



The effect of rate of torque development on motor unit recruitment and firing rates during isometric voluntary trapezoidal contractions

Jonathan D. Miller¹ · C. J. Lund¹ · Marissa D. Gingrich¹ · Kyle L. Schtul¹ · Mandy E. Wray¹ · Trent J. Herda¹

Received: 4 February 2019 / Accepted: 20 July 2019 / Published online: 8 August 2019
© Springer-Verlag GmbH Germany, part of Springer Nature 2019

Abstract

It is common practice to examine motor unit (MU) activity according to mean firing rate (MFR) and action potential amplitude (MUAP_{AMP}) vs. recruitment threshold (RT) relationships during isometric trapezoidal contractions. However, it is unknown whether the rate of torque development during the linearly increasing torque phase affects the activity of MUs during such contractions. Sixteen healthy males and females performed two isometric trapezoidal muscle actions at 40% of maximum voluntary contraction (MVC), one at a rate of torque development of 5% MVC/s (SLOW₄₀) and one at 20% MVC/s (FAST₄₀) during the linearly increasing torque phase. Surface electromyography (EMG) was recorded from the vastus lateralis (VL) via a 5-pin surface array sensor and decomposed into action potential trains of individual MUs, yielding MFRs and MUAP_{AMP} which were regressed against RT separately for each contraction. Surface EMG amplitude recorded from leg extensors and flexors was used to quantify muscle activation and coactivation. MFR vs. RT relationship slopes were more negative ($P=0.003$) for the SLOW₄₀ (-0.491 ± 0.101 pps/%MVC) than FAST₄₀ (-0.322 ± 0.109 pps/%MVC) and the slopes of the MUAP_{AMP} vs. RT relationships ($P=0.022$, SLOW₄₀ = 0.0057 ± 0.0021 mV/%MVC, FAST₄₀ = 0.0041 ± 0.0023 mV/%MVC) and muscle activation of the extensors ($P < 0.001$, SLOW₄₀ = $36.3 \pm 7.82\%$, FAST₄₀ = $34.0 \pm 6.26\%$) were greater for SLOW₄₀ than FAST₄₀. MU firing rates were lower and action potential amplitudes were larger in relation to recruitment thresholds for a contraction performed at a slower rate compared to a faster rate of isometric torque development. Differences in MU activity can exist as a function of rate of torque development during commonly performed isometric trapezoidal contractions.

Keywords Rate of torque development · Motor unit decomposition · Vastus lateralis · Recruitment · Firing rate

Introduction

The Onion-Skin scheme of motor unit (MU) control describes the organization of MU recruitment with regard to firing rate activity during submaximal isometric voluntary contractions in humans (De Luca and Erim 1994; Masakado et al. 1995; De Luca and Hostage 2010; De Luca

and Contessa 2012, 2015), where earlier recruited lower-threshold MUs maintain greater firing rates than later recruited higher-threshold MUs regardless of force and time. In addition, action potential amplitudes are correlated with the diameter of muscle fibers within a MU (Hakansson 1956) and, therefore, the size principle (Henneman 1957) can be observed by regressing action potential amplitudes against recruitment thresholds (Milner-Brown and Stein 1975; Goldberg and Derfler 1977; Masakado et al. 1994; Conwit et al. 1999; Hu et al. 2013a; Pope et al. 2016; Sterczala et al. 2018b; Martinez-Valdes et al. 2018; Miller et al. 2018). The Onion-Skin scheme and the size principle as measured with the MU action potential amplitudes regressed against recruitment thresholds (Hu et al. 2013a; Sterczala et al. 2018b) are most apparent when MU activity is characterized on a subject-by-subject and contraction-by-contraction basis. As a result, it is common practice to examine potential differences in MU activity as a function of contraction intensity (De Luca and Contessa 2012; Hu et al.

New and Noteworthy: It is common practice to characterize motor unit activity during submaximal isometric trapezoidal contractions, however, it is unknown whether the rate of torque development during such contractions influences motor unit activity. The current study revealed larger action potential amplitudes and decreased firing rates in relation to recruitment thresholds for contractions performed with a slower compared to a faster rate of torque development, suggesting motor unit activity is altered by rate of torque development.

✉ Trent J. Herda
t.herda@ku.edu

Extended author information available on the last page of the article

2013a), fatigue (Adam and De Luca 2005; Contessa et al. 2016), exercise interventions (Stock et al. 2012; Pope et al. 2016), coactivation (Contessa et al. 2018), and contractile properties of the muscle (Trevino et al. 2016; Colquhoun et al. 2018a) by comparing the MU firing rate and action potential amplitude vs. recruitment threshold relationships.

Many studies analyzing individual MU activity in humans use isometric trapezoidal contractions with a linearly increasing torque (ramp-up) phase preceding a constant torque phase where a submaximal torque level relative to maximum voluntary contraction (MVC) is maintained followed by a linearly decreasing torque (ramp-down) phase where torque is returned to baseline (De Luca and Hostage 2010; Stock et al. 2012; Hu et al. 2013a; Trevino et al. 2016; Del Vecchio et al. 2018; Martinez-Valdes et al. 2018). It is also common amongst such researchers to use contraction intensities of 40% MVC (Vander Linden et al. 1991; Hu et al. 2013a; Herda et al. 2015; Trevino et al. 2016; Sterczala et al. 2018b) and analyze motor units from the vastus lateralis (Adam and De Luca 2005; De Luca and Contessa 2012; Stock et al. 2012; Contessa et al. 2016; Colquhoun et al. 2018b). Thus, these methods were also used in the current study. However, very little is known about the effect of the rate of torque development during the linearly increasing torque phase on the activity of MUs, in terms of recruitment, firing patterns, and coactivation during such contractions. Although 10% MVC/s is a common rate of force/torque development used in studies of motor unit activity, various rates of torque development have been used to achieve different contraction intensities (De Luca and Contessa 2012; Stock et al. 2012; Trevino et al. 2016) including 5% MVC/s (Vander Linden et al. 1991; Klein et al. 2001; Del Vecchio et al. 2019) and 20% MVC/s (Seki et al. 1991; Masakado et al. 1995). For the current study, the rates of torque development examined were 5% and 20% MVC/s to ensure the differences in rate of torque development were sufficient to observe any potential differences in motor unit activity.

De Luca and Contessa (2012) performed isometric contractions of the first dorsal interosseous and the vastus lateralis (VL) with three different rates of linearly increasing force development of 2%, 4%, and 10% MVC/s to achieve different contraction intensities of 100%, 80%, and 50% MVC, respectively. The authors reported greater firing rates in relation to recruitment threshold for the higher intensity contraction that was performed at a faster rate of force development. Greater excitation required to achieve higher intensity contractions will result in greater MU firing rates (Farina et al. 2010). However, there could also be changes in firing rates in relation to recruitment thresholds as a function of altered recruitment strategies during different rates of force development. Desmedt and Godaux (1977) reported that MUs of the tibialis anterior were recruited at progressively lower forces with increase in rates of force

development during ankle dorsiflexion ballistic contractions with no differences observed during slower rates of isometric force development. However, the target force was set at an absolute 12 kg for each subject and few MUs were recorded per contraction, which did not allow for a systematic examination of MU recruitment and firing rate patterns as can be performed with relationship-based analyses. In contrast, Masakado et al. (1995) observed non-significant differences in recruitment and firing rate patterns between different slower rates of force development (10% MVC/s vs. 20% MVC/s) for the first dorsal interosseous. However, similar to Desmedt and Godaux (1977), a thorough examination of MU activity on a contraction-by-contraction basis could not be performed as few MUs were recorded. Therefore, it remains unclear if MU recruitment and firing rate patterns differ between different slower rates of force development. While some studies have investigated altered motor unit activity (Desmedt and Godaux 1977; Masakado et al. 1995; De Luca and Contessa 2012) or muscle activation (Tomko et al. 2018) during contractions at different rates of torque development, limitations in their methodologies inhibit the generalizability of their findings to current methods of collecting and analyzing MU activity during voluntary contractions. To our knowledge, no study has compared MU activity across slower rates of torque development at the same relative submaximal force levels while using high-yield decomposition techniques that allow for MU activity to be analyzed on a subject-by-subject and contraction-by-contraction basis to avoid biases of recruitment thresholds and inter-individual variability (De Luca and Hostage 2010; De Luca and Contessa 2012).

Currently, interpretations of motor unit activity are made without respect for the influence of the rate of torque development on the findings. If MU activity is significantly affected by the rate of torque development, (1) the findings of such studies may not be generalizable to all rates of torque development, (2) additional care may be needed to ensure compliance with torque trajectories during ramp phases, and (3) it is possible that relationships observed between MU properties and contractile properties of the muscle may be better elucidated at other rates of torque development. Therefore, the examination of MU activity during different rates of torque development via firing rate and action potential amplitude vs. recruitment threshold relationships and EMG amplitude is warranted. We have examined mean firing rate and MU action potential amplitude vs. recruitment threshold and mean firing rate vs. MU action potential amplitude relationships of the VL between two 40% MVC leg extensions which only differed with respect to the rate of torque development (5% MVC/s vs. 20% MVC/s) during the linearly increasing torque phase. In addition, muscle activation (EMG) of the leg extensors [VL, vastus medialis (VM) and rectus femoris (RF)] and flexors [semitendinosus (ST)

and biceps femoris (BF)] was measured to examine potential differences in coactivation that may have altered MU activity of the VL (Contessa et al. 2018) between the contractions with different rates of torque development.

Methods

Subjects

Ten healthy males (age = 21.1 ± 2.1 years, stature = 170.4 ± 24.8 cm, mass = 82.4 ± 32.4 kg) and six healthy females (age = 19.6 ± 1.2 years, stature = 167.8 ± 5.7 cm, mass = 63.8 ± 9.9 kg) participated in this study. Exclusion criteria included any previous or current neuromuscular diseases or musculoskeletal injuries to the ankle, knee or hip joints.

Compliance with ethical standards

The authors declare that they have no conflict of interest. The institutional review board for human subjects research at The University of Kansas approved this study and it was conducted in accordance with the Declaration of Helsinki. All subjects read and signed an informed consent form and completed a pre-exercise health status questionnaire.

Isometric testing

The participants visited the laboratory two times separated by at least 24 h. The first visit was a familiarization trial followed by an experimental trial. During the first visit, the participants completed 4 practice MVCs (2 extension and 2 flexion) and 6–10 practice submaximal trapezoidal contractions depending on how quickly they were able to learn the task. The subject's torque output from each practice trial was visually inspected for accuracy with the torque trajectory. Subjects were determined to be properly familiarized when they were able to comply closely with the given torque trajectory.

For isometric testing, each participant was seated with restraining straps over the pelvis, trunk, and contralateral thigh, and the lateral condyle of the femur was aligned with the input axis of the Biodex System 3 isokinetic dynamometer (Biodex Medical Systems, Shirley, NY) in accordance with the Biodex User's Guide (Biodex Pro Manual, Applications/Operations, 1998). All isometric leg extensor strength assessments were performed on the right leg at a flexion of 90° . Isometric strength was measured using the torque signal from the isokinetic dynamometer. A brief warm up consisting of 6 isometric leg extensions between 30 and 90% of perceived MVC was performed prior to the experimental protocol. During the experimental trials, participants

performed two isometric knee extension MVCs and two isometric knee flexion MVCs. Strong verbal encouragement was provided for motivation during each MVC trial. Subjects were asked to give full effort during each of the MVCs. Also, for each MVC, a countdown was given, and the word "push" was spoken at a relatively high frequency and at a volume slightly greater than normal conversational volume for the duration of the MVC. Following the MVCs, subjects completed two submaximal isometric trapezoidal knee extensions at 40% MVC. The highest torque output averaged over a 0.25-s epoch for the MVCs determined the maximal torque output for each participant and the torque level for the 40% MVCs. The average CV between MVCs was 4.8% indicating that the MVC torque was very consistent between MVCs. The two 40% MVCs were completed with different rates of torque development during the linear increasing torque phase. One increased at 5% MVC/s (SLOW₄₀) and the other at 20% MVC/s (FAST₄₀) to the desired torque level, which was held constant for 12 s for a SLOW₄₀ or for 18 s for a FAST₄₀. Torque was decreased to baseline at a rate of 10% MVC/s for both 40% MVCs. Therefore, the duration of each 40% MVC was 24 s. Three minutes of rest were given prior to each MVC, and 5 min of rest were given prior to each 40% MVC. The order of the 40% MVCs with respect to their rate of torque development (SLOW₄₀ vs. FAST₄₀) was randomized for each subject. During the 40% MVCs, participants maintained their torque output as close as possible to the torque trajectory template displayed digitally on a computer monitor.

EMG recording

During the contractions, surface EMG signals were recorded from the vastus lateralis (VL) using a 5-pin surface array sensor (Delsys, Inc., Natick, Massachusetts). The diameter of each pin is 0.5 mm, and they are placed at the corners of a 5×5 -mm square, with the fifth pin in the center of the square. Bipolar surface electrodes (Delsys, Inc., Natick, Massachusetts) recorded EMG activity from the leg extensors (VL, RF, and VM) and flexors (ST and BF) during all contractions. Before sensor and reference electrode placement, the surface of the skin was prepared by shaving, removing superficial dead skin with adhesive tape, and sterilizing with an alcohol swab. To remove the dead layers of skin, hypoallergenic tape (3 M, St. Paul, Minnesota) was applied to the site, then peeled back to remove contaminants (Delsys, Inc., dEMG User Guide). The specific locations of the sensors were as follows: VL, 67% of the distance from the anterior superior iliac spine to the lateral border of the patella; VM, 80% of the distance from anterior superior iliac spine to the medial epicondyle of the femur; RF, 40% of the distance from anterior superior iliac spine to the superior border of the patella; ST, 50% of the distance from ischial

tuberosity to medial epicondyle of tibia; and BF, 50% of the distance from ischial tuberosity to lateral epicondyle of tibia. The sensors were secured in their locations by adhesive tape. The reference electrode was placed over the left patella (Horita and Ishiko 1987; Rattey et al. 2006; Jubeau et al. 2010; Trevino et al. 2016).

EMG decomposition

For the 40% MVCs, the surface array sensor action potentials were extracted into firing events of single MUs from the four separate EMG signals, sampled at 20 kHz, via the precision decomposition III algorithm (version 1.1.0) as described by De Luca et al. (2006). The precision decomposition III algorithm provides four unique action potential waveforms for each EMG channel. Initially, the accuracy of the decomposed firing instances was tested with the reconstruct-and-test procedure (Nawab et al. 2010). Only MUs decomposed with >90% accuracies were included in the analyses. In addition, a secondary spike trigger average (STA) procedure was included to validate the firing times and action potential waveforms generated via the precision decomposition III algorithm. The derived firing times from the precision decomposition III algorithm were used to perform a STA for the four raw EMG signals (Hu et al. 2013a, b, c; McManus et al. 2016). A MU was included in further analyses if there were high correlations ($r > 0.70$) across the four channels between the precision decomposition III algorithm (version 1.1.0) and STA-derived action potential waveforms and the coefficient of variation of the STA-derived peak-to-peak amplitudes across time was < 0.30 (Hu et al. 2013a). For each MU, recruitment threshold (RT), MU action potential amplitude ($MUAP_{AMP}$), and the mean firing rate (MFR) during the constant torque period were determined. A 2000 ms Hanning window was applied to the MU firing instances to “. $MUAP_{AMP}$ was calculated for each MU according to previous methods (Hu et al. 2013a; Pope et al. 2016; Miller et al. 2018; Sterczala et al. 2018a), as the average peak-to-peak amplitude values from each of the four unique action potential waveform templates using a custom-written software program (LabVIEW 2015, National Instruments, Austin, TX, USA). For the 40% MVCs, a linear model was fitted to the MFR vs RT relationships (De Luca et al. 1996; Herda et al. 2015; Miller et al. 2017a) and $MUAP_{AMP}$ vs. RT relationships (Hu et al. 2013a; Sterczala et al. 2018a) for each subject with the y -intercepts and slopes used for statistical analysis. The following exponential model (Sterczala et al. 2018a, b; Miller et al. 2018) was applied to the MFR vs. $MUAP_{AMP}$ relationships:

$$MFR = Ae^{B(MUAP_{AMP})}$$

where A is the theoretical MFR of a $MUAP_{AMP}$ of 0 mV, e is the natural constant and B is the decay coefficient of MFR

with increments in $MUAP_{AMP}$. Pearson product moment correlations were performed to test for significance. Any contractions without an observed recruitment range of MUs $> 12\%$ MVC, or with less than ten MUs accurately decomposed after the reconstruct-and-test and STA procedures were excluded from further analysis.

Signal processing

All 4 channels of the 5-pin EMG sensor, which was the only sensor that recorded EMG from the VL, are needed for decomposition. However, only channel 1 of the 4 channels was used for amplitude analysis to match the bipolar EMG recording sensors used for amplitude analysis of the VM, RF, BF, and ST. The torque (N m) and the EMG (mV) signals from channel 1 of the surface array sensor (VL) as well as the signal from each of the bipolar EMG electrodes recording from the RF, VM, ST, and BF were recorded with a NI cDAQ (National Instruments, Austin, TX USA) for each MVC and with a NI BNC 2090a (National Instruments, Austin, TX USA) for each 40% MVC. The sampling frequency for torque and EMG signals was 2000 Hz for the MVCs and 20,000 Hz for the 40% MVCs. Data were stored on a personal computer for subsequent analysis. The EMG signals were bandpass filtered (zero phase fourth-order Butterworth filter) at 10–500 Hz, while the torque signal was low-pass filtered with a 10-Hz cutoff (zero-phase fourth-order Butterworth filter). EMG amplitude was expressed as root mean square amplitude values calculated by custom-written software (LabVIEW v 15.0; National Instruments, Austin, TX). All EMG calculations were performed on the filtered signals. MVC torque and peak EMG amplitude of agonist muscles (VL, VM, and RF) were recorded during the highest 0.25 s average torque (N m) that occurred during the two extension MVCs, while peak EMG of antagonist muscles (ST and BF) was determined from the highest 0.25 s average torque during the two flexion MVCs. EMG amplitude values from the 40% MVCs were normalized (N-EMG) as a percentage of the peak EMG for further analysis. For the 40% MVCs, MFR, N-EMG, torque, and CV of torque were analyzed over a 10 s epoch at the beginning of the constant torque phase. The total duration of the contraction and the duration of the epoch of analysis were equated between SLOW₄₀ and FAST₄₀ contractions to minimize differences in the time-related changes in motor unit activity such as potentiation, firing rate adaptation, and fatigue (Dorfman et al. 1990; Adam and De Luca 2005; Potvin and Fugle-vand 2017; Miller et al. 2017b). MUs not active in the entire 10 s epoch were excluded from analysis. For analysis of N-EMG, the average N-EMG of the three extensor muscles (VL, VM, and RF) was considered extensor N-EMG and the average of the two flexor muscles (ST and BF) was considered flexor N-EMG. N-EMG amplitude at torque levels of

24–26% MVC during the linearly increasing torque phase was recorded during the SLOW₄₀ and FAST₄₀. This epoch around 25% MVC was selected to quantify N-EMG during the linearly increasing torque phase, as it is near the upper recruitment range of MUs that was observed for the SLOW₄₀ and is also within the recruitment range of the FAST₄₀.

Statistical analysis

Recording only MUs encompassing a small range of RTs could potentially lead to spurious coefficients from the regressions (Pope et al. 2016; Colquhoun et al. 2018b; Herda et al. 2019; Miller et al. 2019). Therefore, contractions were included in the analyses if they met both of the following criteria: 1) at least 10 MUs were identified and 2) the range of RTs of the MUs observed was greater than 12% MVC. Because of the repeated-measures design of the study, subjects who did not meet the inclusionary criteria for both contractions were not included in further analyses. Four subjects were eliminated, thus statistical analyses were completed on the remaining 12 subjects. Males and females were analyzed together as the primary interest was changes in MU activity as a function of different rates of torque development rather than previously reported sex-related differences in firing rates and action potential amplitudes (Tenan et al. 2013; Peng et al. 2018; Trevino et al. 2018). Following the reconstruct-and-test and STA validation procedures, 232 MUs did not meet the criteria and were not included in the analyses. Additionally, 13 MUs which were not active during the entire steady force were not included in the analyses.

Paired samples *t* tests were used to analyze possible differences between SLOW₄₀ and FAST₄₀ for the lowest and highest RT and MUAP_{AMP} of MUs observed in each 40% MVC, for torque and CV of torque during the constant torque period, and for root mean squared error (RMSE) between torque and the torque trajectory template. Paired samples *t* tests were also used to compare the coefficients of the MFR and MUAP_{AMP} vs. RT relationships and the MFR vs. MUAP_{AMP} relationships between SLOW₄₀ and FAST₄₀. Two separate two-way repeated-measures ANOVAs [rate of torque development (SLOW₄₀ vs. FAST₄₀) × muscle group (extensors vs. flexors)] were used to analyze potential differences in N-EMG between the agonists (extensors) and the coactivation of the antagonists (flexors) during the linear increasing torque and the constant torque phases. In addition, paired samples *t* tests were performed as a follow-up to significant interactions where necessary. Nonparametric Wilcoxon signed ranks tests were performed in place of parametric *t* tests for all data that a Shapiro–Wilk's test determined were not normally distributed. An α of 0.05 was used to determine statistical significance. Statistical analyses were performed using IBM SPSS Statistics v. 25 (SPSS Inc.,

Chicago, IL). All figures were created using GraphPad Prism v. 7 (GraphPad Software, San Diego, CA).

Results

A total of 703 MUs met the inclusion criteria following the reconstruct-and-test and STA validation procedures. Subsequently, 26.2 ± 7.4 MUs were analyzed per SLOW₄₀ and 32.4 ± 8.8 MUs were analyzed per FAST₄₀. All MFR vs. RT ($r = -0.84$ to -0.98), MFR vs. MUAP_{AMP} ($r = -0.77$ to -0.96), and MUAP_{AMP} vs. RT ($r = 0.63$ – 0.92) relationships were significant. A representative illustration of the 40% MVCs and the MU data observed from one subject is depicted in Fig. 1.

For all recorded MUs, RTs were similar ($P = 0.978$) between SLOW₄₀ ($6.97 \pm 5.11\%$ MVC) and FAST₄₀ ($6.95 \pm 6.19\%$ MVC) for the lowest-threshold MUs, but differed for the highest-threshold MUs with greater RTs (Wilcoxon: $P = 0.012$) recorded during the FAST₄₀ ($35.8 \pm 7.31\%$ MVC) than SLOW₄₀ ($28.2 \pm 9.87\%$ MVC). However, the range of observed MUAP_{AMPS} was similar between the 40% MVCs as there were no differences between the smallest observed MUAP_{AMPS} ($P = 0.559$, SLOW₄₀ = 0.044 ± 0.015 mV, FAST₄₀ = 0.043 ± 0.013 mV) or the largest observed MUAP_{AMPS} ($P = 0.248$, SLOW₄₀ = 0.195 ± 0.092 mV, FAST₄₀ = 0.208 ± 0.095 mV).

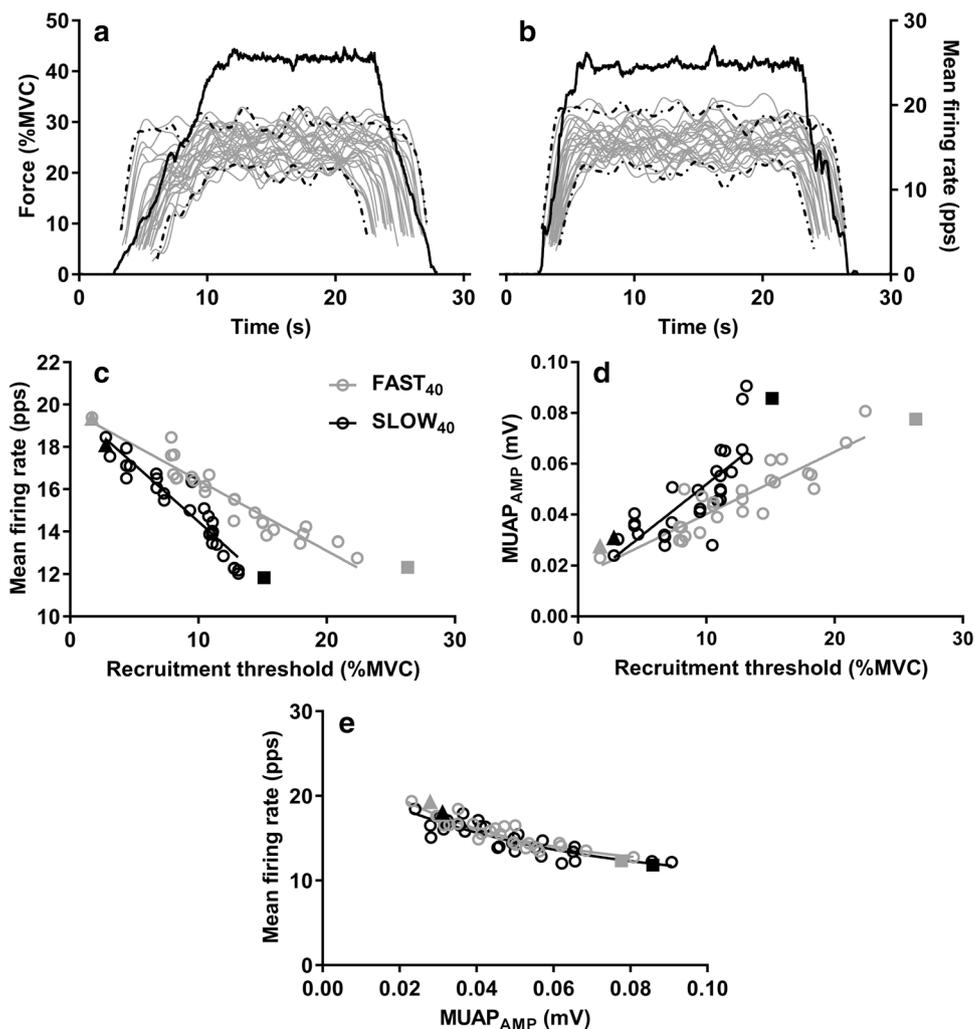
There were no differences in torque ($P = 0.354$, SLOW₄₀ = 85.6 ± 24.6 N m, FAST₄₀ = 86.0 ± 24.5 N m) or CV of torque (Wilcoxon: $P = 0.117$, SLOW₄₀ = $2.24 \pm 1.18\%$, FAST₄₀ = $2.24 \pm 0.71\%$) during the constant torque period between SLOW₄₀ and FAST₄₀. Although compliance with the torque trajectory template was high for both 40% MVCs, the FAST₄₀ torque trajectory template was more difficult to match, as the RMSE between the subject's torque output and the torque trajectory template was greater for FAST₄₀ ($2.50 \pm 0.59\%$ MVC) than SLOW₄₀ ($2.18 \pm 0.61\%$ MVC) ($P < 0.001$).

Motor unit relationships

For the MFR vs. RT relationships, paired samples *t* tests indicated no differences ($P = 0.478$) in the *y*-intercepts between SLOW₄₀ (24.1 ± 3.77 pps) and FAST₄₀ (23.5 ± 4.04 pps). However, the slopes were more negative ($P = 0.003$) for the SLOW₄₀ (-0.491 ± 0.101 pps/%MVC) than FAST₄₀ (-0.322 ± 0.109 pps/%MVC). The higher-threshold MUs had lower firing rates during the SLOW₄₀ (Fig. 2).

For the MUAP_{AMP} vs. RT relationships, there were no differences (Wilcoxon: $P = 0.209$) in the *y*-intercepts between SLOW₄₀ (-0.016 ± 0.043 mV) and FAST₄₀ (-0.006 ± 0.049 mV). However, the slopes were greater ($P = 0.022$) for the SLOW₄₀ (0.0057 ± 0.0021 mV/%MVC)

Fig. 1 Illustration of the slow (SLOW₄₀) (a) and fast (FAST₄₀) (b) rate of torque development contractions from a representative subject. Thick black lines represent the subject's torque tracing. Thin gray lines represent motor unit (MU) mean firing rate [MFR (pulses per second)] curves. The dashed black lines are MFR curves of the first and last recruited MUs which are further illustrated in the subsequent plots. The subject's MFR vs. recruitment threshold (RT) (c), MU action potential amplitude (MUAP_{AMP}) vs. RT (d), and MFR vs. MUAP_{AMP} (e) relationships plotted with lines of best fit



than the FAST₄₀ (0.0041 ± 0.0023 mV/%MVC). For a given higher RT, the MUAP_{AMPS} were greater during the SLOW₄₀ than the FAST₄₀ (Fig. 3).

For the MFR vs. MUAP_{AMP} relationships, paired samples *t* tests indicated no differences in the *A* terms ($P = 0.951$, SLOW₄₀ = 22.7 ± 2.69 pps, FAST₄₀ = 22.8 ± 3.55 pps) or the *B* terms ($P = 0.189$, SLOW₄₀ = -4.72 ± 1.40 pps/mV, FAST₄₀ = -4.44 ± 1.47 pps/mV) between the SLOW₄₀ and FAST₄₀. Therefore, firing rates were equivocal for MUs with similar AP_{AMPS} between SLOW₄₀ and FAST₄₀ (Fig. 4).

Extensor and flexor N-EMG

For N-EMG during the constant torque phase, there was a significant two-way interaction ($P = 0.032$, rate of torque development \times muscle group). Paired samples *t* tests indicated extensor N-EMG was greater than flexor N-EMG for SLOW₄₀ ($P < 0.001$, extensor

N-EMG = $36.3 \pm 7.82\%$, flexor N-EMG = $6.50 \pm 3.82\%$) and FAST₄₀ ($P < 0.001$, extensor N-EMG = $34.0 \pm 6.26\%$, flexor N-EMG = $6.22 \pm 3.52\%$). In addition, extensor N-EMG was greater ($P = 0.015$) for SLOW₄₀ than FAST₄₀, however, flexor N-EMG was not significantly different ($P = 0.183$) between the SLOW₄₀ and FAST₄₀.

For N-EMG at 25% MVC during the linearly increasing torque phase, there was no two-way interaction ($P = 0.142$, rate of torque development \times muscle group) or main effect for rate of torque development ($P = 0.088$). However, there was a main effect for muscle group ($P < 0.001$). Dependent samples *t* tests indicated N-EMG was greater for the extensors than the flexors regardless of contraction ($P < 0.001$). N-EMG was not significantly greater at 25% MVC during the linearly increasing torque phase for SLOW₄₀ than FAST₄₀ for the extensors (SLOW₄₀ = $15.0 \pm 3.28\%$, FAST₄₀ = $13.4 \pm 2.68\%$) or flexors (SLOW₄₀ = $3.48 \pm 2.49\%$, FAST₄₀ = $3.22 \pm 2.61\%$).

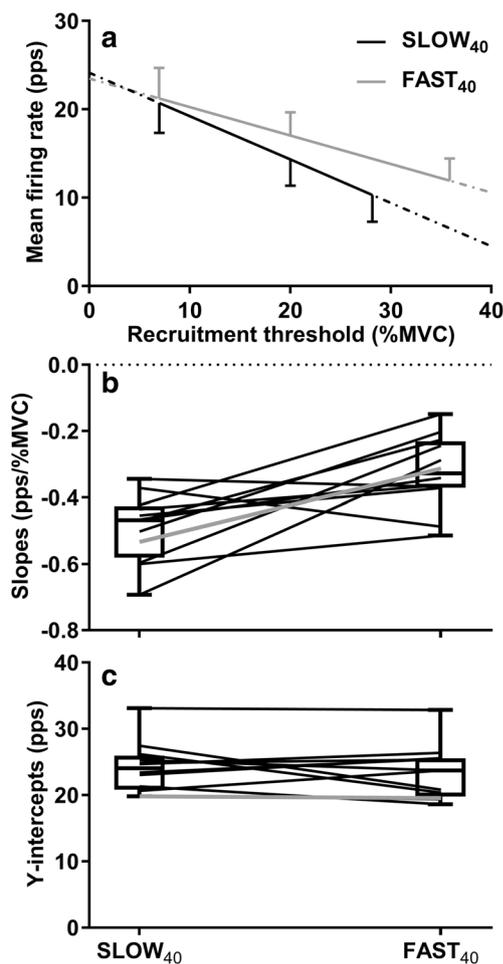


Fig. 2 Average predicted mean firing rate [MFR (pulses per second)] vs. recruitment threshold [RT (%MVC)] relationships (a) for slow (SLOW₄₀) and fast (FAST₄₀) rate of torque development contractions. The solid lines indicate the predicted mean firing rates within the average observed recruitment threshold ranges for each contraction, while the dotted lines extending the predictions indicate the mean firing rates for motor units in the expected real recruitment range. Spaghetti plots of individual responses and box-and-whisker plots of the SLOW₄₀ and FAST₄₀ slopes (b) and y-intercepts (c). The gray lines in b and c indicate the responses from the subject illustrated in Fig. 1

Discussion

MU firing rates were lower and action potential amplitudes were larger in relation to recruitment thresholds for isometric contractions performed at a slower rate compared to contractions performed at a faster rate of torque development. MU activity is commonly observed to be altered by the intensity of the targeted force/torque (Erim et al. 1999; De Luca and Hostage 2010; Hu et al. 2013a; Colquhoun et al. 2018b), different between populations (Erim et al. 1999; Herda et al. 2015; Sterczala et al. 2018a), or altered following exercise interventions (Vila-Chã et al. 2010; Pope et al. 2016). The novel findings of the present study suggest that differences

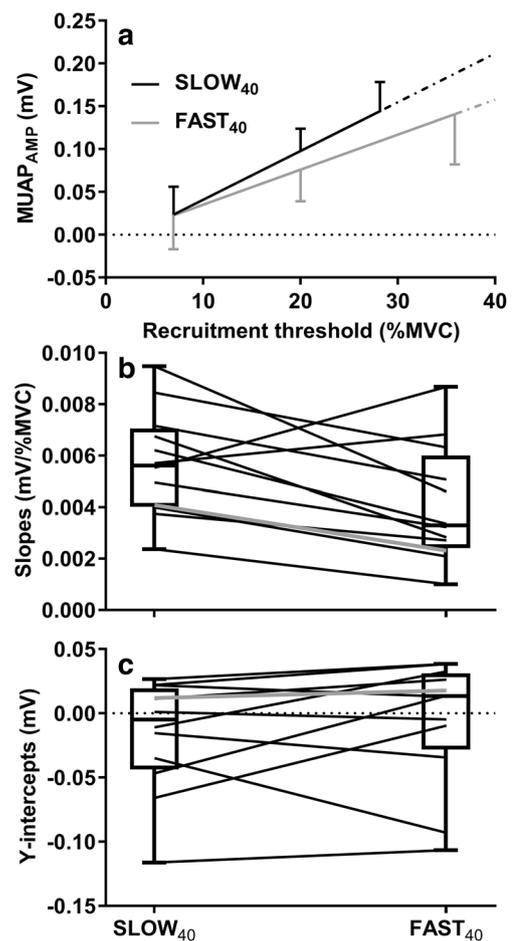


Fig. 3 Average predicted motor unit action potential amplitude [MUAP_{AMP} (mV)] vs. recruitment threshold [RT (%MVC)] relationships (a) for slow (SLOW₄₀) and fast (FAST₄₀) rate of torque development contractions. The solid lines indicate the predicted action potential amplitudes within the average observed recruitment threshold ranges for each contraction, while the dotted lines extending the predictions indicate the action potential amplitudes for motor units in the expected recruitment range for the contraction. However, the predictions were not extended in the 0–6% MVC range as the trajectories would predict action potential amplitudes less than 0 mV for the first recruited MUs which is not physiologically accurate. Spaghetti plots of individual responses and box-and-whisker plots of the SLOW₄₀ and FAST₄₀ slopes (b) and y-intercepts (c). The gray lines in b and c indicate the responses from the subject illustrated in Fig. 1

in MU activity can exist as a function of rate of isometric torque development.

Greater slopes of the MU action potential amplitude vs. recruitment threshold relationships indicated action potential amplitudes were greater at higher recruitment thresholds for the SLOW₄₀ than the FAST₄₀. The largest action potential amplitudes were similar (Fig. 3a) within the average recorded recruitment ranges of MUs for the SLOW₄₀ (RT range = 6.97–28.2% MVC) and FAST₄₀ (RT range = 6.95–35.8% MVC). However, this does not imply that the largest recruited MUs during the contractions

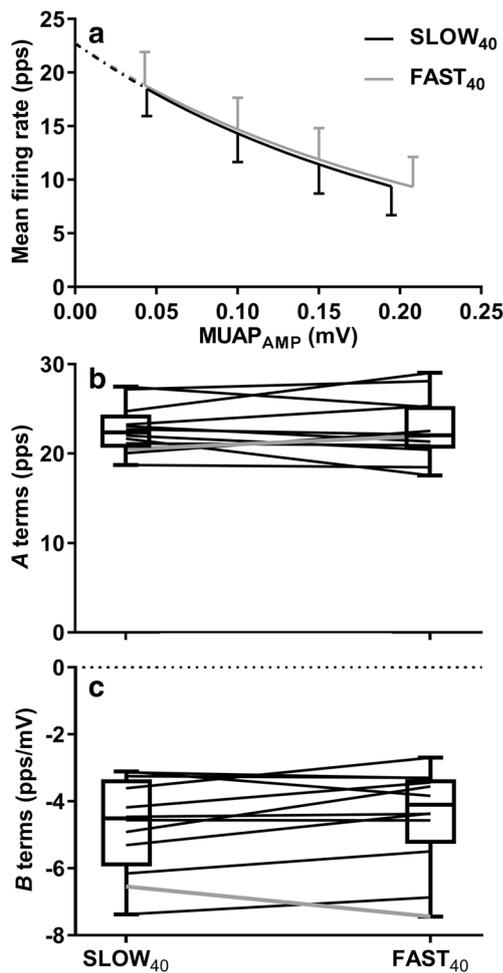


Fig. 4 Average predicted mean firing rate [MFR (pulses per second)] vs. motor unit action potential amplitude [MUAP_{AMP} (mV)] relationships (a) for slow (SLOW₄₀) and fast (FAST₄₀) rates of torque development contractions. The solid lines indicate the predicted mean firing rates within the average observed action potential amplitude ranges for each contraction, while the dotted lines extending the predictions indicate the mean firing rates for motor units in the expected real action potential amplitude range. Spaghetti plots of individual responses and box-and-whisker plots of the SLOW₄₀ and FAST₄₀ A terms (b) and B terms (c). The gray lines in b and c indicate the responses from the subject illustrated in Fig. 1

possessed similar action potential amplitudes. For instance, the VL has been shown to continue recruitment of MUs to 95% MVC (De Luca and Hostage 2010) and, furthermore, N-EMG was doubled from 25% MVC during the linearly increasing torque phase (~15% N-EMG) in comparison to the constant torque phase (~35% N-EMG) for both contractions. Thus, larger MUs continued to be recruited during the linearly increasing torque phase from the observed upper end of the recruitment range of 28.2% MVC to 40% MVC for the SLOW₄₀. The dotted lines in Fig. 3a extend the predicted MUAP_{AMP} vs. RT relationships for SLOW₄₀ and FAST₄₀ beyond the average recorded recruitment range to include

the upper range of recruitment which would be expected during 40% MVCs of the VL. In support of greater recruitment during SLOW₄₀, N-EMG for the extensor muscles was 7% greater during the constant torque phase of SLOW₄₀ relative to FAST₄₀.

A limitation of EMG decomposition is that not all MUs can be recorded during any given contraction. Furthermore, another limitation of this study was that MUs were not tracked across contractions. However, the strong relationships between recruitment thresholds and AP_{AMP}s and firing rates indicate MUs with similar recruitment thresholds will demonstrate similar AP_{AMP}s and firing rates within a contraction. In addition, the relationship-based analysis of MU activity has been shown to be reliable between contractions (Colquhoun et al. 2018b). Therefore, any changes in the characteristics of a MU in relation to recruitment threshold will be easily quantified with the relationship-based approach. Subsequently, it has recently been reported that changes in recruitment thresholds and firing rates in tracked MUs across contractions does not provide any additional information that is not conveyed by the untracked MUs (Del Vecchio et al. 2019). Although unlikely, it cannot be ruled out that a bias in the Precision Decomposition III algorithm contributed to the lack of recorded of higher-threshold (28–40% MVC) MUs during the SLOW₄₀ which would be expected to possess larger action potentials.

The slopes of the mean firing rate vs. recruitment threshold relationships were significantly less negative for the FAST₄₀ than SLOW₄₀, but the y-intercepts were similar. Thus, MUs recruited at similar torque levels had greater firing rates for the FAST₄₀ than the SLOW₄₀ and the effect was more pronounced for higher-threshold MUs (Fig. 2a). When firing rates were expressed relative to MU action potential amplitudes, however, the firing rates were similar between SLOW₄₀ and FAST₄₀ (Fig. 4). Therefore, MUs with similar action potential amplitudes had similar firing rates regardless of rate of isometric torque development. The lower slopes of the mean firing rates vs. recruitment threshold relationships were due to shifting the recruitment of similar MUs to lower torque levels in a contraction at a slower isometric rate of torque development. Together, the mean firing rate vs. recruitment threshold and MU action potential amplitude relationships suggests the additional excitation (N-EMG) necessary to achieve the targeted torque during the SLOW₄₀ primarily resulted in the recruitment of larger MUs rather than significant increase in the firing rates of the already active MU pool.

Previous investigation of MU recruitment and isometric rate of force development yielded partially conflicting results (Desmedt and Godaux 1977; Masakado et al. 1995). Desmedt and Godaux (1977) reported MUs of the tibialis anterior were recruited at lower forces during ankle dorsiflexion contractions at ~50% MVC (12 kg) with greater

rates of force development, and the effect was augmented even up to ballistic speeds where most MUs were recruited prior to the onset of measurable force production. However, the authors reported no changes in recruitment thresholds between the slower isometric rates of force development tested between ~ 1.5 kg/s and ~ 6 kg/s which are similar to the 5% MVC/s and 20% MVC/s rates of torque development tested in the current study. The mechanism responsible for earlier recruitment at greater rates of torque development has yet to be identified (Desmedt and Godaux 1977; Masakado et al. 1995; Maffioletti et al. 2016). A potential explanation for the increased recruitment and MU action potential amplitudes observed during the SLOW₄₀ in the present study may be a function of muscle spindle activity. De Luca and Kline (2012) suggest that at low contraction intensities (i.e., $< 10\%$ MVC) when MUs fire at lower rates where their twitches are not fused, muscle spindles exist in a dynamic state (spindles are shortened and stretched repeatedly), increasing excitation to the motoneuron pool through Ia afferent feedback. With the current protocol, muscle spindles would remain in this dynamic state for four times the duration during SLOW₄₀ in comparison to FAST₄₀, as the subjects would reach 10% MVC in 2 s during SLOW₄₀ or 0.5 s during FAST₄₀. It is plausible the muscle spindles remaining longer in the dynamic state lead to the observed increase in recruitment for SLOW₄₀. In support, Kennedy and Cresswell (2001) reported delayed recruitment of medial gastrocnemius MUs during plantar flexion contractions when muscle fibers were at short, non-optimal lengths, and speculated reduced afferent feedback from muscle spindles may have been responsible for the delayed recruitment. Future research should investigate the current phenomenon under vibration, which is known to remove feedback from muscle spindles (Kouzaki et al. 2000). If this hypothesis is correct, vibration would decrease recruitment during slower rates of torque development.

In the current study, subjects were better able to comply with the torque trajectory template for the SLOW₄₀ than FAST₄₀ as the RMSE was 15% greater for FAST₄₀. It is possible that the increased torque compliance for the SLOW₄₀ was a function of increased synergistic MU activity of the leg extensors and flexors. Thus, earlier recruitment of larger MUs and greater activation of agonists and antagonists may have better modulated the torque output to match the torque trajectory template. In support, extensor N-EMG amplitude was significantly greater for SLOW₄₀, however, there was no significant difference for N-EMG of the leg flexors between SLOW₄₀ ($6.50 \pm 3.82\%$) and FAST₄₀ ($6.22 \pm 3.52\%$). It is unclear how torque could be similar between contractions if overall recruitment was greater for SLOW₄₀ than FAST₄₀ given that firing rates and coactivation of antagonists were also similar. A limitation of the current study is that EMG was only measured from five of the muscles that cross the

knee joint, where EMG of semimembranosus, medial and lateral gastrocnemii, and other muscles of the quadriceps may have fully elucidated the activation strategy of all the muscles in both contractions. It is plausible that the bipolar surface EMG technique used was not sensitive to detect minor differences in already low muscle activation of the leg flexors during a moderate intensity contraction of the leg extensors. Future research should utilize ultrasonography and mechanomyography (Guo et al. 2010) in addition to EMG to examine potential differences in coactivation of the leg flexors at different rates of torque development and/or utilize higher contraction intensities where coactivation would be greater for the leg flexors (Tracy and Enoka 2002).

The results of the present study suggest great care must be taken to ensure the adherence of a subject's torque output with the torque trajectory template provided, as significant deviations in the rate of torque development during the linearly increasing torque phase will alter the recruitment of MUs shifting the slopes of the firing rates and action potential amplitudes in relation to recruitment thresholds. In addition, it should be investigated whether alternate rates of torque development in lieu of the standard 10% MVC/s commonly used for isometric trapezoid contractions are more efficacious for research seeking to determine subtle differences in MU activity between populations or following exercise interventions.

Previously, less negative slopes of mean firing rate vs. recruitment threshold relationships have been observed for contractions performed at greater intensity compared to contractions at lower intensity (De Luca and Hostage 2010) and for individuals with greater type I myosin heavy chain isoform content of the VL (Trevino et al. 2016). Trevino et al. (2016) reported $\sim 73\%$ of the variance in type I myosin heavy chain isoform content of the VL between subjects was explained by the slopes of the mean firing rate vs. recruitment threshold relationships from a 40% MVC. Similarly, Trevino et al. (2018) reported the slopes of the action potential amplitude vs. recruitment threshold relationships during 40% MVC leg extensions were highly correlated with cross-sectional area and myosin heavy chain isoform content of the VL. The current study provides evidence that large changes in the slopes of the mean firing rate and MU action potential vs. recruitment threshold relationships (52% and 28%, respectively) may be observed within subjects at the same contraction intensity by manipulating the rate of torque development of the linearly increasing torque phase of the isometric contraction.

In summary, MUs of similar size were recruited earlier at lower torque levels, and overall recruitment was greater, during an isometric trapezoidal contraction with a slower rate of torque development. This change in recruitment led to altered slopes of the mean firing rate and MU action potential amplitudes vs. recruitment threshold relationships

which are commonly analyzed to characterize firing rate and recruitment patterns of a muscle (De Luca and Hostage 2010; Hu et al. 2013a; Herda et al. 2015; Colquhoun et al. 2018a; Miller et al. 2018; Trevino et al. 2018). However, firing rates were similar when expressed relative to action potential amplitudes. Therefore, MU recruitment, but not firing rates of the motoneurons were altered by modulating rate of torque development during isometric trapezoidal muscle actions of the leg extensors. These findings highlight the necessity of ensuring subjects' torque output matches the provided torque trajectory template in future research. In addition, future research should examine if differences in MU activity as a function of rates of torque develop may be related to sensory processes.

Acknowledgements The authors would like to thank the undergraduate research assistants who aided in the collection and analysis of data. We would also like to thank the subjects for their selfless participation.

Author contributions JDM and TJH developed the research design. CJL, MDG, KLS, MEW collected and analyzed data. JDM analyzed data, performed statistical procedures, and prepared the figures and manuscript. TJH aided in manuscript preparation. All authors edited the manuscript and approved the final version.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki Declaration and its later amendments or comparable ethical standards.

References

- Adam A, De Luca CJ (2005) Firing rates of motor units in human vastus lateralis muscle during fatiguing isometric contractions. *J Appl Physiol* 99:268–280. <https://doi.org/10.1152/jappphysiol.01344.2004>
- Colquhoun RJ, Magrini MA, Haun CT et al (2018a) Muscle phenotype is related to motor unit behavior of the vastus lateralis during maximal isometric contractions. *Physiol Rep* 6:e13636. <https://doi.org/10.14814/phy2.13636>
- Colquhoun RJ, Tomko PM, Magrini MA et al (2018b) The influence of input excitation on the inter- and intra-day reliability of the motor unit firing rate versus recruitment threshold relationship. *J Neurophysiol* 120:3131–3139
- Contessa P, De Luca CJ, Kline JC (2016) The compensatory interaction between motor unit firing behavior and muscle force during fatigue. *J Neurophysiol* 116:1579–1585. <https://doi.org/10.1152/jn.00347.2016>
- Contessa P, Letizi J, De Luca G, Kline JC (2018) Contribution from motor unit firing adaptations and muscle coactivation during fatigue. *J Neurophysiol* 119:2186–2193. <https://doi.org/10.1152/jn.00766.2017>
- Conwit RA, Stashuk D, Tracy B et al (1999) The relationship of motor unit size, firing rate and force. *Clin Neurophysiol* 110:1270–1275. [https://doi.org/10.1016/S1388-2457\(99\)00054-1](https://doi.org/10.1016/S1388-2457(99)00054-1)
- De Luca CJ, Contessa P (2012) Hierarchical control of motor units in voluntary contractions. *J Neurophysiol* 107:178–195. <https://doi.org/10.1152/jn.00961.2010>
- De Luca CJ, Contessa P (2015) Biomechanical benefits of the onion-skin motor unit control scheme. *J Biomech* 48:195–203
- De Luca CJ, Erim Z (1994) Common drive of motor units in regulation of muscle force. *Trends Neurosci* 17:299–305
- De Luca CJ, Hostage EC (2010) Relationship between firing rate and recruitment threshold of motoneurons in voluntary isometric contractions. *J Neurophysiol* 104:1034–1046. <https://doi.org/10.1152/jn.01018.2009>
- De Luca CJ, Kline JC (2012) Influence of proprioceptive feedback on the firing rate and recruitment of motoneurons. *J Neural Eng* 9:016007. <https://doi.org/10.1088/1741-2560/9/1/016007>
- De Luca CJ, Foley PJ, Erim Z (1996) Motor unit control properties in constant-force isometric contractions. *J Neurophysiol* 76:1503–1516. <https://doi.org/10.1152/jn.1996.76.3.1503>
- De Luca CJ, Adam A, Wotiz R et al (2006) Decomposition of surface EMG signals. *J Neurophysiol* 96:1646–1657. <https://doi.org/10.1152/jn.00009.2006>
- Del Vecchio A, Negro F, Felici F, Farina D (2018) Distribution of muscle fibre conduction velocity for representative samples of motor units in the full recruitment range of the tibialis anterior muscle. *Acta Physiol* 222:e12930. <https://doi.org/10.1111/apha.12930>
- Del Vecchio A, Casolo A, Negro F et al (2019) The increase in muscle force after 4 weeks of strength training is mediated by adaptations in motor unit recruitment and rate coding. *J Physiol*. <https://doi.org/10.1113/jp277250>
- Desmedt JE, Godaux E (1977) Ballistic contractions in man: characteristic recruitment pattern of single motor units of the tibialis anterior muscle. *J Physiol* 264:673–693. <https://doi.org/10.1113/jphysiol.1977.sp011689>
- Dorfman LJ, Howard JE, McGill KC (1990) Triphasic behavioral response of motor units to submaximal fatiguing exercise. *Muscle Nerve* 13:621–628. <https://doi.org/10.1002/mus.880130711>
- Erim Z, Beg MF, Burke DT, de Luca CJ (1999) Effects of aging on motor-unit control properties. *J Neurophysiol* 82:2081–2091. <https://doi.org/10.1152/jn.1999.82.5.2081>
- Farina D, Holobar A, Merletti R, Enoka RM (2010) Decoding the neural drive to muscles from the surface electromyogram. *Clin Neurophysiol* 121:1616–1623. <https://doi.org/10.1016/j.clinph.2009.10.040>
- Goldberg LJ, Derfler B (1977) Relationship among recruitment order, spike amplitude, and twitch tension of single motor units in human masseter muscle. *J Neurophysiol* 40:879–890. <https://doi.org/10.1152/jn.1977.40.4.879>
- Guo J-Y, Zheng Y-P, Xie H-B, Chen X (2010) Continuous monitoring of electromyography (EMG), mechanomyography (MMG), sonomyography (SMG) and torque output during ramp and step isometric contractions. *Med Eng Phys* 32:1032–1042. <https://doi.org/10.1016/j.medengphy.2010.07.004>
- Hakansson CH (1956) Conduction velocity and amplitude of the action potential as related to circumference in the isolated fibre of frog muscle. *Acta Physiol Scand* 37:14–34. <https://doi.org/10.1111/j.1748-1716.1956.tb01338.x>
- Henneman E (1957) Relation between size of neurons and their susceptibility to discharge. *Science* 126:1345–1347
- Herda TJ, Siedlik JA, Trevino MA et al (2015) Motor unit control strategies of endurance- versus resistance-trained individuals. *Muscle Nerve* 52:832–843. <https://doi.org/10.1002/mus.24597>
- Herda TJ, Trevino MA, Sterczala AJ et al (2019) Muscular strength and power are correlated with motor unit action potential amplitudes, but not myosin heavy chain isoforms in sedentary males

- and females. *J Biomech* 86:251–255. <https://doi.org/10.1016/j.jbiomech.2019.01.050>
- Horita T, Ishiko T (1987) Relationships between muscle lactate accumulation and surface EMG activities during isokinetic contractions in man. *Eur J Appl Physiol* 56:18–23. <https://doi.org/10.1007/BF00696370>
- Hu X, Rymer WZ, Suresh NL (2013a) Motor unit pool organization examined via spike-triggered averaging of the surface electromyogram. *J Neurophysiol* 110:1205–1220. <https://doi.org/10.1152/jn.00301.2012>
- Hu X, Rymer WZ, Suresh NL (2013b) Assessment of validity of a high-yield surface electromyogram decomposition. *J NeuroEng Rehabil* 10:99. <https://doi.org/10.1186/1743-0003-10-99>
- Hu X, Rymer WZ, Suresh NL (2013c) Reliability of spike triggered averaging of the surface electromyogram for motor unit action potential estimation. *Muscle Nerve* 48:557–570. <https://doi.org/10.1002/mus.23819>
- Jubeau M, Gondin J, Martin A et al (2010) Differences in twitch potentiation between voluntary and stimulated quadriceps contractions of equal intensity. *Scand J Med Sci Sports* 20:e56–e62. <https://doi.org/10.1111/j.1600-0838.2009.00897.x>
- Kennedy PM, Cresswell AG (2001) The effect of muscle length on motor-unit recruitment during isometric plantar flexion in humans. *Exp Brain Res* 137:58–64. <https://doi.org/10.1007/s002210000623>
- Klein CS, Ivanova TD, Rice CL, Garland SJ (2001) Motor unit discharge rate following twitch potentiation in human triceps brachii muscle. *Neurosci Lett* 316:153–156. [https://doi.org/10.1016/S0304-3940\(01\)02389-8](https://doi.org/10.1016/S0304-3940(01)02389-8)
- Kouzaki M, Shinohara M, Fukunaga T (2000) Decrease in maximal voluntary contraction by tonic vibration applied to a single synergist muscle in humans. *J Appl Physiol* 89:1420–1424. <https://doi.org/10.1152/jap.2000.89.4.1420>
- Maffiuletti NA, Aagaard P, Blazevich AJ et al (2016) Rate of force development: physiological and methodological considerations. *Eur J Appl Physiol* 116:1091–1116. <https://doi.org/10.1007/s00421-016-3346-6>
- Martinez-Valdes E, Negro F, Falla D et al (2018) Surface electromyographic amplitude does not identify differences in neural drive to synergistic muscles. *J Appl Physiol* 124:1071–1079. <https://doi.org/10.1152/jap.2017.115.2017>
- Masakado Y, Noda Y, Nagata M et al (1994) Macro-EMG and motor unit recruitment threshold: differences between the young and the aged. *Neurosci Lett* 179:1–4. [https://doi.org/10.1016/0304-3940\(94\)90920-2](https://doi.org/10.1016/0304-3940(94)90920-2)
- Masakado Y, Akaboshi K, Nagata M et al (1995) Motor unit firing behavior in slow and fast contractions of the first dorsal interosseous muscle of healthy men. *Electroencephalogr Clin Neurophysiol* 97:290–295
- McManus L, Hu X, Rymer WZ et al (2016) Muscle fatigue increases beta-band coherence between the firing times of simultaneously active motor units in the first dorsal interosseous muscle. *J Neurophysiol* 115:2830–2839. <https://doi.org/10.1152/jn.00097.2016>
- Miller JD, Herda TJ, Trevino MA et al (2017a) Age-related differences in twitch properties and muscle activation of the first dorsal interosseous. *Clin Neurophysiol* 128:925–934. <https://doi.org/10.1016/j.clinph.2017.03.032>
- Miller JD, Herda TJ, Trevino MA et al (2017b) Time-related changes in firing rates are influenced by recruitment threshold and twitch force potentiation in the first dorsal interosseous: recruitment threshold, potentiation and motor unit firing rates. *Exp Physiol* 102:950–961. <https://doi.org/10.1113/EP086262>
- Miller JD, Sterczala AJ, Trevino MA, Herda TJ (2018) Examination of muscle composition and motor unit behavior of the first dorsal interosseous of normal and overweight children. *J Neurophysiol* 119:1902–1911. <https://doi.org/10.1152/jn.00675.2017>
- Miller JD, Sterczala AJ, Trevino MA et al (2019) Motor unit action potential amplitudes and firing rates during repetitive muscle actions of the first dorsal interosseous in children and adults. *Eur J Appl Physiol*. <https://doi.org/10.1007/s00421-019-04090-0>
- Milner-Brown HS, Stein RB (1975) The relation between the surface electromyogram and muscular force. *J Physiol* 246:549–569. <https://doi.org/10.1113/jphysiol.1975.sp010904>
- Nawab SH, Chang S-S, De Luca CJ (2010) High-yield decomposition of surface EMG signals. *Clin Neurophysiol* 121:1602–1615. <https://doi.org/10.1016/j.clinph.2009.11.092>
- Peng Y-L, Tenan MS, Griffin L (2018) Hip position and sex differences in motor unit firing patterns of the vastus medialis and vastus medialis oblique in healthy individuals. *J Appl Physiol* 124:1438–1446. <https://doi.org/10.1152/jap.2017.124.1438>
- Pope ZK, Hester GM, Benik FM, DeFreitas JM (2016) Action potential amplitude as a noninvasive indicator of motor unit-specific hypertrophy. *J Neurophysiol* 115:2608–2614. <https://doi.org/10.1152/jn.00039.2016>
- Potvin JR, Fuglevand AJ (2017) A motor unit-based model of muscle fatigue. *PLoS Comput Biol* 13:e1005581. <https://doi.org/10.1371/journal.pcbi.1005581>
- Rathey J, Martin PG, Kay D et al (2006) Contralateral muscle fatigue in human quadriceps muscle: evidence for a centrally mediated fatigue response and cross-over effect. *Pflüg Arch Eur J Physiol* 452:199–207. <https://doi.org/10.1007/s00424-005-0027-4>
- Seki K, Miyazaki Y, Watanabe M et al (1991) Surface electromyogram spectral characterization and motor unit activity during voluntary ramp contraction in men. *Eur J Appl Physiol* 63:165–172. <https://doi.org/10.1007/BF00233842>
- Sterczala AJ, Herda TJ, Miller JD et al (2018a) Age-related differences in the motor unit action potential size in relation to recruitment threshold. *Clin Physiol Funct Imaging* 38:610–616. <https://doi.org/10.1111/cpf.12453>
- Sterczala AJ, Miller JD, Trevino MA et al (2018b) Differences in the motor unit firing rates and amplitudes in relation to recruitment thresholds during submaximal contractions of the first dorsal interosseous between chronically resistance-trained and physically active men. *Appl Physiol Nutr Metab*. <https://doi.org/10.1139/apnm-2017-0646>
- Stock MS, Beck TW, Defreitas JM (2012) Effects of fatigue on motor unit firing rate versus recruitment threshold relationships. *Muscle Nerve* 45:100–109. <https://doi.org/10.1002/mus.22266>
- Tenan MS, Peng Y-L, Hackney AC, Griffin LK (2013) Menstrual cycle mediates vastus medialis and vastus medialis oblique muscle activity. *Med Sci Sports Exerc* 45:2151–2157. <https://doi.org/10.1249/MSS.0b013e318299a69d>
- Tomko PM, Colquhoun RJ, Magrini MA et al (2018) Global electromyographic signal characteristics depend on maximal isometric contraction method in the knee extensors. *J Electromyogr Kinesiol* 42:111–116
- Tracy BL, Enoka RM (2002) Older adults are less steady during submaximal isometric contractions with the knee extensor muscles. *J Appl Physiol* 92:1004–1012. <https://doi.org/10.1152/jap.2001.92.4.1004>
- Trevino MA, Herda TJ, Fry AC et al (2016) Influence of the contractile properties of muscle on motor unit firing rates during a moderate-intensity contraction in vivo. *J Neurophysiol* 116:552–562. <https://doi.org/10.1152/jn.01021.2015>
- Trevino MA, Sterczala AJ, Miller JD et al (2018) Sex-related differences in muscle size explained by amplitudes of higher-threshold motor unit action potentials and muscle fibre typing. *Acta Physiol*. <https://doi.org/10.1111/apha.13151>

- Vander Linden DW, Kukulka CG, Soderberg GL (1991) The effect of muscle length on motor unit discharge characteristics in human tibialis anterior muscle. *Exp Brain Res* 84:210–218. <https://doi.org/10.1007/BF00231776>
- Vila-Chã C, Falla D, Farina D (2010) Motor unit behavior during sub-maximal contractions following six weeks of either endurance or strength training. *J Appl Physiol* 109:1455–1466. <https://doi.org/10.1152/jappphysiol.01213.2009>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Affiliations

Jonathan D. Miller¹ · C. J. Lund¹ · Marissa D. Gingrich¹ · Kyle L. Schtul¹ · Mandy E. Wray¹ · Trent J. Herda¹

Jonathan D. Miller
jdmiller@ku.edu

C. J. Lund
cjlund9@ku.edu

Marissa D. Gingrich
marissa_gingrich@ku.edu

Kyle L. Schtul
kyle.schtul@ku.edu

Mandy E. Wray
mandy_wray@ku.edu

¹ Neuromechanics Laboratory, Department of Health, Sport and Exercise Sciences, University of Kansas, 1301 Sunnyside Ave, Room 101BE, Lawrence, KS 66045, USA