the brachialis muscle. A recent report has indicated that the relative involvement of the various elbow flexor muscles during submaximal fatiguing contractions depends on arm posture (32), and it is possible that the extent of the change in EMG after eccentric exercise may vary depending on the position of the arm. Furthermore, we found that the extent of the exercise-induced increase in elbow flexor EMG was not consistent among the elbow flexor muscles in individual subjects, suggesting that the differences in T2-weighted MRI between biceps brachii and brachialis muscles that is indicative of muscle damage (25) may be reflected in an altered muscle activation strategy between these muscles during submaximal contractions.

Eccentric exercise resulted in a larger than proportional increase in elbow flexor EMG for a given level of force at low activation levels. Before exercise, the first 50% of maximum force was achieved with 44% of maximum EMG, whereas it increased to 70% of maximum EMG after eccentric exercise. These responses were specific to eccentric exercise, because there was no change in the EMG-force relation after concentric exercise, where 50% of maximum force was achieved with ~40% of elbow flexor EMG. Under these circumstances, variations in the EMG-force relation are likely to occur due to changes in the timing of motor unit action...
potentials that are not consistent throughout the full force range of the muscle (see Ref. 11) or to changes in the activity from other accessory muscles that contribute to the force but were not measured in the present study (32). Furthermore, the increase in EMG was observed even though the target force was expressed relative to the new (lower) maximum force after eccentric exercise. One possible confounding factor that could contribute to the reduced force after eccentric exercise is a reduction in maximum voluntary activation when measured by twitch interpolation (28). However, this would mean that the actual submaximal target force used after eccentric exercise in the present study would have been underestimated relative to the real (voluntary activation adjusted) maximum. Despite this, the EMG amplitude remained elevated at all submaximal target forces, and correcting for a decrease in voluntary activation would only accentuate the currently observed increases in EMG after eccentric exercise.

There are several possible explanations for a larger EMG obtained at low levels of activation after eccentric exercise. The most obvious explanation is that some muscle fibers belonging to a single motor unit that have been damaged by eccentric exercise are contributing little to the force but are still producing a sarcolemmal action potential that is contributing to the EMG. Under this scheme, increased motor unit recruitment and rate coding would be necessary to achieve the required target force to compensate for losses from the damaged motor units. However, two lines of evidence suggest that this rationale is unlikely. First, no change in the EMG-force relation was observed after concentric exercise that was sufficient to induce significant declines in muscle strength. The reduction in force with fatigue after concentric exercise would also be expected to involve motor units that are contributing a smaller amount to the overall force but still contributing equally to the EMG, although this effect would be less after fatigue from concentric exercise compared with fatigue and muscle damage from eccentric exercise. Second, the increased elbow flexor EMG is largest at low forces and is not proportional throughout the full force range of the muscle, suggesting that there needs to be selective damage to low-threshold motor units or a greater impairment of force at low firing frequencies in the damaged motor units to generate this effect. The increased EMG obtained at low forces does suggest damage to low-threshold motor units, which supports a previous finding in intact muscles of exercising animals (1). However, the available evidence obtained in calf muscles following eccentric exercise in humans indicates that fast-twitch motor units are more susceptible to damage from active lengthening of muscle (18). Therefore, although the present results do suggest damage to low-threshold motor units, we have no evidence to suggest that selective damage has occurred to this population of motor units without concomitant damage to high-threshold motor units.

There remain at least three plausible explanations for an increase in elbow flexor EMG at low activation levels after eccentric exercise. First, an increase in antagonist muscle coactivation, as has been observed during wrist extension (21), would result in additional elbow flexor EMG to achieve the required elbow flexion force. We have recorded from the triceps brachii muscle during submaximal isometric contractions of the elbow flexor muscles and found a twofold increase in coactivation after eccentric exercise (Fig. 6). This finding suggests that an increase in coactivation of triceps brachii muscle, which may represent an attempt to increase joint stability to maintain movement precision in the face of a growing muscle weakness (2), contributes to enhanced elbow flexor EMG during submaximal contractions after eccentric exercise. Second, many different types of exercise result in an excessive loss of force generated at low frequencies (17), known as low-frequency fatigue (9). The presence of motor units experiencing low-frequency fatigue would require additional recruitment and increased discharge rate of the already active motor units to compensate for the loss of force, resulting in increased EMG. Several studies suggest that low-frequency fatigue is enhanced after eccentric exercise compared with isometric or concentric exercise (8, 19, 23), although this effect is partly due to a shift in the optimal muscle length for force generation that is often not accounted for (26). Finally, computer simulation data indicates that motor unit synchronization can have a marked effect on the amplitude of the EMG, even without altering the number of motor units recruited or their discharge rate (45). Although motor unit synchronization is enhanced during slow eccentric contractions of a hand muscle (35), it is not known whether synchronous motor unit activity is altered following a period of fatiguing eccentric exercise.

Increased Force Fluctuations After Eccentric Exercise

Matching a target force as closely as possible usually results in a force that is not constant but fluctuates about the mean target value. In healthy young adults, the amplitude of the force fluctuations are influenced by the muscle group performing the task, and the type and intensity of the muscle contraction (10). In contrast to other muscle groups, the normalized (CV) force fluctuations of the elbow flexors remain relatively constant with increasing contraction intensity (3, 12, 20). However, after a period of eccentric exercise, we found a striking increase in the amplitude of the elbow flexor force fluctuations, even though the target forces were expressed relative to the new maximum voluntary force capability of the muscle after exercise. The extent of the increase was greatest at low force levels, where the force fluctuations were three to four times larger at the 5 and 20% target forces but were only two times larger at the 35 and 50% target forces after eccentric exercise (Fig. 3). A consistent increase in force fluctuations after eccentric exercise has previously been shown during isometric elbow flexion at contraction levels of 30, 50, and 80% of maximum force (20). Here we provide new evidence that the greatest influence of eccentric exercise on force fluctuations occurs at low (<25% MVC) levels of voluntary activation.

When examining the force fluctuations in the frequency domain, in unexercised muscle the majority (70–80%) of the fluctuations occur at low (0–4 Hz) frequencies (7, 38, 39). However, a smaller involuntary oscillation also occurs at a higher frequency (~8–12 Hz), and it is often referred to as physiological tremor. Although there were increases in absolute power of the force fluctuations at all frequencies, we found that there was a twofold increase in the relative power of force fluctuations at 8–12 Hz after eccentric exercise (Fig. 7), which is indicative of enhanced physiological tremor. Using an accelerometer located at the wrist, Saxton et al. (33) reported increased postural tremor of the forearm after eccentric exercise of the elbow flexor muscles. Although significant tremor peaks were observed at 3–5 and 8–12 Hz in the previous...
investigation, no change in the tremor frequency was detected after exercise. Because the spectral profile of force is influenced by contraction intensity (38), it is possible that the increased oscillations in the physiological tremor range observed after eccentric exercise in the present study are only apparent during moderate levels of voluntary activation, as opposed to the low activation levels necessary to perform postural tasks. The frequency of the force fluctuations returned to normal 24 h after exercise, suggesting that any changes in muscle stiffness or swelling did not influence tremor.

The mechanisms that produce force fluctuations must ultimately include factors that influence motor neuron activation for the motor unit population (38). The most likely factors responsible for the increased force fluctuations after eccentric exercise include alterations in discharge rate variability and correlated motor unit activity. For example, motor unit discharge rate variability (22), motor unit synchronization (45), and motor unit coherence (15) have all been credited with a role in accentuating force fluctuations during simulated and voluntary contractions. Furthermore, the presence of low-frequency fatigue could force the muscle to rely more heavily on motor unit recruitment at lower forces to compensate for the force loss in motor units discharging at low (10–20 Hz) rates. The increased recruitment of larger motor units, according to the Size Principle, would result in increased force fluctuations, because the extent of force fluctuations within a muscle is largely dependent on the force contributed by the most recently recruited motor units (10). This effect would be most pronounced at low forces, because the relative contribution of each newly recruited motor unit to the net force is greatest at low forces because there are a smaller number of active motor units. Additionally, these are the forces where most motor units are likely to be discharging at low rates.

Interaction Between Fatigue and Muscle Damage

Eccentric exercise that induced muscle damage resulted in an increase in EMG amplitude and force fluctuations that was greatest at low forces. However, this effect was observed only in the presence of fatigue that occurred after eccentric exercise and not 24 h later (Figs. 3 and 4), when there was still considerable muscle damage (24, 40). This information suggests that muscle damage alone, shown by the data obtained 24 h after eccentric exercise, is not associated with appreciable changes in EMG and force fluctuations. Importantly, damage and subsequent recovery of intramuscular fibers of muscle spindles cannot explain this effect, as it has been shown previously in the anesthetized cat that there is no change in the spindle afferent response following a series of eccentric contractions that had led to a fall in peak force by 40% (13). Furthermore, under these experimental conditions, fatiguing exercise alone does not cause an increase in EMG and force fluctuations during subsequent submaximal contractions, because there was no change in these variables after concentric exercise. One possible explanation for this phenomenon is that an interaction exists between the factors involved in muscle damage and fatigue that act together to increase EMG amplitude and force fluctuations after eccentric exercise, and these effects are not seen when fatigue has subsided. For example, we would expect that fatigue and muscle damage together would result in greater low-frequency fatigue and changes in motor unit activity (recruitment and rate coding, synchronization) compared with muscle damage alone, which would promote larger increases in EMG and force fluctuations after eccentric exercise. This possibility could be confirmed by examining EMG and force fluctuations at the time of maximum muscle damage without fatigue (~2 h after exercise). An alternative explanation is that the presence of muscle damage and fatigue may induce a unique neural activation strategy, as we show evidence for increased antagonist muscle coactivation that was observed after eccentric exercise, but was not present 24 h later.

In conclusion, the performance of eccentric exercise resulted in a decline in muscle strength after and 24 h after exercise, which is indicative of damage to muscle fibers. This decline in strength after exercise was associated with increased EMG of all elbow flexor muscles, particularly the biceps brachii and brachialis muscles. Furthermore, there was an increase in force fluctuations after eccentric exercise, with a greater proportional increase in force fluctuations within the physiological tremor (8–12 Hz) range. The increased elbow flexor EMG and force fluctuations were most pronounced at low forces, suggesting that alterations in motor unit activation are responsible for the impaired neural control of force after eccentric exercise. We suggest that changes in the relative contributions of recruitment and rate coding, or correlated motor unit discharge, may be responsible for the altered neural control of force after eccentric exercise. Although it is well known that eccentric exercise leads to substantial strength losses, we show that it is also detrimental for the precision of force production, and it should be avoided in individuals and athletes whose sporting activity involves fine motor control and where motor skills are critical for an adequate performance in the presence of significant fatigue.

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