Reduced motor unit discharge rates of maximal velocity dynamic contractions in response to a submaximal dynamic fatigue protocol

B. Harwood,1 I. Choi,1 and C. L. Rice1,2

1School of Kinesiology, The University of Western Ontario, London, Ontario, Canada; and 2Department of Anatomy and Cell Biology, The University of Western Ontario, London, Ontario, Canada

Submitted 23 July 2012; accepted in final form 15 October 2012

Harwood B, Choi I, Rice CL. Reduced motor unit discharge rates of maximal velocity dynamic contractions in response to a submaximal dynamic fatigue protocol. J Appl Physiol 113: 1821–1830, 2012. First published October 18, 2012; doi:10.1152/japplphysiol.00879.2012.—Fatigability is highly task dependent wherein motor unit (MU) discharge rates and recruitment thresholds are affected differently depending on whether contractions are performed at maximal or submaximal intensities. Although much is described for isometric tasks, the behavior of MU properties during the production of maximal velocity dynamic contractions following submaximal fatiguing contractions is unknown. In seven young men, we evaluated changes in MU recruitment thresholds and MU discharge rates of the anconeus muscle during both submaximal and maximal dynamic elbow extensions following a submaximal dynamic fatiguing protocol of moderate intensity to velocity task failure. Velocity and power of the maximal dynamic contractions declined ~45% and ~55%, respectively, but these variables were unchanged for the submaximal target velocity contractions. Discharge rates of the 12 MUs at task failure were unchanged for submaximal dynamic contractions, but were decreased ~20% for maximal dynamic and ballistic isometric contractions at task failure. MU recruitment thresholds of submaximal dynamic contractions decreased 52% at task failure, but were similar throughout the fatiguing protocol for maximal contractions. These findings support the concept of a common neural mechanism responsible for the relative declines in MU discharge rate associated with submaximal fatigability in both isometric and dynamic contractions.

THE EXPRESSION OF NEUROMUSCULAR fatigability (13), or more recently termed fatigability (29), is highly dependent on a number of variables, including, but not limited to, the nature of the task (11), the muscle under investigation (3, 38), the age (3, 19) and sex (46) of the participants, and the method used to quantify fatigability (30). Consideration of these variables is essential in any investigation of fatigability and motor unit (MU) behavior, especially during voluntary tasks (69). Unlike isometric tasks, additional important variables related to movement through a range of motion (ROM) may affect the assessment of fatigability (30), and these have limited the amount of information that is available concerning MU properties during dynamic contractions. In an attempt to minimize some of these movement-related influences, several studies have used constant velocity (isokinetic) contraction tasks to investigate MU properties (4–6, 22, 61). However, less power output is generally observed for isokinetic movements compared with more natural human movements (48, 62), especially when movements are performed rapidly (15). In the present study, the term dynamic contractions will be used to indicate contractions in which a relatively constant load is moved voluntarily at angular velocities that can vary freely throughout the joint ROM, and from which power (torque × velocity) can be calculated.

During any type of dynamic contraction, the ability to successfully record and analyze single MUs potentially is affected adversely, mainly by changes in the electrode-muscle interface during active contractile shortening of fibers and whole muscle architectural changes (32, 56). These factors are further compounded during repetitive contractions, which can lead to neuromuscular fatigue in which alterations in both muscle forces and velocities add extra challenges in the ability to record from single MUs (26, 34). Consequently, investigations of MU control properties during fatiguing protocols (FPs), especially those dynamic in nature, are very limited in humans.

Only two studies (41, 57), both in the triceps brachii, have investigated MU control strategies of dynamic contractions in response to a submaximal dynamic FP. These recordings were accomplished during very slow (50°/s) and lightly loaded [20% of maximal voluntary isometric contraction (MVC)] elbow extensions. Discharge rates of MUs recorded during those submaximal efforts changed variably (in some units, rates were unchanged, some increased, and some decreased) resembling results of isometric studies in which no change (20, 33, 41, 49, 66, 70), increased (1, 2), or decreased (16, 31, 36, 37, 39, 59, 64, 68) discharge rates were observed in response to submaximal isometric FPs. Studies of sustained or repeated maximal isometric contractions, however, consistently reported a decline in MU discharge rates with fatigability (10, 12, 54, 63, 66). Furthermore, in the few studies that investigated MU discharge behavior during isometric FPs comprised of both submaximal and periodic maximal (MVC) contractions, pre-to postfatigability MU discharge rates were unchanged for the submaximal target contractions, but MU discharge rates recorded at MVC postfatigability were reduced ~30% (9, 70) (consistent with results above).

Critically, however, it is unknown how MU discharge rates may change for maximal dynamic contractions in response to a submaximal dynamic FP and their relationship to fatigability-related reductions in shortening velocity and muscle power (17, 18). It has been reported that higher MU discharge rates than those observed at isometric MVC (23, 24, 43, 73) are required to summate twitch tensions of MUs with faster contractile properties (24), which subsequently generate the high rates of force development (24, 73) required for the production of maximal dynamic contraction velocities (43). These characteristics of dynamic contractions imply reductions in MU discharge rate related to fatigability may be greater relatively for dynamic contractions compared with...
those reported for isometric contractions, but this has not been evaluated.

The effect of submaximal fatiguing contractions on MU recruitment thresholds is less well defined than for discharge rates. One isometric study of intermittent submaximal fatiguing contractions at 30–50% MVC observed an ~10% decrease in recruitment thresholds of the lateral head of the triceps brachii (20). Lower average MU recruitment thresholds may arise as a consequence of two mechanisms: 1) MU recruitment threshold reductions across the entire motoneuron pool, or 2) reductions in recruitment thresholds of a subsection of the MU population (i.e., higher threshold MUs). The latter mechanism may manifest as a compression in the recruitment threshold range, providing that larger reductions in MU recruitment threshold are observed in high-threshold MUs. Compression of the MU recruitment threshold range has been reported in response to submaximal intermittent isometric fatiguing contractions (16) and separately shown to contribute substantially to the production of nonfatiguing dynamic contractions (45). High-threshold MUs possess fast-twitch contractile properties (58, 65) that are related to maximal shortening velocities in a human extensor muscle model (72). Thus fatigability-related changes in recruitment of high-threshold MUs may represent a mechanism by which high rates of torque development, and, therefore, maximal contraction velocities and muscle power, are maintained in an effort to minimize fatigability (12, 13, 16).

The purpose of the present study, therefore, was to evaluate anconeus MU properties in relation to the generation of submaximal and maximal dynamic elbow extensions in response to a submaximal dynamic FP. To minimize some of the technical limitations of successfully recording MUs during dynamic contractions, the anconeus muscle, which has been shown to be a very useful model for exploration of MU properties for this task (40, 41), was investigated. Briefly, the anconeus is a small elbow joint extensor muscle (47), but one that is active consistently throughout the whole elbow joint ROM and at all elbow extension forces and velocities (51–53). It modulates force through a combination of recruitment and rate coding and is active at lower relative forces compared with those of the triceps brachii (main elbow extensor) (51). Unlike the triceps brachii, anatomical features of the anconeus (44, 60) allow relatively clear recording of MU properties that can be tracked reliably during rapid shortening movements.

Using this muscle model, it was hypothesized, based on earlier studies of MUs recorded at MVC following high-intensity isometric FPs (20, 33, 41, 49, 66, 70), that MU discharge rates related to the production of maximal dynamic contractions will decrease as task failure is approached, but, as shown previously (38, 55), will be unchanged for the submaximal or target dynamic contractions. Also, it was hypothesized that MU recruitment thresholds of submaximal dynamic contractions will decrease with increased time to task failure (TTF) in accordance with earlier studies of submaximal isometric fatigability (37, 70). For maximal dynamic contractions, it was hypothesized that MU recruitment thresholds will be reduced to compensate for fatigability-associated changes to twitch contractile properties and to sustain maximal contraction velocities and muscle power.

METHODS

Seven young men free from orthopedic, neuromuscular, and cardiorespiratory limitations, participated in the study. Subjects provided informed, written and verbal consent before participation, and all procedures were approved according to the policies and guidelines of the local Research Ethics Board for human participants and conformed to the Declaration of Helsinki.

Elbow extension torque, position, and velocity measures were recorded using a Biodex System 3 multijoint dynamometer (Biodex Medical Systems, Shirley, NY), while single MU action potentials from the anconeus and global intramuscular electromyography (EMG) of the anconeus, and lateral and long heads of the triceps brachii were recorded. The unpredictable nature of single MU recordings required that subjects visit the laboratory one to three times (~1.5 h/visit) to ensure an adequate quantity and quality of single MU recordings. Visits in which a MU recording did not meet the inclusion criteria for analysis (see Data analyses) were not considered.

Setup and baseline measures. Subjects were seated in the Biodex dynamometer with their shoulder flexed 90° and their nondominant arm abducted 20°, resting on a support positioned ~10 cm proximal to the olecranon process of the ulna. Single twitches of the elbow extensors (100-μs pulse width) were electrically evoked using a stimulator (DS7AH; Digitimer, Welwyn Garden City, Hertfordshire, UK) and two custom gel-coated aluminum foil stimulation electrodes (5 × 6 cm to 5 × 12 cm in size). The stimulating electrodes were each placed transversely over the muscle belly of the triceps brachii, the anode ~10 cm proximal to the olecranon process of the ulna and the cathode ~10 cm distal to the axilla. The current intensity (80–160 mA) was increased until no additional twitch force was generated and then increased by 15% to ensure supramaximal stimulation. Three consecutive twitches were elicited, each separated by 1 s, to ensure maximal twitch torques were generated. Next, three brief (~5 s) isometric elbow extension MVCs at 90° elbow flexion (0° = full extension), which represented the start point of the elbow extensor ROM, were performed with a supramaximal twitch stimulus delivered before the MVC: one during the plateau in torque during MVC (interpolated twitch), and one immediately following a return to baseline torque levels (post-MVC twitch). Subjects were asked to perform the MVCs “as fast as possible”, so that the torque development phase of the MVC was ballistic. Percent voluntary activation was calculated using the twitch interpolation technique formula: \[ 1 - \left( \frac{\text{interpolated twitch torque}}{\text{post-MVC twitch torque}} \right) \] × 100. Three minutes of rest were given between MVCs. The highest MVC value was used to establish isometric target torques and to determine the load (40% MVC) for all subsequent dynamic contractions.

Following MVCs, three pairs (1 per muscle investigated) of custom-made insulated stainless steel fine wire electrodes (100 μm, California Fine Wire, Grover Beach, CA) were each passed through separate 27.5-gauge hypodermic needle (Becton Dickinson, Franklin Lanes, NJ), and the needles were inserted into the muscle bellies of the anconeus and the lateral and long heads of the triceps brachii to record intramuscular EMG signals in a bipolar configuration. The insulation of the fine wires for this type of EMG recording was removed before insertion into the muscle by applying a flame to the tips of the wires so that ~5 mm in length of uninsulated recording area were exposed, allowing a more global recording to be obtained. The global intramuscular EMG recording resembles that of surface EMG, but provides a distinct advantage in that it minimizes the low-pass filtering effect of subcutaneous tissue and the existence of movement artifact as a consequence of the skin-electrode interface (21). The intramuscular electrode pairs (inter electrode distance of ~2 cm) were inserted in alignment with the muscle fascicles of the following: 1) the lateral head of the triceps brachii above the midshaft of the posterolateral humerus; 2) the long head of the triceps brachii midshaft above the posteriomedial humerus; and 3) the anconeus ~1-2 cm distal to the midpoint between the lateral epicondyle of the...
humerus and the olecranon process of the ulna. The corresponding
ground electrode for these recordings was positioned on the clavicle
just proximal to the acromion to record MU action potentials from
the corresponding MU.

Additional fine-wire electrodes, specifically designed for selectivity,
were inserted into the anconeus to record single MU action potential trains from this muscle. The tips of these fine-wire pairs were also exposed briefly to a flame, but were severed so that the length of exposed wire was minimal (<1 mm). Two pairs of hooked tip fine wires (15–30 cm length) were inserted into the belly of the anconeus. The tips of these fine-wire pairs were placed over the styloid process of the radius and secured with surgical tape.

With all electrode wires inserted, three to five loaded (40% MVC) maximal dynamic elbow extensions \(V_{\text{max40}}\) through 60° ROM (90° elbow flexion to 30° elbow flexion) were performed, during which subjects were encouraged verbally and provided torque and velocity feedback on a computer screen placed ~1 m in front of them. Following determination of MVC and \(V_{\text{max40}}\), a familiarization period was given in which subjects performed practice contractions at 60% of \(V_{\text{max40}}\), the target peak velocity selected for the FP. The 60% \(V_{\text{max40}}\) target peak velocity was chosen because, during pilot testing, it represented the highest peak velocity for which single MU action potentials could be recorded consistently during repetitive contractions at a load of 40% MVC. Subjects were instructed to target 60% \(V_{\text{max40}}\), ensuring that they did so while extending the elbow joint through the prescribed joint ROM (60°). The forearm support was returned automatically to the start point at a rate of 60°/s following each elbow extension, and subjects were asked to relax during this passive elbow flexion phase. Three sets of three contractions with at least 1-min rest between each set were repeated until the subjects, and the investigators, were confident the task could be performed accurately (within ±5% of target peak velocity). Following a 5-min rest period, subjects performed one isometric MVC and two consecutive loaded (40% MVC) maximal dynamic elbow extensions, separated by 3-min rest to be used for baseline measures.

**Submaximal dynamic FP.** A schematic depiction of the FP is presented in Fig. 1A. Following 30-s rest, subjects began the FP, which consisted of sets, each one composed of 10 submaximal dynamic contractions (40% MVC, 60% \(V_{\text{max40}}\)), followed by two maximal dynamic contractions (40% MVC, \(V_{\text{max40}}\)). Horizontal cursors were displayed on the monitor indicating \(V_{\text{max40}}\), the 60% \(V_{\text{max40}}\) target peak velocity, a maximum error margin, and a minimum error margin. The maxima and minima error margins were calculated as greater or lesser than 5% of the target peak velocity, respectively (10% error range). At the completion of each set, subjects began a subsequent set with the only rest provided during the return to starting position for each repetition. The FP sets were continued to task failure, which was defined as the point at which two consecutive elbow extensions failed to reach the minimum error margin. Irrespective of their position within a set, the final two contractions of the whole FP were performed at maximal dynamic effort. Immediately following task failure, the arm was returned to 90° elbow flexion, and subjects performed an isometric MVC sustained for ~3 s with no percutaneous electrical stimulation delivered.

High-pass filtered (10 Hz) intramuscular EMG of the anconeus, global intramuscular EMG of the anconeus, and lateral and long heads of the triceps brachii were preamplified (100–1,000X, Neurolog, Welwyn City, UK) and digitized with an analog-to-digital converter (Cambridge Electronics Design, Cambridge, UK) at a rate of 10 kHz. Torque, position, and velocity data were sampled at 100 Hz, and all data were stored offline for analysis. Offline, intramuscular and global intramuscular EMG signals were high-pass filtered at 100 Hz to remove any remaining movement artifact.

**Data analyses.** All offline data analyses were performed using custom software package (Spike 2, version 7.0, CED, Cambridge, UK). An average peak twitch torque, peak MVC torque, peak elbow extension velocity, and peak percentage of voluntary activation were determined for each subject from the baseline contractions preceding the FP, and a peak MVC torque was assessed from the post-FP MVC. Percent change between pre- and post-MVCs was calculated for each subject, and a group average was generated. For contractions comprising the FP, a peak elbow extension torque, velocity, and power were determined for each elbow extension in which a MU was recorded. Peak elbow extension velocity and peak power for each contraction were expressed relative to the highest peak velocity and power, respectively, recorded during the baseline \(V_{\text{max40}}\) elbow extensions. Peak torque of each contraction was normalized to the highest MVC recorded.

Average root mean square of the anconeus and lateral and long heads of the triceps brachii global intramuscular EMG (EMGANC, EMGLT, and EMGLH, respectively) was determined for each dynamic elbow extension in which a MU discharge rate was obtained. Average root mean square was calculated for a period of time beginning with the initial rise in EMG amplitude from baseline to peak elbow extension velocity because the cessation of the initial agonist burst in the triphasic EMG pattern, which is characteristic of fast single-joint movements, is related to peak contraction velocity (7). Each EMGANC, EMGLT, and EMGLH was first expressed relative to the highest \(E_{\text{max40}}\), the 60% \(V_{\text{max40}}\), and one for maximal \(V_{\text{max40}}\) elbow extensions, respectively. Percent changes from the relative baseline values of EMGANC, EMGLT, and EMGLH were then calculated for each subsequent contraction.

Single MU analysis was performed with a template matching algorithm (Spike 2 version 7.0, CED, Cambridge, UK) that identified single MU action potentials using waveform shape by overlaying sequential action potentials with respect to temporal and spatial characteristics. The ultimate determinant of whether a MU action potential belonged within a MU train was made by visual inspection by an experienced investigator. Single MU action potentials were identified for baseline contractions, post-FP isometric MVCs, and for the dynamic elbow extensions comprising the FP. The criteria for inclusion in the statistical analysis required that MUs 1) fired at least five consecutive action potentials; 2) fired continuously following MU recruitment threshold (no interspike intervals >150 ms); and, for dynamic contractions, were 3) active during both the initiation phase (torque development) and movement phase of each dynamic elbow extension, and 4) present during at least two-thirds of the FP. MU discharge times \((s)\) were determined for each MU action potential, and MU discharge rates were calculated as the number of MU action potentials fired per second for each contraction. Short interspike intervals (<10 ms) usually recorded at recruitment were removed from the analysis. Absolute MU discharge rates of the anconeus were determined for the torque development (ballistic isometric) phase (MU recruitment threshold to attainment of MVC torque) of baseline and post-FP MVCs and for baseline \(V_{\text{max40}}\) contractions. MU discharge rates of the dynamic contractions comprising the FP were expressed relative to the maximal MU discharge rate recorded during the baseline \(V_{\text{max40}}\) elbow extensions (% \(V_{\text{max40}}\)). The relative torque at which a MU fired its first action potential was considered the MU recruitment threshold and was expressed relative to the MVC of the subject from whom the MU was recorded (V%MVC). Descriptive statistics were calculated for all dependent variables. A paired Student’s t-test was used to determine whether MVC torque changed in response to the FP.

Within each subject, two average values for each set were determined for dependent variables: one for submaximal (60% \(V_{\text{max40}}\)), and one for maximal \(V_{\text{max40}}\) elbow extensions. Given that the number of sets completed before task failure varied among subjects, average values (submaximal and maximal) each were associated with the percentage of TTF at which they were recorded. For example, a
Fig. 1. Schematic diagram of protocol and representative data. A: velocity and torque profiles of baseline measures, fatiguing protocols (FP), and post-FP contractions. Vertical dashed lines separate each phase of the protocol. The top horizontal dashed lines in both traces indicate the target torque and velocity, and the bottom dashed lines represent the approximate torque and velocity at task failure. B: representative intramuscular electromyography (EMG) (top), single motor unit (MU) action potentials (MUAPs; middle), and relative velocity (bottom) for submaximal and maximal dynamic contractions at <25% of time to task failure (TTF; left) and ≥75% of TTF (right). C: overlays of the 12 single MUs tracked in the present study. The subject (SUB) from whom each MU was recorded is indicated above each overlay, along with the number of individual MU action potentials contributing to each overlay. $V_{\text{max}40}$, maximal peak velocity with a 40% maximal voluntary torque load; MVC, maximal voluntary isometric contraction; S, submaximal contraction; M, maximal contraction; N, number.
subject completing three sets before task failure contributed one submaximal average and one maximal average at 33, 66, and 99% TTF for each dependent variable, whereas a subject completing 10 sets before task failure contributed a total of 10 submaximal and 10 maximal averages for each dependent variable, corresponding to every 10% interval of TTF. Average values for each dependent variable were stratified according to four TTF ranges (<25, 25 to <50, 50 to <75, and ≥75% TTF). The result of stratification was 8, 14, 17, and 22 points for both submaximal and maximal groups of each dependent variable in the <25, 25 to <50, 50 to <75, and ≥75% TTF ranges, respectively.

Using SPSS 17.0 (IBM, Armonk, NY), Kolmogorov-Smirnov tests of normality verified that all measures, with the exception of MU recruitment threshold of \( V_{\text{max}40} \) contractions, exhibited a normal distribution following standardization to TTF (\( P > 0.05, D = 0.06–0.10 \)). MU recruitment thresholds of \( V_{\text{max}40} \) contractions (\%maximum) displayed a nonnormal distribution (\( P < 0.05, D = 0.16 \)). Therefore, one-factor (%TTF) ANOVAs were performed for submaximal and maximal MU discharge rate values separately for the percent changes in the dependent variables of EMG\(_{\text{ANC}}\), EMG\(_{\text{LT}}\), and EMG\(_{\text{LH}}\); relative peak elbow extension torque, velocity, and power; and relative anconeus MU recruitment threshold (%maximum) of submaximal velocity contractions and MU discharge rate (\%\( V_{\text{max}40} \)) of both submaximal and \( V_{\text{max}40} \) contractions. MU recruitment thresholds of \( V_{\text{max}40} \) contractions were ranked and evaluated using a Kruskal-Wallis test for nonparametric data.

Levine’s test for equality of variances determined that four of these dependent variables (MU recruitment threshold, MU discharge rate, and peak elbow extension torque and power) were homoscedastic (\( P > 0.05 \)) following standardization to TTF. Accordingly, Tukey’s honestly significant difference post hoc comparisons were used to examine differences between the four TTF ranges when a main effect was observed. Games-Howell post hoc comparisons were used for the remaining four dependent variables (relative peak elbow extension velocity and percent change in EMG\(_{\text{ANC}}\), EMG\(_{\text{LT}}\), and EMG\(_{\text{LH}}\)) due to the heteroscedasticity of these measures. Paired \( t \)-tests were used to compare maximal and submaximal MU discharge rates and MU recruitment thresholds at each %TTF range. Effect sizes were calculated (28) and expressed as Hedge’s \( g \) effect size metric (\( g \)) for group data exhibiting equal variance and Glass’s \( \Delta (\Delta) \) for data exhibiting unequal variance. An \( \alpha \)-level of \( P \leq 0.05 \) was set for all statistical procedures, and all values in the text and Figs. 2 and 3 are means ± SDs.

**RESULTS**

MU properties and global intramuscular EMG of the anconeus and lateral and long heads of the triceps brachii were tracked in seven subjects throughout baseline and post-FP isometric MVCs, baseline \( V_{\text{max}40} \) elbow extensions, and during sets composed of 10 submaximal fatiguing (60% \( V_{\text{max}40} \)) and two maximal dynamic elbow extensions to task failure. Representative data of a MU recorded during maximal and submaximal dynamic contractions at <25% TTF and ≥75% TTF are provided in Fig. 1B. Anthropometric, baseline, and fatigue characteristics are summarized in Table 1. Twelve MUs (1–2 per subject) satisfied the strict inclusion criteria (see Data analyses) and were included in the statistical analysis (Fig. 1C).

The FP did not affect the peak elbow extension torque (\( P = 0.96 \)) or power (\( P = 0.90 \)) of the submaximal dynamic contractions. A main effect of %TTF was determined for peak velocity of submaximal dynamic contractions (\( P < 0.05 \)), but post hoc comparisons did not reveal any differences between the four TTF ranges (Fig. 2A). In comparison, main effects for peak torque (\( P < 0.05 \)), velocity (\( P < 0.05 \)), and power (\( P < 0.05 \)) of the maximal dynamic elbow extensions occurred in response to the FP (Fig. 2B). Both velocity and power were lower for the 50–<75% TTF (18 and 30%, respectively) and ≥75% TTF (44 and 55%, respectively) ranges compared with the <25% TTF range (\( P < 0.05 \), Fig. 2B). Post hoc comparisons also revealed a difference between ≥75% TTF and <25% TTF for torque (\( P < 0.05 \)) of maximal dynamic elbow extensions, and the average isometric MVC torque following the FP decreased ~35% (\( P < 0.05 \)).

Analyses of variance for submaximal dynamic contractions revealed main effects of relative TTF (%TTF) for percent change in EMG\(_{\text{ANC}}\) (\( P < 0.05 \)) and EMG\(_{\text{LT}}\) (\( P < 0.05 \)), and a trend for an effect of %TTF for percent change in EMG\(_{\text{LH}}\) (\( P = 0.06 \)). Post hoc analyses demonstrated increases of 64, 45, and 55% at ≥75% TTF compared with <25% TTF for EMG\(_{\text{ANC}}\), EMG\(_{\text{LT}}\), and EMG\(_{\text{LH}}\), respectively (\( P < 0.05 \)) for submaximal dynamic elbow extensions. Whereas, for maximal dynamic elbow extensions, main effects of %TTF were observed for EMG\(_{\text{ANC}}\) (\( P < 0.05 \)) and EMG\(_{\text{LT}}\) (\( P < 0.05 \)), but not EMG\(_{\text{LH}}\) (\( P = 0.57 \)). Relative EMG was 34 and 44% greater at ≥75% TTF compared with <25% TTF in the anconeus and lateral head of the triceps brachii, respectively (\( P < 0.05 \)), for maximal dynamic contractions.

The maximal average MU discharge rate recorded during \( V_{\text{max}40} \) contractions (39.6 ± 5.8 Hz, Table 1) was greater compared with MU discharge rates recorded during the ballistic isometric phase of baseline MVCs (33.3 ± 6.1 Hz) (\( P < 0.05, g = 1.03 \)) and post-FP MVC (26.8 ± 5.2 Hz) (\( P < 0.05, g = 1.03 \)). The average absolute MU discharge rate and

### Table 1. Subject, anthropometric, baseline, and fatigue characteristics

<table>
<thead>
<tr>
<th>Subject</th>
<th>Subject 2</th>
<th>Subject 3</th>
<th>Subject 4</th>
<th>Subject 5</th>
<th>Subject 6</th>
<th>Subject 7</th>
<th>Average ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age, yr</td>
<td>25</td>
<td>26</td>
<td>23</td>
<td>23</td>
<td>23</td>
<td>23</td>
<td>23.7 ± 1.3</td>
</tr>
<tr>
<td>Height, cm</td>
<td>183.0</td>
<td>177.0</td>
<td>180.0</td>
<td>180.0</td>
<td>183.0</td>
<td>178.5</td>
<td>175.0</td>
</tr>
<tr>
<td>Weight, kg</td>
<td>83.2</td>
<td>77.0</td>
<td>90.0</td>
<td>78.0</td>
<td>89.0</td>
<td>76.1</td>
<td>56.0</td>
</tr>
<tr>
<td>VA, %</td>
<td>93.5</td>
<td>100.0</td>
<td>94.6</td>
<td>94.9</td>
<td>95.5</td>
<td>100.0</td>
<td>96.8</td>
</tr>
<tr>
<td>mMVC, Nm</td>
<td>89.4</td>
<td>101.3</td>
<td>117.8</td>
<td>109.6</td>
<td>81.4</td>
<td>71.3</td>
<td>48.2</td>
</tr>
<tr>
<td>( V_{\text{max}40} ), /s</td>
<td>223.0</td>
<td>297.4</td>
<td>297.5</td>
<td>251.4</td>
<td>247.3</td>
<td>247.8</td>
<td>241.9</td>
</tr>
<tr>
<td>mPower, W</td>
<td>244.2</td>
<td>322.6</td>
<td>305.8</td>
<td>310.1</td>
<td>244.2</td>
<td>242.3</td>
<td>234.3</td>
</tr>
<tr>
<td>STF, no</td>
<td>3</td>
<td>4</td>
<td>5</td>
<td>10</td>
<td>5</td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td>TFF, s</td>
<td>76.0</td>
<td>115.5</td>
<td>117.7</td>
<td>258.7</td>
<td>136.3</td>
<td>162.1</td>
<td>187.6</td>
</tr>
<tr>
<td>( V_{\text{max}40} ) mMUDR, Hz</td>
<td>34.3</td>
<td>37.5</td>
<td>45.1</td>
<td>51.5</td>
<td>40.5</td>
<td>37.5</td>
<td>34.3</td>
</tr>
</tbody>
</table>

VA, voluntary activation; m, maximal; MVC, maximal voluntary isometric torque; \( V_{\text{max}40} \), maximal velocity-dependent elbow extension; STF, sets to task failure; TFF, time to task failure; MUDR, motor unit discharge rate.
relative MU recruitment thresholds (%MVC) at each %TTF range are summarized in Table 2. Univariate ANOVAs of maximal dynamic elbow extensions showed a main effect of %TTF for MU discharge rate ($P < 0.05$), but the Kruskal-Wallis test did not show an effect for MU recruitment threshold ($P > 0.14$, Fig. 3). Post hoc comparison of MU discharge rates for maximal dynamic elbow extensions revealed an approximate 20% reduction in MU discharge rates at both 50 to 75% TTF (30.7 ± 6.1 Hz) and ≥75% TTF (30.5 ± 7.9 Hz) compared with <25% TTF ($P < 0.05$, Fig. 3B, Table 2). In comparison, there was a main effect of %TTF for MU recruitment thresholds ($P < 0.05$, Fig. 3A), but not for MU discharge rates ($P = 0.36$, Fig. 3B) for submaximal dynamic elbow

Table 2. Motor unit discharge rates and recruitment thresholds of the anconeus relative to time to task failure

<table>
<thead>
<tr>
<th>Time to Task Failure</th>
<th>Average MUDR, Hz</th>
<th>Average MURT, %MVC</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;25%</td>
<td>38.8 ± 5.9</td>
<td>8.2 ± 9.4</td>
</tr>
<tr>
<td>25 to &lt;50%</td>
<td>32.1 ± 7.5</td>
<td>14.5 ± 14.3</td>
</tr>
<tr>
<td>50 to &lt;75%</td>
<td>30.7 ± 6.1*</td>
<td>9.8 ± 11.2</td>
</tr>
<tr>
<td>≥75%</td>
<td>30.5 ± 7.9*</td>
<td>9.9 ± 11.1</td>
</tr>
</tbody>
</table>

Values are means ± SD of average MUDRs and motor unit recruitment thresholds (MURT) from the 12 motor units recorded corresponding to the TTF range in which they were recorded. *Significantly different from <25% of TTF, $P < 0.05$. 
extensions. Post hoc comparison revealed a 52% reduction in MU recruitment threshold at ≥75% TTF compared with <25% TTF (P < 0.05, Fig. 3A, Table 2) for submaximal dynamic elbow extensions. Differences were also observed for MU discharge rates between maximal and submaximal dynamic contractions at the <25 and 25 to <50% TTF ranges (P < 0.05, g = 1.67 and 0.98, respectively).

**DISCUSSION**

The present study has demonstrated that, in response to submaximal dynamic fatiguing contractions, anconeus MU discharge rates of maximal dynamic elbow extensions declined, and that MU recruitment thresholds were unchanged as a function of %TTF. However, for the submaximal dynamic target contractions, MU recruitment thresholds decreased at ≥75% TTF, but MU discharge rates did not change relative to %TTF. These findings emphasize the central role that task occupies both in the manifestation of fatigability and in the evaluation of MU property changes related to fatigability. A unique aspect of the present study to support these results was the effective recording of single MU action potentials and the subsequent determination of fatigability-associated MU property changes during fast dynamic contractions to task failure and the response of these same MUs to isometric contractions. Attainment of suitable MU recordings under these challenging conditions in the anconeus support the concept that MU discharge rates represent an important neural determinant limiting maximal contraction velocity during dynamic contractions and thus likely affect power production.

**MU discharge rates.** Average unfatigued maximal dynamic MU discharge rates of the anconeus in the present study were similar to those previously reported in our laboratory (43) (Table 1). For submaximal dynamic elbow extensions, MU discharge rates were unchanged through all time points leading to task failure (Fig. 3A). These results are similar to observations from prior studies of the elbow extensors (41, 57) during relatively slower, lightly loaded, submaximal dynamic contractions. Here we are able to report that MU discharge rates of maximal dynamic elbow extensions are reduced with fatigability by ~20% for the last half of the FP (Fig. 3B). These reductions in MU discharge rate, which resemble reductions in motoneuron excitability during a submaximal fatiguing contraction (55), are somewhat similar (~30%) to studies of submaximal isometric fatiguing contractions at comparable loads (50% MVC) to that used in this study (40% MVC) (9, 70). Thus, despite differences in the fatiguing task (isometric vs. dynamic), a similar response of maximal MU discharge rates provides support for common underlying factors affecting the response of anconeus MU output to maximal fatiguing isometric and dynamic contractions.

In the present study, velocity and power were reduced (~45 and ~55%, respectively) in the final 25% of the FP (Fig. 2B). However, MU discharge rates did not decline further after the 50 to <75% TTF range (Fig. 3B). The reductions in velocity (~20%) and power (~30%) at the 50 to <75% TTF range were very similar to those observed for MU discharge rates in the same range (~20%, Fig. 3B), to the ballistic isometric phase of the post-FP MVC (~20%, Table 1), and to sustained isometric MVCs of the elbow and knee extensors (~30%) in prior studies of fatigability (9, 70). Therefore, it seems the relative decline in MU discharge rates is comparable across contraction types and is not influenced by absolute rate differences between isometric and shortening contractions commonly reported (27) and observed in the present study.

The average discharge rate of anconeus MUs in the present study for baseline V_{max>40} elbow extensions was 39.6 ± 5.8 Hz (Table 1). At 50 to <75% TTF, anconeus MU discharge rates for maximal dynamic elbow extensions declined to 30.7 ± 6.1 Hz (P < 0.05) (Table 2), which did not differ from the pre-FP (33.3 ± 6.1 Hz) or post-FP (26.8 ± 5.2 Hz) ballistic isometric MU discharge rates (P = 0.30 and P = 0.14, respectively). However, MU discharge rates pre- and post-FP for both maximal dynamic and ballistic isometric contractions were higher (P < 0.05) than those recorded in the absence of fatigability in one earlier study of the anconeus at sustained maximal isometric torques (23.8 ± 7.7 Hz) (43). These comparisons may indicate that, although maximal MU discharge rates declined following submaximal fatigability, they remained sufficiently high to generate and sustain an isometric MVC torque. Furthermore, these observations in the anconeus highlight the importance of maintaining relatively high MU discharge rates for the production of fast dynamic contractions and that mechanisms are modified differently depending on the task.

The lack of additional declines in anconeus MU discharge rates beyond 50% TTF is potentially the result of the resistant nature of this muscle model to fatigability, as indicated by its twitch contractile properties and fiber composition (51). However, a number of additional factors may explain the disproportionate changes between velocity and power, and MU discharge rates of the anconeus as fatigability progressed. Reductions in activating calcium concentrations and cross-bridge kinetics of skeletal muscle related to fatigability (for review, see Refs. 35, 50) are potent modulators of muscle fiber power and velocity. These peripheral factors likely affect both maximal isometric torque and loaded shortening velocity in the elbow extensor model, as demonstrated by reductions in both of these parameters, despite near maximal voluntary activation (92.3 ± 8.8%), as assessed by 50-Hz tetanus delivered at MVC torque (17). Thus, depending on the task, a minimal threshold of MU discharge rate reductions is preserved, despite continuing declines in contractile function.

An additional consideration is that the anconeus is a relatively small contributor to the resultant elbow extension torque (<15%) (75). Despite being active throughout the entire joint ROM (43, 75) and at all elbow extension torques (14, 51, 53) and velocities (43, 52), the possibility exists that neuromuscular changes related to fatigability occur at different amplitudes and rates in the three heads of the triceps brachii compared with the anconeus. This muscle-dependent response to a FP is likely due to differences in muscle fiber-type composition and twitch contractile properties (51), joint angle-dependent mechanical advantages (21, 74), or torque- and velocity-related differences in contribution to the resultant mechanical output (52, 53, 74, 75). Global intramuscular EMG of the elbow extensors in the present study, and one earlier study of sustained isometric fatiguing contractions (21), supports muscle-specific differential responses to fatigability. However, the interpretation of these data is limited, due to changes in MU action potential waveform characteristics related to fatigability, which can alter the global EMG amplitude, independent of mechanical output (25, 26). With these considerations, MU
discharge rates of the anconae for maximal dynamic and ballistic isometric elbow extensions both declined ~20% in response to the FP, demonstrating that isometric and dynamic contractions share common features with respect to MU discharge behavior for maximal contractions. However, differences in the absolute MU discharge rates with torque or velocity loss indicate a task-specific disparity in the relationship between anconae MU discharge rates and task failure as a consequence of submaximal dynamic fatiguing contractions.

**MU recruitment thresholds.** Declines in MU recruitment thresholds related to fatigability were observed for submaximal but not for maximal dynamic contractions. That MU recruitment thresholds of maximal dynamic contractions did not change as a function of %TTF (Fig. 3A) is contrary to our original hypothesis, but is reasonable in view of the results because, to produce maximal dynamic elbow extensions, it seems the anconae may have been operating above the upper limit of its MU recruitment range (43, 52, 53). Recruitment thresholds of MUs for submaximal dynamic contractions were reduced 52% at \( \geq 75\% \) TTF, which corresponded with higher global EMG amplitudes (45–64%) in the three elbow extensors studied. Increases in EMG amplitude are commonly reported in response to fatiguing repeated or sustained submaximal contractions and are often attributed to increases in MU recruitment, but not without limitations of interpretation (26).

Although MU recruitment thresholds have been shown to decrease in response to repeated contractions in the absence of fatigability (40), a more probable explanation for the decline in MU recruitment threshold in relation to increasing %TTF is that recruitment of higher threshold MUs occurred at progressively lower relative torques in response to the FP, resulting in a compression of the MU recruitment threshold range. Maintenance of orderly recruitment is preserved in the production of most dynamic contractions studied to date (42, 67, 71), but Harwood and Rice (45) have shown that a compression of anconae MU recruitment thresholds is related to an increase in peak elbow extension velocity in nonfatiguing contractions. Similar recruitment threshold reductions, largely in higher threshold MUs, during submaximal fatiguing intermittent isometric contractions in the first dorsal interosseus have also been demonstrated (14). This effect provides an advantage for the production of greater rates of torque development (24, 45, 73), peak velocities (45), and peak power (45), because higher threshold MUs, which have higher peak twitch tensions and shorter time to peak tensions (58, 65), require higher excitation rates for maximal summation of twitch tensions (8). For example, a shift to lower MU recruitment thresholds following a 12-wk dynamic training program corresponded to an 82% increase in rate of tension development (24, 45, 73), peak velocities (45), and peak power (45), because higher threshold MUs, which have higher peak twitch tensions and shorter time to peak tensions (58, 65), require higher excitation rates for maximal summation of twitch tensions (8). For any change in anconae MU discharge rates offer evidence in support of MU recruitment threshold range compression for the maintenance of contraction velocity and muscle power in response to the FP. Similar relative MU discharge responses of maximal contractions to submaximal dynamic fatigability in the present study, and to submaximal isometric fatigability in previous studies (9, 70), indicate that a common underlying neural mechanism regulates both contraction types with neuromuscular fatigue. This concept is further supported by similar MU discharge rate reductions with submaximal dynamic fatigability, regardless of the contraction type (maximal dynamic vs. ballistic isometric) used to quantify changes at task failure. However, the disparity between absolute MU discharge rates of different contraction types [maximal dynamic, ballistic isometric, and sustained MVC (43)] before and after the FP stresses the role of high discharge rates of anconae MUs for the production of fast dynamic contractions.

**GRANTS**

This research was supported by the Natural Sciences and Engineering Research Council of Canada.

**DISCLOSURES**

No conflicts of interest, financial or otherwise, are declared by the author(s).

**AUTHOR CONTRIBUTIONS**

Author contributions: B.H. conception and design of research; B.H. and I.H.C. performed experiments; B.H. and I.H.C. analyzed data; B.H. and C.L.R. interpreted results of experiments; B.H. prepared figures; B.H. and C.L.R. drafted manuscript; B.H. and C.L.R. edited and revised manuscript; B.H., I.H.C., and C.L.R. approved final version of manuscript.

**REFERENCES**


59. Harwood B et al. Submaximal Fatigue Reduces Discharge Rates and Velocity • Harwood B et al. 1829


