Impaired neuromuscular function during isometric, shortening, and lengthening contractions after exercise-induced damage to elbow flexor muscles

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and 1-RM load declined by loads of 10, 20, and 40% of 1 RM. Tasks were performed before, immediately after exercise, there was reduced steadiness for the shortening and lengthening contractions. Ten healthy individuals (age 22 ± 4 yr) performed four tasks with the elbow flexor muscles: a maximum voluntary contraction, a one repetition maximum (1 RM), an isometric task at three joint angles (short, intermediate, and long muscle lengths), and a constant-load task during slow (∼7°/s) shortening and lengthening contractions. Task performance was quantified as the fluctuations in wrist acceleration (steadiness), and electromyography was obtained from the biceps and triceps brachii muscles at loads of 10, 20, and 40% of 1 RM. Tasks were performed before, immediately after exercise, and 24 h after eccentric exercise that resulted in damage to muscle fibers. Maximum voluntary contraction force and 1-RM load declined by ∼45% immediately after exercise and remained lower at 24 h (∼30% decrease). Eccentric exercise resulted in reduced steadiness and increased biceps and triceps brachii electromyography for all tasks. For the isometric task, steadiness was impaired at the short compared with the long muscle length immediately after exercise (P < 0.01). Furthermore, despite no differences before exercise, there was reduced steadiness for the shortening compared with the lengthening contractions after exercise (P = 0.01), and steadiness remained impaired for shortening contractions 24 h later (P = 0.01). These findings suggest that there are profound effects for the performance of these types of fine motor tasks when recovering from a bout of eccentric exercise.

motor function; electromyogram; acceleration; elbow flexion

Most tasks of daily living and sporting activities involve the performance of a combination of shortening and lengthening muscle contractions, with greater forces developed during lengthening contractions for some tasks, such as walking downhill, and in slowing or braking movements, such as when landing from a jump. If the intensity or duration of the lengthening contractions is of sufficient magnitude, it will result in damage to muscle fibers, leading to prolonged muscle weakness and a stiff and sore feeling in the muscles a day or so after the exercise (see Refs. 22, 23). One consequence of this exercise-induced muscle damage is a disturbance in the electromyogram (EMG)/force relation in submaximal contractions. Despite no changes in the EMG for maximum contractions, there is a more than proportional increase in EMG at low-force levels after eccentric exercise (27, 32), which presumably reflects an altered neural drive to the damaged muscles. Furthermore, several studies have shown that exercise-induced muscle damage results in an impaired ability to control muscle force or limb position (15, 24, 27), with the greatest impairments evident during low-force contractions (27).

A fundamental property of muscle is that its contractile force depends on the length of the muscle fibers (11) and the velocity of the contraction performed during shortening and lengthening muscle actions (14). To achieve appropriate control of muscle torque or limb position during functional tasks, the nervous system must precisely adjust motor unit activity to account for the altered muscle properties during tasks that require a change in muscle length. However, when the muscle is damaged with repetitive lengthening contractions (i.e., eccentric exercise), the nervous system is presented with at least two additional challenges. First, there is a shift in the length-tension curve to longer muscle lengths (13), indicating that contractions performed at short muscle lengths are further from the optimal length for force generation. Evidence obtained in human elbow flexor muscles suggests that the optimum elbow joint angle shifts by up to 17° after eccentric exercise (21). Second, there is a disturbance in the sense of force (32) and sense of limb position (31) during submaximal tasks, which may influence motor function during changes in muscle length. Although it has been shown that motor performance during submaximal isometric contractions is impaired after eccentric exercise, the ability of the nervous system to accurately control limb position during changes in muscle length in damaged muscles is unknown.

The purpose of this study was to examine the effect of exercise-induced damage of the elbow flexor muscles on steady motor performance during isometric, shortening, and lengthening contractions. The isometric task was performed at three different joint angles that required a load to be held in a constant position while the muscle was at a short, intermediate, and long length. The performance of the isometric task was compared with that achieved during slow shortening and lengthening contractions while lifting and lowering a constant load. We expected to see impaired neuromuscular performance at the short muscle lengths after eccentric exercise due to a shift in the length of optimal force generation to longer muscle lengths (13). In addition, we expected to see the largest...
impairments in motor performance during lengthening contractions when performed with damaged muscles, as the muscle damage is generated primarily through the stretching of active muscle, resulting in sarcomere disruption during the lengthening phase of the contraction (17, 22). These findings may suggest substantial impairments in neuromuscular control during functional tasks requiring a change in muscle length. Such a finding may, inter alia, have implications for particular groups, such as in the elderly or athletes, where injuries may be accentuated by a more variable and less accurate limb position during activities of daily living or in athletic pursuits.

METHODS

Ten subjects were recruited for this study (5 men and 5 women: age 22 ± 4 yr). All subjects reported no recent injury or musculoskeletal pain in their right arm or shoulder. Two subjects performed regular strength training involving their elbow flexor muscles (3–4 times per week), whereas all other subjects were not involved in any form of strength training. Written, informed consent was obtained from all subjects. All experimental procedures conformed to the Declaration of Helsinki and were approved by the Human Research Ethics Committee at The University of Adelaide.

Experimental Arrangement

Subjects were seated comfortably in a modified chair with their right forearm positioned in a custom-made device designed to allow position holding, flexion, and extension of the elbow joint against a constant load (Fig. 1). During all tasks, the upper arm was positioned anteriorly at 90° to the torso. The forearm was supinated and secured to a platform by two wide nylon straps. The platform was connected to a pulley via a perpendicular metal rod. At one end of the rod, an angular displacement transducer (resolution of 4 mV/°) was used to detect the angular displacement about the elbow joint that was generated from flexion extension movements of the forearm. The other end of the rod was attached to a pulley with a radius of 0.23 m that was counterweighted so that resistance was provided only when a load was attached to a line located around the pulley. This setup allowed the elbow joint to move freely throughout its full range of motion. Contractions were performed over 60° throughout the middle of the range of motion, from 120 to 60° elbow flexion (where 180° represented full extension). Furthermore, the pulley could be locked in place to perform isometric contractions at an elbow joint angle of 90°. In this arrangement, force was measured with a force transducer (model MLP-150, Transducer Techniques) that was fixed to the floor and attached to the end of the line placed around the pulley, producing a moment arm of 0.23 m.

Surface EMG signals were recorded with two electrodes (Ag-AgCl, 4 mm diameter) placed 2 cm apart over the distal portion of biceps brachii (elbow flexor), proximal portion of the brachioradialis (elbow flexor), and the distal portion of the triceps brachii (elbow extensor). A grounding strap located around the wrist served as a common reference for the EMG recordings. EMG signals were amplified (100-1000x; V75-04, Coulbourn Instruments, Whitehall, PA), band-pass filtered (high pass at 13 Hz, low pass at 1,000 Hz), displayed on an oscilloscope, and recorded on digital tape. An accelerometer (V94-41, Coulbourn Instruments) with a resolution of 0.01 g was attached onto the platform at the level of the wrist to measure fluctuations in acceleration in the sagittal plane during the tasks.

Experimental Procedures

Relaxed elbow angle was measured using a goniometer, while subjects stood upright with their right arm relaxed by their side. Anatomical landmarks were located at the midpoint between the acromion and coracoboid process, the lateral epicondyly, and the midpoint of the ulnar and radius styloid processes. These points were marked at the beginning of the experiment to ensure reliable location of the location. The experimenter gradually increased the pressure applied by the compression gauge until the subject reported pain. Relaxed elbow angle and muscle pain threshold were obtained from an average of three trials. These measures were obtained before, immediately after, and 24 h after eccentric exercise as indicators of muscle damage.

Experimental tasks. Subjects performed four tasks: a maximum voluntary isometric contraction (MVC), a one repetition maximum (1 RM), holding a constant load at a set elbow angle (isometric task), and performing elbow flexion and extension while supporting a constant extension load (shortening and lengthening contractions). All tasks were performed in the sagittal plane. These tasks were performed before, immediately after, and 24 h after eccentric exercise.

MVC force. The MVC task consisted of a ramp increase in flexion force over 3 s to maximum, with the maximum voluntary effort sustained for a further 2–3 s. The MVC force was determined by the experimenter during the sustained contraction to ensure maximum force production. The greatest force produced during flexion was considered the MVC force. Subjects performed three flexion tasks, with 2-min rest between each contraction. The pulley was then locked at 90° to provide resistance during isometric elbow extension, and this procedure was replicated to obtain maximum EMG in the triceps brachii muscles.

Fig. 1. Schematic drawing of a subject in the experimental apparatus for the constant-load contractions. The right forearm was secured in the device, which was connected to a pulley with a moment arm of 0.23 m. A load was attached to a line located around the pulley that produced an extension torque that was opposed by contraction of the elbow flexor muscles. The task was to match the elbow joint position (angular displacement transducer) as closely as possible to a target line located on the oscilloscope. A flat target line indicated an isometric contraction, whereas a triangular template indicated the lifting (shortening contraction) and lowering (lengthening) of the load. Muscle activity was recorded from the electromyogram (EMG), with electrodes placed over the biceps brachii, brachioradialis, and triceps brachii muscles.
1-RM load. The 1-RM load was defined as the quantity of mass (kg) that the subject could lift no more than once. The 1-RM load was determined with the same apparatus used for the constant-load task. Subjects were required to lift a load from 120 to 60° elbow flexion following a target line displayed on the oscilloscope. The duration of this lift was 9 s (velocity of ~6.7°/s). The experimenter chose the initial weight, and then the weight was increased in increments of 0.5–2 kg, depending on the ease of the previous attempt. Subjects usually performed three to five lifts until the task could not be performed correctly. The last weight lifted successfully over the full range of motion was considered to be the 1 RM. Subjects were given a 1-min rest between each attempt.

Isometric task. A load was attached to the end of the pulley that provided an elbow extension torque that was opposed by contraction of the elbow flexor muscles. The isometric task was performed at 60, 90, and 120° of elbow flexion, which was assumed to represent a short, intermediate, and long length of the biceps brachii muscle, respectively. The task required the subject to hold the load for 9 s while matching a target elbow joint position that was provided by a straight line on the feedback oscilloscope. Subjects performed the isometric task with loads of 10, 20, and 40% of 1 RM, carried out in a pseudo-random order. The load was normalized to the most recently obtained 1 RM in that session.

Shortening and lengthening contractions. The angular position of the elbow joint was displayed on the feedback oscilloscope, along with the target line that corresponded to a triangular template representing the elbow joint movement to be performed. The template represented a constant-velocity contraction (~6.7°/s) in both the flexion and extension directions. Each subject was instructed to match the template as accurately as possible by moving the elbow joint through a 60° range of motion from the starting position (120°). The subjects raised the load during 9 s of flexion (shortening contraction) and lowered the load during 9 s of extension (lengthening contraction). Subjects performed these contractions with loads of 10, 20, and 40% of the most recently obtained 1 RM. Subjects completed three trials at each load.

Eccentric Exercise

The eccentric exercise consisted of lowering a weight that was equivalent to ~50% of the 1-RM load for each subject. Subjects were seated in a chair that consisted of an adjustable height seat and a padded support for the upper arm that was positioned 45° from the torso. The subjects rested their upper arm on the support and held their forearm vertically. The exercise task required subjects to lower the weight starting from 45° flexion (forearm held vertical) to full extension (range of 135°) in 2 s by eccentric contraction of the elbow flexor muscles. Following the contraction, the experimenter removed the load, and the subjects returned their arm to 45° within 4 s. This task was repeated in sets of 10 with 20-s rests between each set until there were visible signs of tremor during the contraction and verbal communication from the subject that they were having difficulty controlling the load. When this occurred, the MVC was measured regularly, and the exercise was stopped when MVC had declined by at least 40% of the preexercise value (21). This protocol was performed to obtain equivalent muscle damage in all subjects and reduces the variability in strength loss between different subjects due to any inherent differences in the subject population.

Data Analysis

Signals were recorded and sampled at 200 Hz (position and force), 1,000 Hz (acceleration), or 2,000 Hz (EMG) using an analog-to-digital converter (CED 1401, Cambridge, UK) and stored on computer. All data were analyzed offline using the Spike2 data analysis system (Cambridge, UK) and custom-designed software. For the MVC task, EMG was full-wave rectified, and the average EMG was calculated over a 1-s interval obtained around the peak force. For the isometric task, steadiness was measured as the SD of acceleration over the middle 6 s of the task, with an increase in the acceleration fluctuations reflecting reduced steadiness. The average rectified EMG from all muscles was calculated over the same 6-s period. The shortening and lengthening contractions were analyzed by placing cursors at the beginning, middle, and end of the movement to mark the raising and lowering phases of the task. The SD of acceleration was calculated for the middle 6 s for both phases and was normalized to the absolute load for each of the tasks. The EMG was full-wave rectified and averaged over the middle 6 s of each phase. The SD of acceleration and EMG was averaged over all three trials to obtain the final measure for each condition.

One-factor ANOVA with a repeated-measures design was used to compare MVC force, 1-RM load, relaxed elbow angle, and muscle pain threshold over time (before, immediately after, and 24 h after exercise). A two-factor ANOVA was used to compare maximal EMG during maximal elbow flexion between muscles (biceps and brachioradialis) over time. As there was no significant difference between the two elbow flexor muscles for any condition, only the data from biceps brachii are reported. A two-factor ANOVA was used to compare maximal EMG during maximal elbow flexion and extension tasks between muscles (biceps and triceps brachii) over time. For the isometric contractions, a three-way repeated-measures ANOVA was used to analyze steadiness (SD of acceleration) and EMG (biceps and triceps brachii) between joint angles (60° short, 90° intermediate, and 120° long muscle length), loads (10, 20, and 40% of 1 RM), and time. For the movement tasks, a three-factor ANOVA with repeated measures was used to analyze steadiness and EMG between the tasks (isometric at 90°, shortening, and lengthening), loads, and time. Significant main effects or interactions in the ANOVA were analyzed with Fisher’s paired least-significant difference post hoc test, which performed all possible comparisons based on the type of factor examined. The level of significance was set at P < 0.05. All values are reported as means ± SD in the text and means ± SE in Figs. 2 and 4.

RESULTS

The main goal of eccentric exercise was to decrease MVC force during elbow flexion by 40% with repeated eccentric contractions, with the expectation that this intervention would induce prolonged declines in strength that are indicative of muscle damage. The decline in force was achieved with a mean exercise load of 7.8 ± 3.1 kg and required an average of 152 ± 77 contractions. This exercise resulted in a ~45% decline in MVC force and 1-RM load immediately after exercise, which remained depressed 24 h later (Table 1). EMG was recorded from biceps brachii during maximal isometric elbow flexion and from the triceps brachii muscle during maximal isometric extension of the elbow joint. No difference in maximal EMG was observed in either muscle when measured at each time point after exercise. Relaxed elbow angle declined after exercise and remained significantly reduced 24 h after exercise. Muscle pain threshold was not significantly different immediately after exercise but had significantly decreased 24 h later, indicating increased muscle soreness (Table 1).

Isometric Task

Wrist acceleration steadiness and biceps and triceps brachii EMG were measured at elbow angles of 60° (short muscle length), 90° (intermediate), and 120° (long), while subjects held loads of 10, 20, and 40% of their 1-RM load. To facilitate comparisons between loads and subjects, the acceleration fluctuations were normalized to the load lifted, and the biceps and triceps brachii EMG was normalized to the MVC EMG ob-
tained in that session. Significant main effects for time, angle, and load were found for all of these dependent variables (Table 2). Most importantly, there was reduced steadiness and an increase in biceps and triceps brachii EMG immediately after exercise. Loads held at short muscle lengths showed reduced steadiness and an increase in biceps and triceps brachii EMG compared with long muscle lengths. Furthermore, contractions performed with the 40% 1-RM load resulted in reduced steadiness and an increase in biceps and triceps brachii EMG compared with the 10 and 20% 1-RM loads.

When examining the effect of exercise and joint angle, the SD of acceleration was significantly greater at the short muscle length (60° angle) compared with the long muscle length (120° angle) immediately after exercise (angle × time interaction, P < 0.01; Fig. 2A). However, there was no difference between muscle lengths before or 24 h after exercise. Furthermore, despite no difference in the SD of acceleration between loads before exercise (values from 0.010 ± 0.004 to 0.013 ± 0.004 m·s⁻²·kg⁻¹), the SD of acceleration increased to a greater extent immediately after exercise at the 10% 1-RM load (0.076 ± 0.052 m·s⁻²·kg⁻¹) compared with the 20% (0.050 ± 0.032 m·s⁻²·kg⁻¹, P < 0.001) and 40% (0.045 ± 0.028 m·s⁻²·kg⁻¹, P < 0.001) loads (load × time interaction, P < 0.001). These data indicate that eccentric exercise resulted in impaired motor performance at short muscle lengths (60° angle), and that this impairment was most pronounced at light loads (10% of 1 RM). The significant increase in biceps brachii EMG after exercise was not influenced by muscle length during the postural contractions (angle × time interaction, P = 0.09; Fig. 2B). In contrast, the triceps brachii EMG was 50% larger (P = 0.01) at the short compared with the long muscle length immediately after eccentric exercise (angle × time interaction, P = 0.002; Fig. 2C), but was not different before or 24 h after the exercise. Compared with before exercise, the triceps brachii EMG was elevated immediately after exercise at the short (P < 0.001) and intermediate (P = 0.01) muscle length and remained elevated 24 h after exercise at the short muscle length only (P = 0.03).

**Shortening and Lengthening Contractions**

Original data from a single subject for the shortening and lengthening task with a 10% 1-RM load performed before and immediately after exercise are shown in Fig. 3. The 1 RM for this subject was 14.9 kg before exercise and 5.2 kg after exercise, representing a 65% decline in strength that remained depressed by 32% 24 h later. Despite lifting and lowering a smaller load, biceps and triceps brachii EMG increased during the shortening and lengthening contractions after eccentric exercise. Furthermore, a substantial decrease in wrist steadiness was observed after exercise, with the most pronounced impairment observed during the shortening contraction.

For comparison of neuromuscular function between isometric tasks and movements, we have compared the EMG and acceleration fluctuations during the shortening and lengthening contractions with the isometric task performed at an intermediate muscle length (90° elbow joint angle), as this represented the midpoint in elbow joint position over which the shortening and lengthening contractions were performed and analyzed. The significant main effects for acceleration fluctuations and biceps and triceps brachii EMG are shown in Table 3. When comparing the effect of exercise time and load on EMG and acceleration fluctuations in all subjects, similar observations for the shortening and lengthening contractions were observed as in the isometric tasks. We have, therefore, focused the

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**Table 1. Absolute and normalized changes in MVC force, EMG, and indicators of muscle damage obtained before, immediately after, and 24 h after eccentric exercise**

<table>
<thead>
<tr>
<th></th>
<th>Before</th>
<th>After</th>
<th>24 h</th>
<th>%Δ_1-B</th>
<th>%Δ_24-B</th>
<th>%Δ_24-A</th>
</tr>
</thead>
<tbody>
<tr>
<td>MVC force, N</td>
<td>181 (79)*</td>
<td>100 (46)†</td>
<td>124 (60)</td>
<td>−45 (6)</td>
<td>−33 (11)</td>
<td>24 (19)</td>
</tr>
<tr>
<td>Biceps MVC EMG, mV</td>
<td>0.58 (0.30)</td>
<td>0.58 (0.26)</td>
<td>0.62 (0.40)</td>
<td>7 (47)</td>
<td>9 (46)</td>
<td>4 (33)</td>
</tr>
<tr>
<td>Triceps MVC EMG, mV</td>
<td>0.29 (0.22)</td>
<td>0.27 (0.23)</td>
<td>0.29 (0.20)</td>
<td>13 (38)</td>
<td>2 (39)</td>
<td>−8 (32)</td>
</tr>
<tr>
<td>1 RM, kg</td>
<td>15.2 (5.0)*</td>
<td>8.2 (3.6)†</td>
<td>10.5 (4.8)</td>
<td>−47 (14)</td>
<td>−32 (16)</td>
<td>35 (40)</td>
</tr>
<tr>
<td>Relaxed elbow angle, °</td>
<td>17.0 (6.9)*</td>
<td>24.8 (7.0)†</td>
<td>20.2 (6.9)</td>
<td>55 (39)</td>
<td>26 (42)</td>
<td>−20 (12)</td>
</tr>
<tr>
<td>Muscle pain threshold, N</td>
<td>32.7 (20.6)</td>
<td>30.7 (28.1)</td>
<td>19.4 (19.6)†</td>
<td>−14 (47)</td>
<td>−42 (43)</td>
<td>−19 (56)</td>
</tr>
</tbody>
</table>

*Values are means (SD). MVC, maximum voluntary contraction; EMG, electromyography; 1 RM, one repetition maximum; Before, before exercise; After, immediately after exercise; 24 h, 24 h after exercise; %Δ_1-B, %Δ_24-B, and %Δ_24-A, normalized change for After vs. Before, 24 h vs. Before, and 24 h vs. After, respectively. *P < 0.05 compared with Before and 24-h. †P < 0.05 compared with 24 h. ‡P < 0.01 compared with Before.

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**Table 2. Main effects of angle, time, and load on the fluctuations in wrist acceleration and biceps and triceps brachii EMG during the isometric task**

<table>
<thead>
<tr>
<th>Angle, °</th>
<th>60</th>
<th>90</th>
<th>120</th>
<th>Before</th>
<th>After</th>
<th>24 h</th>
<th>Load, %</th>
<th>10</th>
<th>20</th>
<th>40</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acceleration SD, m·s⁻²·kg⁻¹</td>
<td>0.039 (0.040)*</td>
<td>0.034 (0.031)</td>
<td>0.027 (0.026)</td>
<td>0.012 (0.005)*</td>
<td>0.057 (0.041)</td>
<td>0.031 (0.023)*</td>
<td>0.039 (0.041)</td>
<td>0.034 (0.030)</td>
<td>0.026 (0.023)*</td>
<td></td>
</tr>
<tr>
<td>Biceps brachii EMG, %MVC</td>
<td>32.9 (22.7)*</td>
<td>20.0 (13.8)</td>
<td>22.7 (18.1)</td>
<td>16.0 (11.8)*</td>
<td>33.4 (20.1)</td>
<td>26.3 (20.7)</td>
<td>15.0 (11.6)</td>
<td>22.2 (15.1)</td>
<td>38.5 (21.7)*</td>
<td></td>
</tr>
<tr>
<td>Triceps brachii EMG, %MVC</td>
<td>21.3 (16.7)*</td>
<td>16.7 (14.0)</td>
<td>17.1 (15.0)</td>
<td>13.7 (11.7)*</td>
<td>23.5 (17.9)</td>
<td>17.8 (14.4)</td>
<td>13.1 (10.5)</td>
<td>16.8 (13.8)</td>
<td>25.2 (18.2)*</td>
<td></td>
</tr>
</tbody>
</table>

Values are means (SD). *P < 0.05 compared with After and 24 h. †P < 0.05 compared with After. *P < 0.005 compared with 120° (long length). †P < 0.005 compared with 90° (intermediate length) and 120° (long length). *P < 0.05 compared with 10 and 20%. †P < 0.05 compared with 10%.
remaining analysis on any task-related differences in EMG and acceleration fluctuations as a result of the exercise.

For all loads and time points, the SD of acceleration was largest for the shortening contractions, intermediate for the lengthening contractions, and least for the isometric task. As expected, substantial task-related differences were observed in the biceps and triceps brachii EMG, with the largest EMG in both muscles observed during the shortening contractions, compared with the lengthening and isometric tasks. No significant differences in biceps and triceps EMG were observed during isometric and lengthening contractions (Table 3).

The magnitude of the acceleration fluctuations between the tasks was influenced by exercise (task × time interaction, \( P = 0.009 \)), where there were significantly larger acceleration fluctuations for shortening compared with lengthening contractions immediately after exercise (\( P = 0.01 \), Fig. 4A). Furthermore, the impaired steadiness for shortening contractions after eccentric exercise was greatest at light loads and declined for heavier loads (task × time × load interaction, \( P = 0.003 \)). At the 10% 1-RM load, the acceleration SD was larger during shortening compared with lengthening (\( P = 0.002 \)) and isometric contractions (\( P < 0.001 \); Fig. 4B) immediately after exercise. However, no difference was observed between isometric, shortening, and lengthening contractions at any time point at the 40% 1-RM load (Fig. 4C). In contrast to the acceleration fluctuations, the pattern of EMG amplitude between the tasks was not influenced by exercise (task × time interaction, \( P = 0.07 \) for biceps, \( P = 0.4 \) for triceps). Furthermore, the EMG between the tasks did not vary with load at the different recording times with exercise (task × time × load interaction, \( P = 0.1 \) for biceps, \( P = 0.4 \) for triceps).

**DISCUSSION**

It is now well established that one consequence of exercise-induced muscle damage is an impairment in the ability to perform steady isometric contractions at submaximal forces (15, 27). The purpose of this study was to examine the effect of eccentric exercise on steady motor performance during more functional tasks that require the maintenance of different elbow joint positions (isometric task) and changes in muscle length (shortening and lengthening contractions) during constant-load contractions. Following this procedure, we found that steadiness was impaired during all contractions after eccentric exercise, but was most affected during isometric contractions at short muscle lengths, and during shortening contractions when lifting a constant load. The impaired steadiness at short compared with long muscle lengths after eccentric exercise was accompanied by increased triceps brachii (antagonist) EMG. However, there was no difference in antagonist activity for the shortening and lengthening contractions after eccentric exercise.

Eccentric exercise was performed in the present study to induce damage to muscle fibers, which was indicated by a prolonged loss of muscle strength, changes in the relaxed elbow joint angle (increased passive tension), and a lower threshold for muscle pain 24 h after the exercise. Minimal changes in these and other markers of muscle damage are observed after concentric exercise (7, 28), which is primarily associated with metabolic fatigue that recovers rapidly (31). Furthermore, several previous studies have indicated that a bout of concentric exercise that results in substantial declines in muscle strength is not accompanied by an increase in EMG force fluctuations during subsequent isometric contractions (15, 27, 32). We, therefore, suggest that the likely explanation for the impaired neuromuscular function observed after eccentric exercise in the present study is due largely to the damaging effects of eccentric exercise.

**Isometric Contractions at Different Muscle Lengths**

In our laboratory’s previous study, we found that there was a twofold increase in elbow flexor force fluctuations during submaximal contractions of 5–50% MVC when performed immediately after eccentric exercise that recovered 24 h later (27). Using a similar protocol of eccentric exercise to damage the elbow flexor muscles, we found, in the present study, that the impairment in motor performance during isometric contractions was five times larger immediately after exercise and...
shorter muscle length, necessitating the recruitment of larger motor units and an increase in EMG. It is the unfused contractions of the largest, most recently recruited motor units that are likely to contribute to the impaired motor performance (1), with greater contributions at low forces because each newly recruited motor unit represents a larger proportion of the net force. However, our laboratory has shown in a preliminary investigation that isometric force fluctuations during submaximal contractions are impaired at short muscle lengths, even when normalized to the maximum force obtained at each joint angle after eccentric exercise (26), suggesting that other factors must be involved.

A contributing factor to the impaired steadiness at short muscle lengths could be due to increased antagonist muscle activity when the muscle is damaged, which may occur through differences in the level of coactivation of the antagonist muscle, or alternating activation of the agonist and antagonist muscles (30). Increased antagonist muscle activity after eccentric exercise has been observed previously during wrist extension (16) and elbow flexion (27), which was supported in the present study. Furthermore, we found that the triceps brachii EMG was greater when the isometric elbow flexor contractions were performed at the short muscle length, but only when the muscle was damaged after eccentric exercise (Fig. 2). It is not yet clear whether this represents a deliberate

remained elevated (3 × larger) 24 h later. These data suggest that the motor impairment after eccentric exercise is more severe and longer lasting when performing isometric contractions with a constant load compared with a restrained isometric task. Furthermore, despite no difference in wrist acceleration fluctuations at different muscle lengths before exercise, there was a greater impairment in performance of the isometric task at short muscle lengths immediately after eccentric exercise. This suggests that the features contributing to this muscle length-dependent effect are due to changes in neuromuscular function resulting from exercise-induced muscle damage.

The impaired motor performance at short muscle lengths after eccentric exercise is likely to be manifested by a change in behavior of the population of active motor units brought about by neuromuscular and mechanical factors. For example, there is a greater loss of strength at short muscle lengths after eccentric exercise (20, 24), possibly due to an impaired ability to maximally activate the muscle at short muscle lengths (21), the shift in optimal muscle length for force generation to longer muscle lengths (13), or impaired calcium kinetics at short muscle lengths with muscle damage (2, 3). These changes would suggest that holding the same load at each joint angle would represent a larger proportion of maximal strength at the shorter muscle length, necessitating the recruitment of larger motor units and an increase in EMG. It is the unfused contractions of the largest, most recently recruited motor units that are likely to contribute to the impaired motor performance (1), with greater contributions at low forces because each newly recruited motor unit represents a larger proportion of the net force. However, our laboratory has shown in a preliminary investigation that isometric force fluctuations during submaximal contractions are impaired at short muscle lengths, even when normalized to the maximum force obtained at each joint angle after eccentric exercise (26), suggesting that other factors must be involved.

A contributing factor to the impaired steadiness at short muscle lengths could be due to increased antagonist muscle activity when the muscle is damaged, which may occur through differences in the level of coactivation of the antagonist muscle, or alternating activation of the agonist and antagonist muscles (30). Increased antagonist muscle activity after eccentric exercise has been observed previously during wrist extension (16) and elbow flexion (27), which was supported in the present study. Furthermore, we found that the triceps brachii EMG was greater when the isometric elbow flexor contractions were performed at the short muscle length, but only when the muscle was damaged after eccentric exercise (Fig. 2). It is not yet clear whether this represents a deliberate

### Table 3. Main effects of task, time, and load on the fluctuations in wrist acceleration and biceps and triceps brachii EMG during isometric, shortening, and lengthening contractions

<table>
<thead>
<tr>
<th>Acceleration SD</th>
<th>Isometric</th>
<th>Shortening</th>
<th>Lengthening</th>
<th>Before</th>
<th>After</th>
<th>24 h</th>
<th>Load, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>m/s² kg⁻¹</td>
<td>0.034 (0.031)</td>
<td>0.079 (0.082)</td>
<td>0.060 (0.048)</td>
<td>0.028 (0.020)</td>
<td>0.093 (0.084)</td>
<td>0.051 (0.039)</td>
<td>0.043 (0.045)</td>
</tr>
<tr>
<td>Biceps brachii</td>
<td>20.0 (13.8)</td>
<td>29.7 (21.5)</td>
<td>19.3 (12.7)</td>
<td>13.7 (9.9)</td>
<td>31.7 (17.6)</td>
<td>23.7 (176)</td>
<td>13.3 (8.4)</td>
</tr>
<tr>
<td>Triceps brachii</td>
<td>16.7 (14.0)</td>
<td>21.2 (16.6)</td>
<td>15.8 (12.8)</td>
<td>13.0 (9.1)</td>
<td>23.3 (16.8)</td>
<td>17.5 (15.1)</td>
<td>12.8 (10.3)</td>
</tr>
</tbody>
</table>

Values are means (SD). *P < 0.05 compared with lengthening and isometric contractions. †P < 0.005 compared with isometric contractions. ‡P < 0.005 compared with Before and 24 h. §P < 0.005 compared with Before. †P < 0.05 compared with 10 and 40%. ||P < 0.0001 compared with 10%.
subjects showing the greatest loss of strength displaying the tracking error up to 3 days after eccentric exercise, with the muscle length, producing mixed results. For example, during a performance during skilled motor tasks that require a change in metric tasks. Only a few studies have examined motor performance such as maximal isokinetic contractions or submaximal isometric tasks. Most observations of impaired neuromuscular function after eccentric exercise have been based on relatively simple tasks, such as maximal isokinetic contractions or submaximal isometric tasks. Only a few studies have examined motor performance during trained muscles when measured 20 min after the exercise. Using slower movements and a sensitive measure of steady motor performance while lifting and lowering loads, we found that the wrist acceleration fluctuations were approximately three times larger during shortening and lengthening contractions immediately after exercise, with the greatest impairments observed during shortening contractions when lifting constant loads. Furthermore, the acceleration fluctuations remained elevated 24 h after exercise compared with before exercise for shortening, but not lengthening, contractions. As the shortening contractions were always performed before the lengthening contractions in the present study, it is possible that a learning response occurred while lifting the constant load that resulted in improved steadiness during the lowering phase of the movement. However, three consecutive trials were performed at the same load, and there was no improvement in performance during the shortening or lengthening contractions between the first and last trial at any time point, suggesting that this possibility is unlikely. The most likely mechanism that could be responsible for the impaired steadiness during shortening and lengthening contractions is a change in the control properties of the motor unit population as a result of the exercise. Several motor unit factors are likely to contribute to the impaired steadiness, including an increase in recruitment to activate larger motor units, increased discharge rate variability, and increased correlation of motor unit activity (see Ref. 10). Our laboratory has recently shown that mean motor unit discharge rate and synchronization are increased during low-force isometric contractions after eccentric exercise (8), suggesting a likely change in motor unit activity during shortening and lengthening contractions in damaged muscles. Importantly, the activity of motor units during lengthening contractions is not simply the inverse of motor unit activity during shortening contractions. From studies examining the activity of the same motor units in fresh muscle, there is increased motor unit recruitment and discharge rate modulation during shortening contractions, whereas the motor unit discharge rates are lower (with less rate modulation) but discharge with higher synchrony during lengthening contractions (9, 18, 25). The greater impairment in steadiness during the shortening contractions when the muscle is damaged could, therefore, be due to the recruitment of larger motor units that discharge with greater variability, or an increase in correlated motor unit activity when the muscle shortens to lift the constant load. How muscle damage influences the relative contribution of motor unit recruitment, rate modulation, and discharge synchrony to the performance of shortening and lengthening contractions remains to be determined.

Motor Performance with Shortening and Lengthening Contractions

Motor strategy to increase joint stability to maintain movement precision when accompanied by increased muscle weakness (4), or if it represents an unintended overflow of neural activity (e.g., Refs. 12, 33).

Motor Performance with Shortening and Lengthening Contractions

Most observations of impaired neuromuscular function after eccentric exercise have been based on relatively simple tasks, such as maximal isokinetic contractions or submaximal isometric tasks. Only a few studies have examined motor performance during skilled motor tasks that require a change in muscle length, producing mixed results. For example, during a fast elbow joint tracking task, Pearce et al. (19) found increased tracking error up to 3 days after eccentric exercise, with the subjects showing the greatest loss of strength displaying the most impaired tracking performance. In contrast, Smith and Newham (29) found no deficit in tracking performance after eccentric exercise of the elbow flexor muscles when measured 20 min after the exercise. Using slower movements and a sensitive measure of steady motor performance while lifting and lowering loads, we found that the wrist acceleration fluctuations were approximately three times larger during shortening and lengthening contractions immediately after exercise, with the greatest impairments observed during shortening contractions when lifting constant loads. Furthermore, the acceleration fluctuations remained elevated 24 h after exercise compared with before exercise for shortening, but not lengthening, contractions. As the shortening contractions were always performed before the lengthening contractions in the present study, it is possible that a learning response occurred while lifting the constant load that resulted in improved steadiness during the lowering phase of the movement. However, three consecutive trials were performed at the same load, and there was no improvement in performance during the shortening or lengthening contractions between the first and last trial at any time point, suggesting that this possibility is unlikely. The most likely mechanism that could be responsible for the impaired steadiness during shortening and lengthening contractions is a change in the control properties of the motor unit population as a result of the exercise. Several motor unit factors are likely to contribute to the impaired steadiness, including an increase in recruitment to activate larger motor units, increased discharge rate variability, and increased correlated motor unit activity (see Ref. 10). Our laboratory has recently shown that mean motor unit discharge rate and synchronization are increased during low-force isometric contractions after eccentric exercise (8), suggesting a likely change in motor unit activity during shortening and lengthening contractions in damaged muscles. Importantly, the activity of motor units during lengthening contractions is not simply the inverse of motor unit activity during shortening contractions. From studies examining the activity of the same motor units in fresh muscle, there is increased motor unit recruitment and discharge rate modulation during shortening contractions, whereas the motor unit discharge rates are lower (with less rate modulation) but discharge with higher synchrony during lengthening contractions (9, 18, 25). The greater impairment in steadiness during the shortening contractions when the muscle is damaged could, therefore, be due to the recruitment of larger motor units that discharge with greater variability, or an increase in correlated motor unit activity when the muscle shortens to lift the constant load. How muscle damage influences the relative contribution of motor unit recruitment, rate modulation, and discharge synchrony to the performance of shortening and lengthening contractions remains to be determined.

Functional Implications

We have shown in the present study that the ability to perform isometric, shortening, and lengthening contractions is impaired for up to 24 h after exercise that was sufficient to induce muscle damage. These fluctuations in motor performance are important, as they are influential in producing a smooth trajectory and to accurately attain a desired target location of a limb (6, 10). We also found that the fluctuations in motor performance were greatest during isometric contrac-
tions at short muscle lengths and when shortening the muscle to lift constant loads. These findings suggest that there may be profound effects for the performance of these types of fine motor tasks when recovering from a bout of eccentric exercise. Furthermore, when combined with the altered proprioception that is commonly observed with fatiguing eccentric exercise (23), these findings may have implications for sports injuries, where an inability to produce a smooth movement trajectory or accurately locate an appropriate target may, at times, lead to more major injuries, such as muscle tears (e.g., Ref. 5).

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