Motor-Unit Activity Differs With Load Type During a Fatiguing Contraction

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Mottram, Carol J., Jennifer M. Jakobi, John G. Semmler, and Roger M. Enoka. Motor-unit activity differs with load type during a fatiguing contraction. J Neurophysiol 93: 1381–1392, 2005. First published October 13, 2004; doi:10.1152/jn.00837.2004. Despite a similar rate of change in average electromyographic (EMG) activity, previous studies have observed different rates of change in mean arterial pressure, heart rate, perceived exertion, and fluctuations in motor output during the performance of fatiguing contractions that involved different types of loads. To obtain a more direct measure of the motor output from the spinal cord, the purpose of this study was to compare the discharge characteristics of the same motor unit in biceps brachii during the performance of two types of fatiguing contractions. In separate tests with the upper arm vertical and the elbow flexed to 157°, the seated subjects maintained either a constant upward force at the wrist (force task) or a constant elbow angle (position task) for a prescribed duration. The force and position tasks were performed in random order at a target force equal to 3.5 ± 2.1% (mean ± SD) of the maximal voluntary contraction (MVC) force above the recruitment threshold of the isolated motor unit. Each subject maintained the two tasks for an identical duration (161 ± 96 s) at a mean target force of 22.2 ± 13.4% MVC (range: 3–49% MVC). The dependent variables included the discharge characteristics of the same motor unit in biceps brachii, fluctuations in motor output (force or acceleration), mean arterial pressure, heart rate, and rating of perceived exertion. Despite similar increases in the amplitude of the averaged EMG (% MVC) for the elbow flexor muscles during both tasks (P = 0.60), the rates of increase in mean arterial pressure (P < 0.001), rating of perceived exertion (P = 0.023), and fluctuations in motor output (P = 0.003) were greater during the position task compared with the force task. Consistent with these differences, mean discharge rate declined at a greater rate during the position task (P = 0.03), and the coefficient of variation for discharge rate increased only during the position task (P = 0.02). Furthermore, more motor units were recruited during the position task compared with the force task (P = 0.01). These findings indicate that despite a comparable net muscle torque, the rate of increase in the motor output from the spinal cord was greater during the position task.

INTRODUCTION

The mechanisms that contribute to the decline in muscle force during a voluntary contraction are known to depend on the details of the task that is being performed (Bigland-Ritchie et al. 1995; Enoka and Stuart 1992; Gandevia 2001). The task variables that appear to influence the prevailing mechanisms include the type and intensity of exercise, the muscle groups involved, and the physical environment in which the task is performed. This report focuses on the influence of the type of load supported during a fatiguing contraction.

Several studies have examined this issue by comparing the performance of individuals on two tasks that required the same net muscle torque by the involved muscles but in which the type of load differed (Hunter and Enoka 2003; Hunter et al. 2002, 2003). The two tasks involved the elbow flexor muscles. In one task, known as the force task, the wrist was rigidly attached to a restraint and the subject was required to sustain an upward force (15–20% of maximum) by contracting the elbow flexor muscles for as long as possible. In the other task, known as the position task, the subject supported an inertial load that was equivalent to the force exerted during the force task and was required to maintain a constant elbow angle for as long as possible. The net muscle torque exerted by each subject was identical for the two tasks.

The time to task failure in these studies was consistently less for the position task. In one study, the time to failure was 1402 ± 728 (SD) s for the force task and 702 ± 582 s for the position task (Hunter et al. 2002). The rate of increase in the electromyographic (EMG) activity for the elbow flexor muscles (biceps brachi, brachialis, brachioradialis) was identical for the two tasks; this is consistent with the assertion that the net muscle torque was similar for both tasks. Despite the comparable increase in average EMG, the subjects terminated the position task earlier than the force task. Nonetheless, the amount of fatigue experienced by the subjects, as indicated by the decline in the maximal voluntary contraction (MVC) force, was similar at the conclusion of the two tasks. In contrast to the similar rate of increase in EMG activity, measures of central neural activity, including mean arterial pressure, heart rate, ratings of perceived exertion, and fluctuations in motor output (force and acceleration), all increased more rapidly during the position task.

Due to the limitations of the surface EMG as an index of the neural drive to muscle (Day and Hulliger 2001; Farina et al. 2004) and the more rapid increases in other indices of neural activity, we hypothesized that the rate of change in the motor output from the spinal cord would be greater for the position task. The purpose of the study was to compare the discharge characteristics of the same motor unit in biceps brachii during the performance of the two types of fatiguing contractions. The findings indicated that the enhanced central activity during the position task was associated with more marked changes in motor-unit activity compared with those that occurred during the force task. These adjustments included a greater reduction in discharge rate, a more pronounced increase in discharge rate variability, and an augmented recruitment of motor units. These results are consistent with the interpretation that the motor neuron pool receives greater amounts of synaptic input during the position task compared with the force task, despite a similar net muscle activity.
torque for the two tasks. Some of these data have been presented previously in abstract form (Jakobi et al. 2002; MacGillis et al. 2003b).

**METHODS**

Fifteen healthy adult men (25.6 ± 5.8 yr; range, 20–39 yr) participated in the study. All subjects were moderately active and were right-handed (average Laterality Quotient score was 0.725 ± 0.22; range: 0.18–1.0) as identified by the Edinburgh Handedness Inventory (Oldfield 1971). None of the subjects had any known neurological disorder or cardiovascular disease, and all subjects were naive to the purpose of the experiment. The Human Research Committee at the University of Colorado approved the procedures and the experiments were performed in accordance with the Declaration of Helsinki. Prior to participation in the study, all subjects gave written informed consent.

Each subject participated in one to three experimental sessions that were separated by ≥1 wk. Each experiment involved recording the discharge of a single motor unit (n = 32) in the biceps brachii of the left arm. Single-motor-unit recordings were obtained from the same motor unit as subjects performed two isometric tasks (force and position) with the elbow flexor muscles.

**Experimental arrangement**

Subjects were seated upright in an adjustable chair with the non-dominant arm abducted ~0.26 rad and the elbow resting on a padded support. The elbow joint was flexed to 1.57 rad and positioned midway between pronation and supination with the forearm parallel to the ground. Activation of the elbow flexor muscles caused an upward force to be applied at the wrist. One strap was placed around the subject’s waist and chair, and two nylon straps were placed vertically over each shoulder to restrain the subject and to minimize shoulder movement. The hand and forearm were secured in a modified wrist-hand-thumb orthosis (Orthomerica; Newport Beach, CA).

The force applied at the wrist in the vertical and horizontal directions was measured with a force transducer that was mounted on a custom-designed, adjustable support. The orthosis was rigidly attached to the force transducer. The MVC force of the elbow flexor muscles was measured in the upward vertical direction at the wrist with the JR-3 force-moment sensor (900-N range, 89.7 N/V; JR-3, Woodland, CA) prior to performance of the force task, and with the JR-3 force-moment sensor (900-N range, 89.7 N/V; JR-3, Woodland, CA) prior to performance of the position task. The MVC force for the elbow extensor and elbow flexor muscles; the MVC force for the biceps brachii, upper trapezius, and triceps brachii muscles was recorded with bipolar surface electrodes (8-mm diam; silver-silver chloride) that were placed 16 mm apart (center-to-center) on the skin overlying the respective muscles. The electrodes for biceps brachii were placed over the septum between the short and long heads of the muscle. The upper trapezius electrodes were placed 2 cm lateral to the midpoint between C2 and the acromium. Electrodes were placed on one side of the innervation zone to minimize signal cancellation. Reference electrodes were placed over the dorsal surface of the ulna at the elbow, and over the superior surface of the acromium. The EMG of the brachialis muscle was measured with an intramuscular bipolar electrode inserted 3–4 cm proximal to the antecubital fold. The electrode comprised two stainless-steel wires (100-μm diam) that were insulated with Formvar (California Fine Wire, Grover Beach, CA). One wire in each pair had the insulation removed for ~2 mm to increase the recording volume of the electrode. A surface electrode (8-mm diam) placed on the lateral epicondyle of the humerus served as the reference electrode. The EMG signals were amplified (500–2,000 times) and band-pass filtered (20–800 Hz for the surface EMG and 20–1500 Hz for the intramuscular EMG) with Coulbourn modules (Coulbourn Instruments, Allentown, PA) prior to being displayed on an oscilloscope and recorded on digital tape.

Muscle fiber action potentials from single motor units in the biceps brachii were recorded with insulated branched bipolar electrodes (stainless steel, 50-μm diam; California Fine Wire). The electrode contained three exposed areas where the insulation was removed: two on one wire (branched) and one on the other wire (monopolar) directly across from the midpoint of the branched pair (Enoka et al. 1988; Gydikov et al. 1986). Each exposed area had a width of 0.75–1 mm, and the space between each exposed area was 0.75–1 mm. Thus the entire length of the branched (2 short-circuited surfaces) and the monopolar-exposed surfaces was 3–5 mm. The wires were secured together with all-purpose gel, leaving the recording sites exposed. A disposable 25-gauge hypodermic needle was used to insert the branched bipolar electrode under the skin (not penetrating the fascia) and over the belly of the biceps brachii muscle for a distance of 3–8 cm, and was removed prior to recording motor-unit activity. The electrode was positioned perpendicular to the direction of the muscle fibers. Prior to determining the recruitment threshold, the position of the electrode was altered to optimize the detection of action potentials from a single motor unit and was not moved again until the experiment was completed. Single-motor-unit recordings were amplified (1,000–2,000 times), band-pass filtered (20–8,000 Hz), displayed on an oscilloscope, and stored on digital tape.

**Experimental procedures**

Subjects performed two submaximal isometric tasks (force and position) with the elbow flexor muscles of the left arm. These two tasks were performed on the same day in random order. Prior to the experimental session, each subject visited the laboratory for an introductory session to become familiar with the equipment and the procedures and to perform several trials of the MVC task. The experimental session consisted of 5 steps: 1) an assessment of the MVC force for the elbow extensor and elbow flexor muscles; 2) isolation and determination of the recruitment threshold of a single motor unit in the biceps brachii; 3) performance of the force task and a subsequent MVC; 4) performance of the position task and a subsequent MVC; and 5) repeat assessment of the recruitment threshold of the isolated motor unit. Steps 3 and 4 were performed in random order. Prior to initiating the second task (force or position), subjects rested until the MVC force was within 5% of the value recorded at the beginning of the protocol.
MOTOR-UNIT ACTIVITY AND LOAD TYPE

MVC FORCE. The protocol began with the subject performing three isometric MVC trials with the elbow extensor muscles and three trials with the elbow flexor muscles. The MVC task consisted of a gradual increase in force from zero to maximum over 3 s, with the maximal force held for 3 s. Efforts that the subject did not regard as maximal were rejected, and the visual gain of the force feedback was varied across trials to minimize the subject’s awareness of differences in performance (Gandevia 2001). Subjects were given a 60- to 90-s rest between trials. When the peak forces from two of the three trials were not within 5% of each other, additional trials were performed until this was accomplished. The greatest force achieved by the subject was defined as the MVC force and was used as the reference for determining the recruitment threshold of the isolated motor unit and the contraction intensity for the force and position tasks.

MOTOR-UNIT RECRUITMENT THRESHOLD. With the nondonnant wrist attached to the force transducer, the subject gradually increased the force exerted by the elbow flexor muscles to a level that was sufficient to sustain a minimal, repetitive discharge of an isolated motor unit. Subjects were given audio feedback of action potential discharge and visual feedback of elbow flexor force to assist in achieving and maintaining a minimal repetitive discharge rate. The force at which the discharge rate of the isolated motor unit was minimal and repetitive was defined as the recruitment threshold (Spiegel et al. 1996). The isolated motor unit was characterized by the shape and amplitude of its action potential, which was monitored on an oscilloscope during the performance of both the force and position tasks. In 3 of 35 experiments, the isolated motor unit was lost between tasks. The recruitment threshold of the isolated motor unit was measured again after completion of the second task.

FORCE AND POSITION TASKS. The position and force tasks were performed at a target force equal to 3.5 ± 2.1% of the MVC force above the recruitment threshold of the isolated motor unit. This target force was selected to ensure that the isolated motor unit would be active during both isometric contractions. For the force task, the subject was required to exert a force in the upward direction by contracting the elbow flexor muscles and matching the target force displayed on a monitor. For the position task, the subject was required to maintain the elbow joint angle at 1.57 rad while supporting an inertial load that was equivalent to the target force during the force task. This was accomplished by hanging a weight (resolution of 0.01 N) from the wrist at the same point on the orthosis as the point of application for the force that was exerted during the force task. Thus the load torque applied at the wrist was identical within subjects for the two tasks. Subjects were provided with visual feedback of the force (0.3% MVC/cm) exerted at the wrist during the force task, and of the elbow angle (2°/cm) during the position task (Hunter et al. 2002).

Contraction time was identical within subjects for the two tasks (161 ± 96 s; range: 45–330 s) and was based on target force. The duration of the task, which did not involve performing the task to failure, was determined from an inverse linear relation between target force (recruitment threshold) and contraction time: the duration was 330 s for target forces that were 0–5% MVC force and declined to 60 s for target forces that were 30–45% MVC force.

MEASURES OF EXERTION. Heart rate and blood pressure were monitored during both tasks with an automated beat-by-beat, blood pressure monitor (Finapres 2300, Ohmeda, Madison, WI). The blood pressure cuff was placed around the middle finger of the dominant hand and the arm was supported on a table at heart level with both the shoulder abducted and the elbow flexed to 1.57 rad. Additionally, the rating of perceived exertion (RPE) was assessed with the modified Borg 10-point scale (Borg 1982). Subjects were instructed to focus the assessment of effort on the arm muscles performing the task. The scale was anchored so that 0 represented the resting state and 10 corresponded to the strongest effort that the arm muscles could perform. The measures of exertion were recorded at 25% intervals of the contraction duration.

Data analysis

Force, acceleration, elbow angle, and EMG were recorded on digital tape and subsequently digitized (A/D converter, 12-bit resolution) and analyzed off-line using the Spike2 (version 5.02) data-analysis system (Cambridge Electronic Design, Cambridge, UK). The single-motor-unit recordings were digitized (18,500 samples/s), along with the associated surface EMG (2,000 samples/s). The force, position, and acceleration signals were digitized at 200 samples/s.

The MVC force was quantified as the peak force obtained during the MVC task. The maximal EMG for each muscle was determined as the average value over a 0.5-s interval that was centered about the peak rectified EMG during the MVC.

Acceleration during the position task and force during the force task were quantified in the vertical and horizontal (side-to-side) directions. The fluctuations in force and acceleration were compared by calculating the SD of acceleration and force for the first 10 s, 5 s on either side of 25, 50, and 75% of endurance time, and the last 10 s of the contraction. The EMG activity of the elbow flexor muscles and elbow extensor muscles during the fatiguing contraction were quantified in two ways: 1) for statistical purposes, as averages of the rectified EMG (AEMG) over the first 10 s, 5 s on either side of 25, 50, and 75% of contraction time, and the last 10 s of the contraction; and 2) for graphic presentation, as averages of the rectified EMG for every 1% of the contraction time. The EMG was normalized to the peak EMG obtained during the MVC for the elbow flexor and extensor muscles, and to a maximal resisted shoulder shrug for the upper trapezius.

Action potentials discharged by single motor units in biceps brachii were discriminated using a computerized, spike-sorting algorithm (Spike2, version 5.02; Cambridge Electronic Design), which identified the potentials belonging to a single motor unit based on waveform amplitude, duration, and shape (Fig. 1). For contractions lasting >60 s, the first, middle, and last 30 s were analyzed. For tasks that lasted for 60 s, the first, middle, and last 20 s were analyzed. For one subject whose target force was 49% MVC and the duration of the two tasks was 45 s, the first, middle, and last 15 s were analyzed. To ensure discrimination accuracy, the interspike intervals of identified motor units were manually examined for every trial. Trials that contained abnormally long or short interspike intervals (force task: 29% of trials, position task: 47% of trials) were visually discriminated on a spike-by-spike basis. Mean discharge rate was determined from the interspike intervals using custom-designed software written in Matlab (Mathworks, Natick, MA). The interspike intervals were detrended prior to determining the SD and coefficient of variation for the discharge rate, and then converted to instantaneous frequencies. For each subject, discharge times that were <4 or ≥50 pps (1.8 ± 5.8% of discharges) were considered outliers and were not included in subsequent analyses.

The recruitment threshold of the isolated motor units ranged from 3–44% of MVC. Based on a k-Means Cluster Analysis, the motor units were classified into two categories: low-threshold motor units (recruitment thresholds ranged from 3 to 21% MVC; n = 20) and moderate-threshold motor units (recruitment thresholds ranged from 26 to 44% MVC; n = 12). Discharge characteristics (mean discharge rate, SD and coefficient of variation for discharge rate) were characterized as well, based on this classification system. In addition to identifying and analyzing the discharge of the primary motor unit in each task, newly recruited motor units were also quantified using the same discrimination methods. These additional motor units, which were not identified prior to task initiation, were considered newly
recruited if they discharged action potentials for \( \geq 10\% \) of task duration, regardless of onset time. With this criterion, one recruited motor unit that discharged for only 3\% of task duration was discarded. The discharge times of the newly recruited motor units were determined for the entire duration of their activity.

**Statistical analysis**

A mixed three-factor ANOVA (2 tasks \( \times 5 \) time points \( \times 2 \) motor-unit types) with repeated measures on task and time (SPSS version 9.0) was used to compare the dependent variables for elbow force, perceived exertion, and change in SD for force and acceleration. Similar mixed three-factor, repeated-measures ANOVAs were used to compare the dependent variables of heart rate and mean arterial pressure (MAP; 2 tasks \( \times 6 \) time points \( \times 2 \) motor-unit types) and the dependent variables for motor-unit discharge rate (mean, SD, and coefficient of variation) (2 tasks \( \times 3 \) time points \( \times 2 \) motor-unit types). A mixed four-factor ANOVA (3 muscles \( \times 2 \) tasks \( \times 5 \) time points \( \times 2 \) motor-unit types) with repeated measures on task and time was used to compare the AEMG during the contraction for the elbow flexor muscles (biceps brachii and brachialis) and triceps brachii. A mixed two-factor ANOVA (2 tasks \( \times 5 \) time points) was used to compare the AEMG for the upper trapezius. The preceding ANOVAs were also used with recruitment threshold (21 different recruitment thresholds, ranging from 3 to 44\% MVC) as a continuous variable to examine differences in the dependent variables as a function of recruitment threshold, rather than simply classifying motor units into groups of low- and moderate-recruitment thresholds.

Dependent \( t \)-tests were used to compare the MVC force before and after task performance, the recruitment threshold of the isolated motor unit before and after the experiment was completed, and the same additional motor units that were newly recruited during the force task with those newly recruited during the position task. Independent \( t \)-tests were used to compare the different motor units recruited during the force task with those recruited during the position task. In addition, the mean and coefficient of variation for discharge of the newly recruited units were compared with mixed two-factor, repeated-measures ANOVAs (2 tasks \( \times 3 \) time points). When ANOVAs yielded significant interactions, post hoc comparisons using the Bonferroni adjustment for multiple comparisons were performed to locate differences between and within tasks at the appropriate time points. The alpha level for all statistical tests was 0.05 except for paired comparisons when the alpha level was adjusted with a Bonferroni correction.
correction. Data are reported as means ± SD within the text and displayed as means ± SE in the figures.

RESULTS

In an attempt to compare changes in the motor output from the spinal cord during the two types of fatiguing contractions, changes in the discharge rate and the recruitment threshold of the same motor unit in biceps brachii were assessed during performance of the position and the force tasks. The results indicated that the differences in central neural activity observed previously (Hunter and Enoka 2003; Hunter et al. 2002, 2003) are accompanied by distinct changes in motor-unit activity that contrast with the similar increases in the average EMG for the two tasks.

Task performance

The two tasks were performed one after the other, in a randomized order, at a target force equal to 3.5 ± 2.1% of MVC force above the recruitment threshold of the isolated motor unit. The target force was 22.2 ± 13.4% MVC force (range: 3–49% MVC force). The mean contraction duration, which was identical between tasks for each motor unit, was 161 ± 96 s (range: 45–330 s). The average decline in MVC force after this duration was similar between tasks: 10.4 ± 11.3% for the force task and 6.7 ± 11.8% for the position task; (P = 0.15), and achieved an average value of 8.5 ± 11.6% (P < 0.001). Subjects rested for 15–20 min between the two tasks; this was sufficient to ensure that the MVC forces were similar (P = 0.40) prior to the start of the first and second tasks (1st task: 265 ± 50 N; 2nd task: 262 ± 57 N). The similarity in the net muscle torque for the two tasks was underscored by comparable values for the mean vertical force exerted under the elbow joint during the position (67 ± 40 N) and force tasks (73 ± 46 N, P = 0.79), and at the start (74 ± 45 N and 74 ± 33 N) and end of the two tasks (64 ± 40 N and 69 ± 62 N for the position and force tasks, respectively, P = 0.48).

The two tasks involved comparable levels of EMG activity. The amplitude of the averaged EMG (% MVC) for the biceps brachii and brachialis muscles increased progressively during both tasks (Fig. 2; P < 0.001). Additionally, the averaged EMG (AEMG) was similar within muscles for both tasks (P = 0.60). A muscle × task × time interaction indicated that the AEMG of the brachialis muscle was greater than that for biceps brachii muscle during both tasks (Fig. 2; P = 0.003). The mean AEMG for the brachialis muscle during the position and force tasks (25.0 ± 18.8 and 26.6 ± 24.9%, respectively) was significantly greater than that for biceps brachii (16.7 ± 14.8 and 16.8 ± 14.4%, respectively; P = 0.003). Furthermore, the mean AEMG was similar in both the antagonist muscle (triceps brachii) during the position (6.8 ± 1.9%) and force tasks (4.7 ± 1.0%, P = 0.73) and in an ancillary muscle (upper trapezius; recorded in 9 of the 15 subjects) during the position (36.6 ± 22.4%) and force task (38.3 ± 22.2%, P = 0.48).

Measures of central neural activity

Despite the similarity in the forces exerted during the two tasks, there were differences in the rates of change for MAP, heart rate, RPE, and the fluctuations in motor output (force and acceleration). Although MAP increased during both tasks, the rate of increase was greater for the position task compared with the force task (P < 0.001, Fig. 3A). MAP was greater at all time points during the position task except at 25% of contraction time with the greatest difference occurring at task termination (125 ± 22 and 113 ± 18 mmHg for the position and force tasks, respectively; P < 0.001). Similarly, heart rate was greater at all time points during the position task: heart rates were 86 ± 15 and 79 ± 12 bpm at the start (P = 0.004) and 89 ± 17 and 83 ± 15 bpm at 80 s (P < 0.001) and 94 ± 19 and 90 ± 21 bpm at 160 s (P = 0.03) for the position and force tasks, respectively. Furthermore, RPE was similar at the start of the contraction (2.0 ± 2.0 position task, 2.0 ± 1.5 force task; P = 0.44) but increased more rapidly during the position task (P = 0.023, Fig. 3B).

The amplitude of the fluctuations in force and acceleration in the vertical and horizontal directions increased progressively during the two tasks (Fig. 4). The relative increase in the
vertical fluctuations in acceleration during the position task (132 ± 150% at task termination) was greater than the relative increase in the vertical fluctuations in force during the force task (29 ± 92% at task termination, \( P = 0.003 \); Fig. 4A). Similarly, the relative increase in the horizontal fluctuations in acceleration during the position task (160 ± 187% at task termination) was greater than the relative increase in the horizontal fluctuations in force during the force task (30 ± 93% at task termination, \( P = 0.003 \); Fig. 4B).

**Motor-unit activity**

The force exerted by the elbow flexor muscles during the two tasks was set relative to the recruitment threshold for each of the 32 motor units. Target force was 13.4 ± 7.6% MVC (range: 3–26% MVC) for low-threshold motor units and 37.0 ± 5.4% MVC (range: 31–49% MVC) for moderate-threshold motor units. Contraction time was 222 ± 66.47 s (range: 105–330 s) for low-threshold units and 58.75 ± 4.33 s (range: 45–60 s) for moderate-threshold units. Recruitment threshold for all motor units declined from 19.6 ± 12.1% MVC at the start of the two tasks to 16.5 ± 11.4% MVC at the end of the two tasks (\( P < 0.001 \)). For the two groups of motor units, recruitment threshold declined from 11.7 ± 5.9 to 9.6 ± 7.2% MVC (\( P = 0.001 \)) for the low-threshold motor units and from 33.4 ± 5.9 to 28.3 ± 6.6% MVC (\( P = 0.002 \)) for the moderate-threshold units (Table 1).

Discharge rate declined during both tasks (main effect for time, \( P < 0.001 \)); the reduction was greater for the position

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**Fig. 4.** The relative increase in the fluctuations in motor output was greater for the position task. The fluctuations in motor output were quantified as the SD of force during the force task and the SD of acceleration during the position task in the vertical (A) and horizontal (B) directions. The data (mean ± SE) are graphed as the percent increase from the beginning of the task for each 25% increment in task duration. The vertical and horizontal fluctuations increased more rapidly during the position task (task \( \times \) time interaction, \( P < 0.001 \)).

* \( P < 0.02 \), † \( P < 0.002 \), and ‡ \( P < 0.0006 \) between the 2 tasks (post hoc paired t-test with Bonferroni correction).
A main effect for motor-unit type indicated that the coefficient of variation for discharge rate was greater for moderate-threshold units (28.1 ± 9.6%) compared with low-threshold units (20.6 ± 7.3%, P = 0.001, Fig. 6B, Table 1). There was a significant correlation between the coefficient of variation for discharge rate at the beginning (1st 20–30 s) of the contraction and recruitment threshold during the two tasks (force task: P = 0.006, r² = 0.23; position task: P < 0.001, r² = 0.47).

Table 1. Average discharge characteristics of low- and moderate-threshold motor units

<table>
<thead>
<tr>
<th></th>
<th>Low Threshold</th>
<th>Moderate Threshold</th>
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<tr>
<td>Discharge rate, pps</td>
<td>11.6 ± 2.8</td>
<td>12.9 ± 2.6</td>
</tr>
<tr>
<td>Coefficient of variation, %</td>
<td>20.7 ± 7.3</td>
<td>28.1 ± 9.9*</td>
</tr>
<tr>
<td>Coefficient of variation, pps</td>
<td>2.3 ± 1.0</td>
<td>3.5 ± 1.3†</td>
</tr>
<tr>
<td>Recruitment threshold, % decline</td>
<td>29.0 ± 29.8**</td>
<td>15.3 ± 11.9***</td>
</tr>
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</table>

Data are means ± SD for motor units with low and moderate recruitment thresholds. The data indicate the average values during the fatiguing contractions with the position and force tasks combined. *P < 0.002 compared with the low-threshold units. †P < 0.001 compared with the low-threshold units. **P < 0.002 compared with the initial recruitment threshold.
There were no differences between tasks in the times of recruitment (P = 0.006, \( r^2 = 0.23 \)), this was not the case for the position task (P = 0.357, \( r^2 = 0.03 \)).

The subcutaneous electrode over biceps brachii detected newly recruited motor units during 31 of the 32 sessions (Fig. 7). The average number of newly recruited motor units was greater during the position task (1.4 \( \pm 0.8 \), range: 0–4 motor units) compared with the force task (1.0 \( \pm 0.7 \), range: 0–3 motor units), which resulted in a greater number of newly recruited units during the position task trials (n = 46) compared with the force task trials (n = 32, P = 0.01). Twenty six of these units were newly recruited during both tasks (Table 3). There were no differences between tasks in the total percent of task duration that the 26 motor units discharged action potentials (96.3 \( \pm 8.9\% \) task duration, P = 0.58). As well, there were no differences between tasks in the times of recruitment (2.3 \( \pm 6.3\% \); range: 0–33% task duration) and derecruitment (98.1 \( \pm 6.2\% \); range 73–100% task duration, P = 0.87).

Furthermore, the mean discharge rate of these units (n = 24 due to insufficient discharges for 2 units) declined from 11.9 \( \pm 2.1 \)pps during the first 30 s of the position task to 10.6 \( \pm 2.4 \)pps during the last 30 s of the position task, whereas it did not change (11.2 \( \pm 2.6 \)pps) during the force task (P = 0.03). In contrast, the coefficient of variation for discharge rate (23.1 \( \pm 8.9\% \)) was similar for the 24 motor units that were newly recruited in both tasks (P = 0.29).

The subcutaneous electrode detected an additional 20 newly recruited motor units during the position task trials that were not recruited during the force task trials, compared with only six additional newly recruited motor units during the force task trials that were not recruited during the position task trials (Table 3). The additional newly recruited units discharged for 77.1 \( \pm 28.4\% \) of contraction duration during the position task (n = 20) and for 85.0 \( \pm 36.7\% \) of contraction duration during the force task (n = 6, P = 0.57). The newly recruited units began discharging action potentials at 20.2 \( \pm 27.1\% \) of contraction duration (range: 0–76% of task duration) during the position task and 12.5 \( \pm 30.6\% \) of contraction duration (range: 0–75% task duration, P = 0.56) during the force task. The time at which these motor units were derecruited was similar for the two tasks (position task: 96.7 \( \pm 7.7\% \) of task duration; force task: 97.5 \( \pm 6.1\% \) of task duration; P = 0.99).

Although the correlation between mean discharge rate at the beginning of the contraction and recruitment threshold was similar for the force task (P = 0.006, \( r^2 = 0.23 \)), this was not the case for the position task (P = 0.357, \( r^2 = 0.03 \)).

The discharge rate of the 20 additional newly recruited units during the position task (10.2 \( \pm 2.3 \)pps) was similar to the discharge rate of the six additional newly recruited units recruited during the force task (10.9 \( \pm 2.0 \)pps, P = 0.55). Furthermore, mean discharge rate declined during the fatiguing contractions for both sets of newly recruited motor units (P = 0.002): from 11.5 \( \pm 3.2 \)pps (n = 19 due to insufficient discharges for 1 unit) during the first 30 s to 9.7 \( \pm 2.4 \)pps during the last 30 s of the position task and from 11.6 \( \pm 2.9 \)pps (n = 6) during the first 30 s to 10.5 \( \pm 2.3 \)pps during the last 30 s of the force task. The coefficient of variation for discharge rate of the additional newly recruited units did not change during the fatiguing contractions and was 22.0 \( \pm 9.6\% \) during the position task and 19.8 \( \pm 7\% \) during the force task (P = 0.59).

**DISCUSSION**

The purpose of this study was to compare the discharge characteristics of the same motor unit in biceps brachii during the performance of two types of fatiguing contractions. Despite a comparable net muscle torque for the two tasks, the results indicated that the central demands and peripheral feedback associated with supporting an inertial load were greater than those that occurred when exerting an equivalent force against a rigid restraint. This was demonstrated by enhanced motor-unit activity that included a greater reduction in discharge rate, a more pronounced increase in discharge rate variability, and an augmented recruitment of motor units to compensate for the greater decline in discharge rate during the position task compared with the force task.

The ability to sustain a submaximal target force for several minutes requires an increase in the descending drive onto the motor neuron pool to compensate for the declining force capacity of the activated motor units. The gradual enhancement of the activation signal contributes to progressive increases in the rating of perceived exertion, MAP, heart rate, transient activation of motor units, the amplitude of the interference EMG, and the fluctuations in muscle force (Hunter and Enoka 2003; Hunter et al. 2002, 2003). Similar adjustments were observed for a range of target forces in the current study (3–49% MVC force) compared with constant target forces of 15–20% MVC force in the previous studies. The greater rate of
increase in most of these signals for the position task suggests that augmentation of the descending drive occurred more rapidly during the position task compared with the force task.

Although the observation of greater changes in motor-unit activity during the position task is consistent with the enhanced rates of increase in the other measures of central neural activity, it contrasts with a similar rate of increase in average EMG activity for the two tasks. It has been recognized for several decades, however, that the amplitude of the interference EMG underestimates the motor output from the spinal cord (Adrian 1925). The magnitude of deficit can be substantial and reach values of ~60% at maximal levels of muscle activation (Day and Hulliger 2001; Farina et al. 2004). More recently, it has been established that the amplitude of the EMG cannot be used to predict motor-unit recruitment (Farina et al. 2002). The results of the current study demonstrate that the surface EMG is insensitive to modest changes in motor-unit activity during a sustained contraction and underscores that it is an inadequate index of the neural drive to muscle.

It appears, therefore, that the rate of increase in the motor output from the spinal cord is more rapid when light loads are supported during the position task compared with exerting a submaximal force against a rigid restraint. Based on the associated adjustments, the increase in motor-unit activity likely involves an augmentation of both the descending drive and sensory feedback from the periphery. Regulation of MAP and heart rate during static contractions of moderate intensity, for example, can be achieved primarily by the motor command (Gandevia and Hobbs 1990; Gandevia et al. 1993; Ogoh et al. 2002), whereas activation of the group III and IV afferents during fatiguing contractions contributes to the reflex-mediated increase in the MAP (Alam and Smirk 1937; Kaufman et al. 1988; Rowell 1993; Rowell and O’Leary 1990). Similarly, the rating of perceived exertion appears to involve an interaction between a corollary of the central motor command and peripheral afferent feedback (Carson et al. 2002). Furthermore, the fluctuations in motor output (force and acceleration) are monotonically related to increases in motor-unit activity during brief contractions of varying intensity (Christou et al. 2002; Galganski et al. 1993) but are also influenced by changes in peripheral afferent feedback during sustained contractions (Cresswell and Löscher 2000; Hagbarth and Young 1979; McAuley and Marsden 2000). Accordingly, the more rapid increases in MAP, heart rate, ratings of perceived exertion, and fluctuations in motor output during the position task suggest that the rates of increase in the descending drive and afferent feedback were greater during this task compared with the force task.

Although the greater recruitment of motor units during the position task can be explained by an increase in the descending drive to the motor neuron pool (Löscher et al. 1996), the greater decrease in mean discharge rate and increase in discharge rate variability likely involves other mechanisms. Because the discharge of the same motor unit was monitored in the two tasks, the differential change in discharge rate likely involved synaptic mechanisms rather than intrinsic motor neuron properties. One example of a potential difference in synaptic input involves the demonstration that neurochemical excitation of group III–IV afferents, which occurs during fatiguing contractions, can increase the fluctuations in the membrane trajectory during the afterhyperpolarization (Windhorst et al. 1997), and this is known to increase the variability
in discharge rate (Calvin and Stevens 1968; Matthews 1996). This effect is likely mediated by presynaptic inhibition of the group Ia afferents rather than by direct inhibitory effects onto the motor neuron pool (Butler et al. 2003; Duchateau and Hainaut 1993; Duchateau et al. 2002; Ellrich et al. 1998; Pettorossi et al. 1999; Rossi et al. 1999). Additionally, the discharge rate of motor units becomes more variable when local anesthesia presumably blocks fusimotor axons (Hagbarth et al. 1986), which might correspond to the greater disfacilitation of group Ia feedback during the position task.

The differential adjustments in discharge rate exhibited by the low- and moderate-threshold units during the two tasks suggest significant differences in the synaptic input to the motor neuron pool during these conditions. When these inputs decreased mean discharge rate, there was a corresponding increase in discharge rate variability (Person and Kudina 1972). For example, the mean discharge rate for the low-threshold motor units decreased and their coefficient of variation increased during the position task but not during the force task. Conversely, there was no task effect for the different newly recruited units (20 units position task, 6 units force task) as also observed for the same motor units (n = 26) that were newly recruited in both tasks; mean discharge rate declined during the position task but not during the force task. Twenty motor units were recruited during the position task trials that were not recruited during the force task trials, whereas only 6 motor units were recruited during the force task trials that were not recruited during the position task trials.

### Table 3. Discharge characteristics of recruited motor units

<table>
<thead>
<tr>
<th></th>
<th>Position Task</th>
<th>Force Task</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mean discharge rate, pps</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>n = 26</td>
<td>11.0 ± 1.7</td>
<td>11.3 ± 2.4</td>
</tr>
<tr>
<td>n = 20</td>
<td>10.2 ± 2.3</td>
<td>—</td>
</tr>
<tr>
<td>n = 6</td>
<td>10.9 ± 2.0</td>
<td>—</td>
</tr>
<tr>
<td><strong>Coefficient of variation, pps</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>n = 26</td>
<td>2.5 ± 0.8</td>
<td>2.5 ± 1.1</td>
</tr>
<tr>
<td>n = 20</td>
<td>2.2 ± 0.8</td>
<td>—</td>
</tr>
<tr>
<td>n = 6</td>
<td>2.1 ± 0.4</td>
<td>—</td>
</tr>
<tr>
<td><strong>Coefficient of variation, %</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>n = 26</td>
<td>23.6 ± 9.3</td>
<td>22.7 ± 8.7</td>
</tr>
<tr>
<td>n = 20</td>
<td>22.0 ± 9.6</td>
<td>—</td>
</tr>
<tr>
<td>n = 6</td>
<td>19.8 ± 3.7</td>
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</tr>
</tbody>
</table>

Data are means ± SD for recruited motor units. Forty-six motor units were recruited during the position task trials, and 32 motor units were recruited during the force task trials. Twenty-six of these motor units were recruited during both tasks. Twenty motor units were recruited during the position task trials that were not recruited during the force task trials, whereas only 6 motor units were recruited during the force task trials that were not recruited during the position task trials.
Recruited units during the force task were not observed during the force task trials. Thus 6 of the 32 (19%) newly recruited units during the position task trials and 6 additional units subcutaneous electrode detected 26 newly recruited motor units in the two tasks. The exerted by the biceps brachii muscle during the two tasks. The discharge rate variability at the start of the position task was strongly associated with recruitment threshold, whereas mean discharge rate was not. Perhaps the inputs to the motor neurons were modulated differently by descending input from the brain stem for the two tasks as has been shown for tonic and repetitive motor activity (Heckman 2003; Heckman et al. 2003; Jacobs et al. 2002).

Furthermore, the presence of different newly recruited motor units in the two tasks underscores a potential role for either some specificity in the input received by the motor neuron pool or slight differences in the force (magnitude or direction) exerted by the biceps brachii muscle during the two tasks. The subcutaneous electrode detected 26 newly recruited motor units that were activated during both tasks, but 20 additional units during the position task trials and 6 additional units during the force task trials. Thus 6 of the 32 (19%) newly recruited units during the force task were not observed during the position task. This variability is greater than the <10% coefficient of variation reported for repeat measurements of recruitment threshold of motor units in the elbow flexor muscles (Denier van der Gon et al. 1985) but is consistent with the observed variability in motor-unit discharge during fatiguing contractions (Carpentier et al. 2001; Enoka et al. 1989).

The observation that the rate of change in motor-unit activity differed for the force and position tasks begs the question of why there was a difference when the net muscle torque was similar. Evidence suggests that the control strategy differs for the two tasks (Buchanan and Lloyd 1995). For example, muscle spindle sensitivity is augmented during precision tasks and reinforcement maneuvers (Hulliger 1993; Kakuda and Nagaoka 1998; Kakuda et al. 1996, 1997), and the amplitude of the stretch reflex is enhanced when the limb acts against a compliant load compared with a rigid restraint (Akazawa et al. 1983; De Serres et al. 2002). Consistent with the possibility of enhanced fusimotor drive, interventions (e.g., prolonged vibration, ischemia) that reduce the feedback transmitted by large-diameter afferents during a sustained submaximum contraction are associated with less pronounced increases in the force fluctuations and bursting in the interference EMG (Cresswell and L"oscher 2000). Furthermore, the gain of the feedback signal during the position task influences the time to task failure (MacGillis et al. 2003a). A likely consequence of heightened sensitivity of the stretch reflex pathway is a greater demand on the motor neuron pool (Maluf et al. 2004).

In conclusion, the current results support our hypothesis that the rate of change in motor output from the spinal cord was greater for the position task compared with the force task despite the two tasks requiring a comparable net muscle torque. Both the adjustment in discharge rate and the recruitment of additional motor units were greater during the position task. The greater adjustments in motor-unit activity during the position task suggests that the briefer time to failure that has been reported for this task may be attributable to a more rapid fatigue of the motor-unit population.

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