Motor unit activity in biceps brachii of left-handed humans during sustained contractions with two load types

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Gould JR, Cleland BT, Mani D, Amiridis IG, Enoka RM. Motor unit activity in biceps brachii of left-handed humans during sustained contractions with two load types. J Neurophysiol 116: 1358–1365, 2016. First published June 22, 2016; doi:10.1152/jn.00147.2016.—The purpose of the study was to compare the discharge characteristics of single motor units during sustained isometric contractions that required either force or position control in left-handed individuals. The target force for the two sustained contractions (24.9 ± 10.5% maximal force) was identical for each biceps brachii motor unit (n = 32) and set at 4.7 ± 2.0% of maximal voluntary contraction (MVC) force above its recruitment threshold (range: 0.5–41.2% MVC force). The contractions were not sustained to task failure, but the duration (range: 60–330 s) was identical for each motor unit and the decline in MVC force immediately after the sustained contractions was similar for the two tasks (force: 11.1% ± 13.7%; position: 11.6% ± 9.9%). Despite a greater increase in the rating of perceived exertion during the position task (task × time interaction, P < 0.006), the amplitude of the surface-recorded electromyogram for the agonist and antagonist muscles increased similarly during the two tasks. Nonetheless, mean discharge rate of the biceps brachii motor units declined more during the position task (task × time interaction, P < 0.01) and the variability in discharge times (coefficient of variation for interspike interval) increased only during the position task (task × time interaction, P < 0.008). When combined with the results of an identical study on right-handers (Mottram CJ, Jakobi JM, Semmler JG, Enoka RM. J Neurophysiol 93: 1381–1392, 2005), the findings indicate that hand edness does not influence the adjustments in biceps brachii motor unit activity during sustained submaximal contractions requiring either force or position control.

NEW AND NOTEWORTHY

Adjustments in discharge characteristics of biceps brachii motor units during sustained submaximal contractions differ when the arm supports an inertial load (position control) compared with pulling against a rigid restraint (force control). The present study demonstrates that the adjustments occur more rapidly and to a greater extent during position control than those involving force control.

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Address for reprint requests and other correspondence: J. R. Gould, Scientific Affairs, ZOLL Medical Corp., Chelmsford, MA 01824-4105 (e-mail: jgould@zoll.com).
the adjustments in motor unit activity during the force and position tasks by left-handed individuals.

The purpose of the present study was to compare the discharge characteristics of single motor units during sustained isometric contractions that required either force or position control in left-handed individuals. Because of the absence of a difference between limbs (dominant and nondominant) in endurance time for these types of sustained contractions in left- and right-handers (Gordon et al. 2012), the results of the present study were compared with those for right-handers obtained by Mottram et al. (2005). The comparison assessed the influence of handedness on the adjustments in motor unit activity during isometric contraction requiring either force or position control. To assess the potential influence of limb dominance on the performance of these tasks, a secondary purpose in the present study was to compare the performance of both limbs of left-handers on standardized tests of motor function. Based on the findings of Gordon et al. (2012) and in contrast to Mottram et al. (2005), the hypothesis was that the adjustments in the discharge characteristics of the biceps brachii motor units in left-handers would not differ during the sustained isometric contractions requiring either force or position control. Some of these data have previously been presented in abstract form (Cleland et al. 2013).

METHODS

Twenty-one healthy adults (21.9 ± 1.9 yr; 8 women, 13 men; height: 173.3 ± 9.5 cm; body mass: 70 ± 12 kg) participated in the study after written informed consent was obtained. All subjects were left-handed and free of neurological disease. The Institutional Review Board at the University of Colorado, Boulder (Protocol 11-0423) approved the experimental procedures.

Participants visited the laboratory on two occasions. The first visit lasted ~30 min and was used to familiarize the volunteer with the details of the study, to obtain written informed consent, and to assess hand preference and function. The second visit lasted ~2 h and involved recording the activity of single motor units in biceps brachii (32 motor units were recorded from 21 participants) during two sustained isometric contractions (force and position control). The goal was to compare the adjustments in the discharge characteristics of isolated motor units when encountering two different load conditions. To normalize the challenge across motor units, the target force for the two loads was set relative to the recruitment threshold of each motor unit.

Handedness and motor function. Handedness was assessed with the Edinburgh Handedness inventory, which comprises a self-report questionnaire that indicates the level of preference to use the left or right limb when performing 12 different tasks. The laterality quotient was −0.58 ± 0.22, which indicated a preference for left-handedness. Participants then performed three tests of motor function: 1) grip strength, 2) grooved pegboard test, and 3) handwriting test (Porac and Coren 1981; Provins and Magliao 1993). Grip strength and the grooved pegboard test represent the two measures of upper extremity function in the set of five assessments that comprise the motor domain of the NIH Toolbox (Reuben et al. 2013). The handwriting test comprised the time required to write the alphabet three consecutive times as quickly as possible. The three tests (grip strength, grooved pegboard test, writing test) were performed with each hand in a randomized order and quantified as the mean of three trials.

Experimental setup. Subjects were seated comfortably with the upper left arm perpendicular to the ground and slightly abducted from the trunk. The elbow was flexed to ~1.57 rad, and the wrist and forearm were oriented in a neutral position between pronation and supination and placed in a wrist-hand-thumb orthosis (Orthomerica, Newport Beach, CA). The orthosis was connected to a strain gauge force transducer (JR3, Woodland, CA) to measure the force transmitted to the load. The applied force was displayed on a monitor located at eye level ~60 cm in front of the subject. Before the start of the position task, an electromyographiometer (Biometrics, Cwmfelinfach, UK) was attached to the lateral aspect of the arm and forearm to measure elbow angle and the signal was displayed on the monitor.

Electromyographic recordings. Interference electromyographic (EMG) signals were recorded from muscles in the left arm with either surface electrodes (biceps brachii, brachioradialis, and triceps brachii) or an intramuscular electrode (brachialis). The surface electrodes (silver-silver chloride electrodes, 8-mm diameter; Coulbourn Instruments, Allentown, PA) were arranged in a bipolar configuration and placed ~15 mm apart on one side of the innervation zones for each muscle. The intramuscular signals were recorded with a fine-wire bipolar electrode that comprised two Formvar-insulated, stainless steel wires (50-µm diameter) fastened together with an all-purpose adhesive gel. The bipolar recording was made between the cut end of one wire and a ~1–2 mm region on the other wire from which the insolation was removed. A surface electrode was used as a reference for the intramuscular recording. The surface and intramuscular EMG signals were amplified (1,000×), band-pass filtered (13–1,000 Hz; Coulbourn Instruments), sampled at 2 kHz by a Power 1401 (Cambridge Electronic Design, Cambridge, UK), and stored on a computer (Dell, Plano, TX). The EMG data were normalized to values obtained during maximal voluntary contractions (MVCs) performed before the fatiguing contraction.

Single-motor unit action potentials were recorded in the short head of the biceps brachii muscle with subcutaneous fine-wire, branched bipolar electrodes that have been described in detail previously (Enoka et al. 1988; Gydikov et al. 1986; Mottram et al. 2005; Pascoe et al. 2013). Single-motor unit recordings were amplified (5,000×) and band-pass filtered (0.3–8.5 kHz; Coulbourn Instruments). The motor unit signal was sampled at 20 kHz by a Power 1401 and stored on a computer for off-line analysis.

Experimental protocol. The primary outcome of the study was the discharge times of the same motor unit during sustained submaximal contractions that required either force or position control. Prior to performing the sustained contractions, each participant performed MVCs with the elbow flexor muscles and the motor unit to be tracked during the two sustained contractions was identified.

Maximal voluntary contractions. MVC force was measured before and after each sustained contraction. The first MVC was used to determine maximal strength, to provide a reference for motor unit recruitment threshold force, and to record peak EMG activity. The second MVC was performed after the first sustained contraction, and the decline in peak elbow flexor force was used as an index of performance fatigability. The third and fourth MVCs were performed before and after the second sustained contraction to assess recovery and to provide another index of performance fatigability, respectively. The second and fourth MVCs were done within 30 s after completing the preceding sustained contraction.

The MVCs involved a gradual (~3 s) increase in the force exerted by the elbow flexor muscles up to maximum and maintaining this
force for ~3 s. The investigators provided strong verbal encourage-
ment during each MVC. Participants performed at least two MVC trials before the first sustained contraction to become familiar with the task. There was ~90 s of rest between consecutive trials, and the gain of the visual feedback was adjusted between contractions. If the peak forces were not within 5% of each other for the first two trials, or if a participant indicated that one of the efforts was not maximal, additional MVCs were performed until those criteria were met. The greatest peak force was taken as maximum and used as a reference for the submaximal sustained contractions. A single MVC was performed after the first sustained contraction and before and after the second sustained contraction. If the MVC force before the second sustained contraction was less than <95% of the initial MVC force, the subjects were given another 5 min of rest before MVC force was measured again. Before the first sustained contraction a single MVC was performed with the elbow extendors to record peak EMG amplitude.

Motor unit recruitment threshold. The recruitment threshold of motor units was determined before the sustained contractions. Par-
ticipants were asked to gradually increase the elbow flexor force up to a target force of 60% MVC over the course of 10 s. Motor unit recruitment threshold was identified as the force at which an observed motor unit began discharging action potentials repetitively (interspike intervals <250 ms). Recruitment threshold was estimated online as the force corresponding to the third spike in a consistent train of motor unit action potentials (Moritz et al. 2005). Participants briefly matched a target force set at ~3.5% MVC force above the identified recruit-
ment threshold to ensure that the motor unit discharged action poten-
tial repetitively. Small adjustments in target force were made to optimize the quality of the recorded signal before beginning the two sustained contractions.

Sustained isometric contractions. Based on the protocol of Mot-
tram et al. (2005), participants performed two submaximal isometric contractions that were sustained for a prescribed duration. The net torque about the elbow joint was the same during both contractions for each individual, but one task required the participant to exert a constant force against a rigid restraint (force control) whereas the other task required the individual to maintain a constant elbow angle (1.57 rad) while supporting an inertial load (position control). Participants were provided with visual feedback on the monitor during both the force (gain: 3% MVC force/cm) and position (gain: 2° elbow flexion or extension/cm) tasks (Hunter et al. 2002; Mottram et al. 2005). The two contractions were performed in random order, but consecutively to record the same motor unit with the subcutaneous electrode. The participant rested for ~25 min before starting the second contraction.

The two tasks required participants to match the control parameter (force or angle) to the target displayed on a monitor. The duration of the two sustained contractions was the same for each participant (motor unit) but differed across participants (152 ± 84 s; range: 60–330 s). As described in Mottram et al. (2005), task duration was inversely related to the recruitment threshold of the isolated motor unit. Task duration was set at 330 s for target forces in the range of 0–5% MVC force and declined linearly to 60 s for target forces in the range of 30–45% MVC force.

Rating of perceived exertion (RPE) was measured with the modi-
fied Borg scale (0–10) during the sustained contractions. The scale was anchored so that 0 represented rest or no exertion and 10 represented the strongest possible effort. The recorded signals (force, elbow angle, and EMG) were sampled by an analog-to-digital converter (Power 1401) and stored on a computer for off-line analysis using Spike2 data acquisi-
tion/analysis software. The signals recorded from biceps brachii with the subcutaneous fine-wire electrodes (Fig. 1) were processed with an automatic decomposition algorithm in EMGLAB (McGill et al. 2005). The action potentials discharged by the identified motor unit were tracked for the prescribed duration of each sustained contraction, and the discharge times were used to determine the associated interspike intervals. The output of the algorithm was then visually inspected to verify individual spike times and edited to correct for missing or incorrectly identified spikes based on timing of interspike intervals and the residual of the signal (Mottram et al. 2005). To ensure that the same motor unit was tracked during both sustained contractions, its action potentials were superimposed and visually compared for consistency (Fig. 1). To accommodate the different durations of the sustained contractions, the discharge characteristics of each motor unit were determined for 10-s intervals at the start, middle, and end of the contraction. Discharge rate was calculated as the reciprocal of the mean interspike interval for each of these 10-s intervals.

MVC force was measured as the greatest peak force exerted during one of the MVC trials. The maximal EMG amplitude during that MVC trial corresponded to the average value during a 0.5-s interval centered about the peak of the rectified EMG. The interference EMG signals recorded during the sustained contractions were rectified and quantified as the average amplitude (aEMG) normalized to the peak EMG obtained during the selected MVC trial. aEMG values were obtained during three 10-s intervals at the start, middle, and end of each sustained contraction.

Statistics. Dependent t-tests were used to compare motor function scores of the left and right hands, MVC forces, and motor unit recruitment thresholds before and after each task. Two-factor analysis of variance was used to examine changes in dependent variables over time (3 time points; start, middle, and end) and differences between tasks (2 tasks; force control and position control). Significant main effects and interactions were examined with the Fisher’s least signific-
differe test. Dependent variables included motor unit discharge characteristics (mean and coefficient of variation for interspike interval), EMG amplitude of agonist and antagonist muscles, and RPE. α-Levels for significance were set at 0.05 for all statistical tests unless otherwise noted.

RESULTS

There was no difference in two measures of motor function for the dominant and nondominant arms of the left-handed participants as indicated by the time to complete the grooved pegboard test (59.1 ± 8.1 s and 62.9 ± 7.2 s, respectively) and grip strength (40 ± 12 kg and 41 ± 12 kg). However, the dominant (left) hand (42.0 ± 9.0 s) completed the writing test more quickly (P < 0.001) than the nondominant hand (68.2 ± 16.9 s).

The force produced during the two sustained contractions (24.9 ± 10.5% MVC force) depended on the recruitment threshold of the identified motor unit (21.6 ± 11.7% MVC force). To elicit a repetitive discharge of motor unit action potentials, the target force was set to 4.7 ± 2.0% MVC force above recruitment threshold of the identified motor unit. The duration of the two sustained contractions was the same for each motor unit (152 ± 84 s; range: 60–330 s), which resulted in similar reductions (P = 0.77) in MVC force immediately after each sustained contraction: 11.1 ± 13.7% decline in MVC after the force task and 11.6 ± 9.9% decline after the position task. MVC forces performed before the first sustained contraction (252 ± 89 N) did not differ significantly (P = 0.41) from MVC forces performed after ~25 min of rest and before the start of the second sustained contraction (230 ± 88 N). Similarly, there were no statistically significant differences between the aEMG values during the MVCs performed before the force and position tasks (brachioradialis, P = 0.53; triceps brachii, P = 0.19; brachialis, P = 0.67; biceps, P = 0.79).

RPE increased during both sustained contractions (main effect for time, P < 0.001; Fig. 2), but there was a greater
increase during the position task (time × task interaction, \( P = 0.006 \)). The final RPE values, which were obtained at the same time for the two sustained contractions for each participant, were 7.0 ± 2.2 for the force task and 8.0 ± 1.5 for the position task, confirming that the sustained contractions were not performed to task failure.

Because of the absence of a significant interaction (muscle × time) for aEMG of the agonist muscles (biceps brachii, brachioradialis, and brachialis) during each sustained contraction, the results were averaged across the three agonists (Table 1). The aEMGs at the end of both sustained contractions were increased significantly \( (P = 0.001) \) relative to the values at the start (%\( \Delta \)) for both the agonist (force: 39 ± 25%, position: 26 ± 24%; \( P = 0.001 \)) and antagonist (force: 21 ± 18%, position: 26 ± 27%) muscles. The increases in aEMG were not statistically different across tasks. Similarly, the values for force steadiness (quantified as the coefficient of variation for force) were collapsed across task because of the absence of a significant task × time interaction \( (P = 0.053) \), which yielded a significant main effect for time \( (P = 0.046) \) (Table 2).

The subcutaneous electrode recordings obtained from 23 experimental sessions (2 participants volunteered for a second session) were analyzed to determine the discharge times of at least one clearly identifiable motor unit. Most recordings \( (n = 16) \) yielded a single motor unit, but it was possible to discriminate two motor units in six recordings and four motor units in one recording. The recruitment thresholds of the 32 motor units ranged from 0.5% to 41.2% MVC force. The discharge characteristics of each motor unit were analyzed during both sustained contractions. Consistent with the magnitude of the two loads being matched, the mean discharge rate for the 32 motor units was similar at the start of the two sustained contractions (Table 2). A significant task × time interaction

Fig. 1. Representative activity of the same motor unit recorded during a 5-s window at the beginning and end of both the force and position tasks. To right of each motor unit recording is the expanded waveform overlay for the isolated motor unit, and above each recording is a trace indicating the low-pass filtered (8 Hz) version of the instantaneous discharge rate and the force recorded at the wrist of the left hand. Mean discharge rate for the illustrated motor unit started and ended at 15.2 pps and 12.6 pps, respectively, during the force task and at 14.5 pps and 12.5 pps during the position task. An additional motor unit was identified at the end of the position task (shown in gray).

Fig. 2. Mean (±SE) rating of perceived exertion (RPE; 0–10 Borg scale) increased during both force (filled circles) and position (open circles) tasks, but more so during the position task.

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for the position task. The relative change (% decrease in mean discharge rate at the start and end of the sustained contraction was −24 ± 16% for the position task and −15 ± 17% for the force task. Moreover, a main effect for task (P = 0.004) indicated that the decline in discharge rate was greater during the position task (Table 2). The absolute (Δpps) and relative (%Δ) changes in discharge rate during the two tasks are shown in Fig. 3 for both the left-handers (present study) and a preceding study on right-handers (Mottram et al. 2005).

The variability in discharge times was quantified as the coefficient of variation for interspike interval. A significant task × time interaction (P = 0.008) indicated that the coefficient of variation for interspike interval increased during the position task (Table 2). The relative change (%Δ) in coefficient of variation for interspike interval at the end of the sustained contraction was −4 ± 35% for the force task and 21 ± 42% for the position task.

Table 1. Average rectified EMG amplitudes for agonist (biceps brachii, brachialis, and brachioradialis) and antagonist (triceps brachii) muscles during force and position tasks

<table>
<thead>
<tr>
<th></th>
<th>Force Task</th>
<th></th>
<th>Position Task</th>
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<tbody>
<tr>
<td></td>
<td>Start</td>
<td>Middle</td>
<td>End</td>
<td>Start</td>
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<tr>
<td>Biceps brachii</td>
<td>14.6 ± 9.8</td>
<td>20.6 ± 12.4</td>
<td>22.8 ± 15.6</td>
<td>15.3 ± 8.3</td>
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<tr>
<td>Brachialis</td>
<td>25.5 ± 14.8</td>
<td>28.3 ± 15.6</td>
<td>30.4 ± 16.0</td>
<td>25.0 ± 14.9</td>
</tr>
<tr>
<td>Brachioradialis</td>
<td>16.1 ± 9.6</td>
<td>19.4 ± 11.0</td>
<td>22.0 ± 12.3</td>
<td>14.7 ± 7.6</td>
</tr>
<tr>
<td>Agonists</td>
<td>18.7 ± 11.4</td>
<td>22.8 ± 13.0</td>
<td>25.1 ± 14.6*</td>
<td>18.3 ± 10.3</td>
</tr>
<tr>
<td>Antagonist</td>
<td>6.6 ± 5.5</td>
<td>7.6 ± 6.2</td>
<td>8.1 ± 6.4*</td>
<td>6.9 ± 5.5</td>
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Data are mean ± SD average rectified EMG amplitudes (aEMG, expressed as % MVC value). *P < 0.05 relative to aEMG at the start.

DISCUSSION

The main finding of the present study on left-handed individuals was that adjustments in discharge rate and the variability in discharge times of biceps brachii motor units differed during sustained submaximal contractions requiring either force or position control. Similar results were reported previously for right-handed individuals using the same protocol (Mottram et al. 2005). The absence of a difference in motor unit activity between left- and right-handers during these two tasks suggests that the influence of handedness on the relative endurance times for sustained contractions with the two load types requires an alternative explanation (Gordon et al. 2012).

Handedness. Although the present study was performed on the dominant arm of left-handers and that of Mottram et al. (2005) examined the nondominant arm of right-handers, the results were likely not influenced by limb dominance. The main reason for dismissing a role for limb dominance in these types of tasks is that Gordon et al. (2012) found no difference in endurance time between limbs when left- and right-handers sustained submaximal contractions requiring either force or position control to task failure. Moreover, the present study found no differences in two tests of motor function (NIH Toolbox) between the limbs of left-handers: the strength of forearm-hand muscles (handgrip) and time to complete a pegboard test (Brouwer et al. 2001). Comparison of the present findings with those of Mottram et al. (2005), therefore, examined the potential influence of handedness on the adjustments in motor unit activity during sustained contractions requiring either force or position control.

Some reports suggest that the discharge characteristics of motor units can differ between left- and right-handed individuals, although the findings are mixed. The differences do not seem to involve conventional measures of discharge characteristics, such as mean discharge rate and the variability in discharge times (Adam et al. 1998; Schmied et al. 1994), but rather the extent to which discharge times are correlated across motor units (Kamen et al. 1992). Short-term motor unit synchronization, which is often used as an index of the relative strength of common input to pairs of motor neurons, was reported to be greater in a hand muscle of the dominant arm than the nondominant arm of right-handers, but there was no difference between limbs in left-handers (Semmler and Nordstrom 1995). Cortical projections to motor neurons can likely modulate this measure of motor unit synchronization (Datta et al. 1991; Farmer et al. 1993; Mills and Schubert 1995). Therefore, one potential explanation for the difference between limbs of right-handers but not left-handers is the influence of handedness on the distribution of descending pathways onto populations of spinal motor neurons (Brouwer et al. 2001; Buckingham et al. 2012; Pereira et al. 2012; Pool et al. 2014; Przybyle et al. 2012; Semmler and Nordstrom 1995). In contrast, Schmied et al. (1994) found that the level of short-term motor unit synchronization between pairs of motor units in the extensor carpi radialis muscle was greater in the dominant arm.
than the nondominant arm for both left- and right-handers, with no difference attributable to handedness.

The contrasting results on the influence of handedness on motor unit synchronization are likely attributable to limitations of the technique used to quantify the level of correlation. The classic approach is based on quantifying the peak of the cross-correlation histogram derived from the discharge times of action potentials from pairs of motor units (Kirkwood 1979; Nordstrom et al. 1992; Sears and Stagg 1976). However, the time at which a motor neuron generates an action potential depends on both the synaptic input it receives and its intrinsic properties. Because of the nonlinear association between synaptic current and action potential generation for each motor neuron, the amount of correlation in the discharge times for pairs of motor neurons is only weakly associated with the relative strength of common synaptic input (Farina et al. 2016; Farina and Negro 2015). Measures of short-term motor unit synchronization, therefore, are expected to be highly variable even for the same relative proportion of common synaptic input.

Taken together, these results suggest that motor unit activity during submaximal isometric contractions with upper extremity muscles is not influenced by handedness and is unlikely to be responsible for the differences reported by Gordon et al. (2012). Nonetheless, this interpretation needs to be confirmed with contemporary technology that can record the concurrent activity of multiple motor units to infer details about the synaptic input received by populations of motor units (Farina et al. 2016).

Force and position control. When sustaining a submaximal isometric contraction, the discharge rates of the motor units active from the beginning of the task decline progressively and the variability in interspike intervals increases (Carpentier et al. 2001; Enoka et al. 1989; Jensen et al. 2000; Kelly et al. 2013; Riley et al. 2008). These adjustments in motor unit activity are attributable to changes in the synaptic input and the intrinsic properties of the motor neurons (Baudry et al. 2011; Dideriksen et al. 2010). The rate of change in motor unit activity depends on the characteristics of the load against which the limb is acting. The adjustments occur more quickly when the task is to maintain the position of the limb while supporting an inertial load (position control) than when the limb pushes against a rigid restraint to maintain a constant force (force control) (Baudry et al. 2009; Mottram et al. 2005; Rudroff et al. 2010). Consistent with the different rates of decline in motor unit activity, the rate of increase in RPE is greater during position control than during force control even though the net muscle torque is matched during the two tasks (Hunter et al. 2002; Maluf et al. 2005; Rudroff et al. 2011). However, the rate of increase in EMG amplitude was similar during the two tasks because of the relative insensitivity of the interference signal to modest changes in motor unit activity (Farina et al. 2010; Mottram et al. 2005).

In the present study on left-handers, mean discharge rate (10-s intervals) declined (%Δ) during both tasks (152 ± 84 s) but with a greater reduction during the position task (−24 ± 16%) relative to the force task (−15 ± 17%). Similar values were observed in the preceding study on right-handers (Mottram et al. 2005), with reductions of −20 ± 16% and −9 ± 17% during the position and force tasks, respectively. Moreover, there were statistically significant increases in the variability in discharge times, but only during the position task for both left-handers and right-handers. Despite these mean changes in discharge characteristics for the two tasks, there was considerable variability across motor units in these adjustments. As indicated in Fig. 3, six of the motor units for left-handers and nine of the motor units for right-handers exhibited a relative increase in discharge rate during the force task. In contrast, only two and four motor units, respectively, increased discharge rate during the position task. Moreover, the distributions shown in Fig. 3 indicate more consistent and substantial reductions in discharge rate during the position task.

The variance in the adjustments in discharge rate observed in the present study are consistent with those reported by other investigators for the changes in motor unit properties during sustained isometric contractions (Carpentier et al. 2001; Enoka et al. 1989; Garland et al. 1994; Rudroff et al. 2010). In an attempt to explain the variance in the absolute (pps) and relative (%) changes in discharge rate in the present study, the associations for the force and position tasks were examined for
the left- and right-handers. There were no significant associations ($r^2 \leq 0.17$) among these variables. Moreover, the change in discharge rate appears to be unrelated to recruitment threshold, as there were no significant associations between any of the changes in discharge rate and task duration ($r^2 \leq 0.07$).

One of the limitations of the present study that constrains the interpretation of the observed changes in discharge rate is that most of the recordings were obtained for only one motor unit during each contraction. To identify differences in the net synaptic input received by motor neurons during these two tasks, it is necessary to record the discharge of several concurrently active motor units and estimate the proportion of common synaptic input received by the motor neuron pool (Castronovo et al. 2015; Farina et al. 2016).

On average, therefore, the more marked decrease in discharge rate during the position task indicates a greater decline in net excitatory synaptic input onto motor neurons during this task for both left- and right-handers. One source of excitatory input that declines more rapidly during sustained contractions requiring position control is that provided by group Ia afferents, as indicated by a more rapid reduction in the amplitude of the H reflex during fatiguing contractions performed with the elbow flexor muscles (Klass et al. 2008). Although the responsiveness of the stretch reflex pathway is greater during position control (Akazawa et al. 1983; Doemges and Rack 1992; Maluf et al. 2007), the greater reduction in H-reflex amplitude is mediated by an increase in the level of Ia presynaptic inhibition (Baudry et al. 2010, 2011; Baudry and Enoka 2009). The depression of group Ia input onto motor neurons during the position task is likely necessary to minimize reflex-related oscillations in limb position (Cresswell and Löschner 2000; Stein and Oguztöreli 1976) that would compromise the ability of an individual to maintain a constant joint angle.

Another finding consistent with a difference in the synaptic inputs received by the motor neurons during the two tasks was the significant increase in the coefficient of variation for interspike interval during the position task but not the force task. The variability in the times at which motor neurons discharge action potentials is attributable to the fluctuations in membrane potential during the afterhyperpolarization phase of the action potential due to the arrival of excitatory and inhibitory postsynaptic potentials (Berg et al. 2007; Calvin and Stevens 1968; Matthews 1999). The variability in discharge times for a single motor unit is typically greater at target forces slightly (~3%) above the recruitment threshold force (Barry et al. 2007; Moritz et al. 2005). This suggests that the progressive increase in the coefficient of variation for interspike interval during the position task indicated a gradual decline in the net excitatory synaptic input received by the motor neurons (Pascoe et al. 2014).

Although initial studies on force steadiness suggested an association between the coefficients of variation for force and interspike interval (Galganski et al. 1993; Laidlaw et al. 2000; Moritz et al. 2005), the present findings underscore the relative independence of the two measures. Whereas the coefficient of variation for force increased by similar amounts during the two sustained contractions, the coefficient of variation for interspike interval increased only during the position task. This result is consistent with the observation that the fluctuations in force in position steady-state, submaximal contractions appear to depend more on the common modulation of motor unit discharge rate than on the variability in discharge times (Farina and Negro 2015; Negro et al. 2009).

Given the range of factors that can modulate motor unit activity during sustained contractions requiring force or position control, the question arises as to whether handedness might have a similar influence (Pool et al. 2014). Gordon et al. (2012) found that, in contrast to right-handers, the endurance times for fatiguing contractions requiring either force or position control were not correlated in left-handers. One potential explanation for this difference is that the adjustments in motor unit activity during force- and position-control tasks may be modulated by handedness. The findings of the present study, however, indicate that left-handers exhibit greater declines in discharge rate and increases in discharge variability during sustained contractions requiring position control relative to force control, similar to a previous report for right-handers (Mottram et al. 2005). Therefore, the absence of a correlation between the endurance times for the two fatiguing contraction in left-handers but not right-handers cannot be explained by the influence of handedness on the modulation of motor unit activity.

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DISCLOSURES

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AUTHOR CONTRIBUTIONS


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