



The relationship of agonist muscle single motor unit firing rates and elbow extension limb movement kinematics

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Received: 11 March 2021 / Accepted: 26 June 2021 / Published online: 8 July 2021
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Abstract

This study explored the relationship between single motor unit (MU) firing rates (FRs) and limb movement velocity during voluntary shortening contractions when accounting for the effects of time course variability between different kinematic comparisons. Single MU trains recorded by intramuscular electromyography in agonist muscles of the anconeus ($n = 15$ participants) and lateral head of the triceps brachii ($n = 6$) were measured during each voluntary shortening contraction. Elbow extension movements consisted of a targeted velocity occurring along the sagittal plane at 25, 50, 75 and 100% of maximum velocity. To account for the effect of differences in contraction time course between parameters, each MU potential was time locked throughout the shortening muscle contraction and linked with separated kinematic parameters of the elbow joint. Across targeted movement velocities, instantaneous FRs were significantly correlated with elbow extension rate of torque development ($r = 0.45$) and torque ($r = 0.40$), but FRs were not correlated with velocity ($r = 0.03$, $p = \text{n.s.}$). Instead, FRs had a weak indirect relationship with limb movement velocity and position assessed through multiple correlation of the stepwise kinematic progression. Results show that voluntary descending synaptic inputs correspond to a more direct relationship between agonist muscle FRs and torque during shortening contractions, but not velocity. Instead, FRs were indirectly correlated to preparing the magnitude of imminent movement velocity of the lagging limb through torque.

Keywords Concentric · Discharge rate · Human · Rate coding · Skeletal muscle · Voluntary

Introduction

The rate of limb movement is ultimately determined by the shortening contraction speed of the agonist muscle (Edman 2014). Under voluntary control, tension in the muscle, and its corresponding force, are mediated by motor unit (MU) recruitment and firing rate (FR) modulation from descending synaptic inputs (Heckman and Binder 1991; Fuglevand et al. 1993; Devanne et al. 1997). Yet, understanding how FRs correspond to movement kinematics is largely based on inference from isometric contraction.

From the few comparisons in human tibialis anterior, soleus, hand and upper limb muscles (Desmedt and Godaux 1979; Gydikov et al. 1986; Howell et al. 1995; Garland et al. 1996; Harwood et al. 2011; Harwood and Rice 2012, 2014; Kallio et al. 2013; Oliveira and Nergro 2021), averaged FRs increase during muscle shortening as compared to isometric contraction, and is positively related to movement speed (Desmedt and Godaux 1979; Gydikov et al. 1986; Garland et al. 1996; Harwood et al. 2011; Harwood and Rice 2014). Whereas, in extra-ocular muscles in non-human primates FRs are directly related to eye movement velocity with proportional changes throughout the contraction duration (Robinson 1970; Van Gisbergen et al. 1981). This work has been used to inform theory on goal directed arm movements (Harris and Wolpert 1998). However, in understanding relationships between FRs and limb kinematics, the effect of differences in contraction lag (i.e., time shifted or electro-mechanical delay) between individual kinematic parameters are not well integrated; despite the importance of maximal work and contraction duration being described in some of the first analyses of fast movements (Hill 1922). Recently,

Communicated by Winston D Byblow.

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this has been supported from experiments investigating the cortical (Churchland and Shenoy 2007; Churchland et al. 2012) and spinal (Gydikov et al. 1986; Weiler et al. 2019) control of muscle activity and movement (Hallett et al. 1975; Flash and Hogan 1985; Harris and Wolpert 1998) framing neuromuscular control as changing time-evolving process throughout volition. The importance of understanding which kinematic parameters are directly or indirectly related to FRs throughout contraction duration would provide a clearer understanding of the underlying timing of descending or sensory synaptic inputs that predict and shape movement. Therefore, in building on relatively few prior MU studies during voluntary limb movements (Garland et al. 1996; Harwood et al. 2011; Harwood and Rice 2014), our aim was to compare the strength of relationships between FRs and separated kinematic parameters when accounting for an effect of contraction lag.

Unlike eye movement (Robinson 1970; Van Gisbergen et al. 1981), limb movement has relatively larger intrinsic force lag in response to FR inputs during the onset of isometric contractions (Partridge 1965; Baldissera et al. 1998) or load-moving shortening contractions (Buchthal and Rosenfalck 1960; Partridge 1966; Brown et al. 1999), with force lag attributed to the electromechanical delay (EMD) across muscle fibres and tendon structures in transferring intrinsic muscle tension (Ebashi and Endo 1968; Ford et al. 1977; Balnave and Allen 1996; Kjaer 2004; Herzog et al. 2012). During limb movement, EMD, which represents the time between measured electromyography activity and a kinematic movement response, is greater during muscle shortening as compared to isometric or lengthening contraction (Cavanagh and Komi 1979; Norman and Komi 1979), and is attributed to differences in muscle stiffness, because frequency-dependent catch-like responses of human muscle can be more enhanced during shortening contractions (Binder-Macleod and Lee 1996). Therefore, during shortening contractions, the relationship of FRs to kinematic parameters with minimal contraction lag are expected to be more directly predictive of each other (Robinson 1970; Van Gisbergen et al. 1981; Goldberg et al. 1998), as compared to relationships with greater lag, for example FRs with limb movement velocity.

From this, FRs would be expected to have a weaker direct relationship with limb movement velocity as compared with torque, however, there is little evidence to support this at the single MU level during whole muscle shortening contractions. The analysis of the experiments were designed to account for the effect of differences in contraction lag between correlations of FRs and measured kinematic comparisons. This was accomplished by time-locking each FR interval from single MU train recordings throughout agonist muscle shortening contractions (Fig. 1, panels A and B), and linking these time coordinates with the separated kinematic

parameters. We hypothesized a stronger relationship will occur between FRs and elbow extension torque as compared with either velocity or position.

Methods

Participants

Fifteen adults (11 males and 4 females, 20–34 years old) free of neurological or orthopaedic illness consented and participated in 34 experimental sessions.

Experimental set-up

Seated upright in a dynamometer (humac norm, computer sports medicine Inc., MA, USA) the upper limb, shoulders and hip were secured. The left elbow was aligned to the axis of rotation and the range of motion (ROM) occurred along the sagittal plane with the forearm in the neutral or semi-pronated position. Signal acquisition of calibrated torque, angular velocity, and position from the dynamometer during elbow extensions were analogue–digital converted (power-1401, Cambridge electronic design, Cambridge, UK) and each sampled at 1 kHz (spike2, version 7, Cambridge electronic design).

Intramuscular electromyography (EMG)

Sterilized intramuscular electrodes (102 µm diameter insulated steel wire, California fine wire company, USA) were inserted into the mid-point and distal aspect of the anconeus and distal aspect of the lateral head of the triceps brachii using a 27-gauge hypodermic needle. Intramuscular EMG in the anconeus was recorded from a bi-polar configuration and grounded over the clavicle with a 2.5 × 2.5 cm surface electrode (Harwood et al. 2011; Harwood and Rice 2012, 2014). A monopolar intramuscular electrode configuration was used for the lateral head of the triceps brachii with a reference and ground surface electrode placed on the acromion process and deltoid muscle, respectively. Through pilot testing, a monopolar configuration resulted in clearer MU train recordings in the triceps brachii (Fig. 1, panels A, B and D), likely due to anatomical features that differ from the anconeus (Stevens et al. 2014) in which a bi-polar electrode configuration provided better recordings (Harwood et al. 2011; Harwood and Rice 2012, 2014). Each EMG channel was differentially hardware amplified (× 100–500), band pass filtered (0.01–10 kHz, neurolog, digitimer, UK) and sampled at 25 kHz.

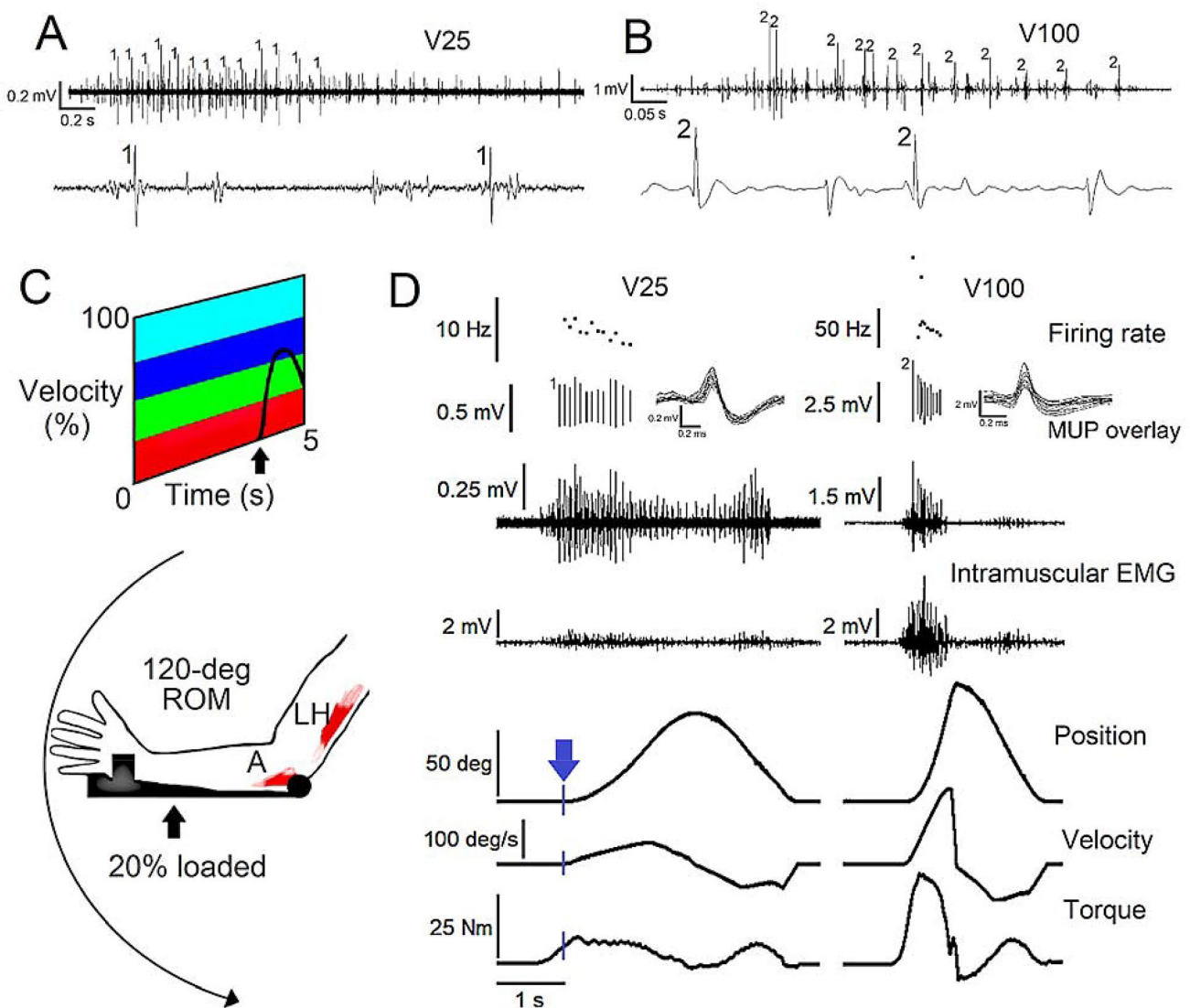


Fig. 1 The relationship of agonist muscle single MU EMG activity with measured limb kinematics during voluntary elbow extension movement. Intramuscular EMG of the lateral head (LH) of the triceps brachii muscle with a MU train identified and followed within each targeted velocity movement at **A** V25% and **B** V100% of maximum velocity during a MVC (i.e., V_{max}). **C** Cartoon depiction of the targeted velocity and elbow extension during 120 deg range of motion (ROM). For intramuscular sites, the location of the anconeus (**A**) and LH of the triceps brachii muscles are depicted. **D** Summary raw data for V25 and V100 targeted velocity conditions from an adult male

participant (age 23 years old). Kinematic parameters were linked to each FR interval throughout the common contraction time course. The MU potential (MUP) waveforms for MU1 and MU2 identified in panels A and B, are overlaid for each targeted movement velocity, respectively. As an example, the blue arrow denotes the relationship between the FR, torque, velocity, and position tracings linked to the first FR interval for MU1 at the same time coordinate, with 12.7 Hz, 17.2 Nm, 0.6 deg s^{-1} , and 0.2 deg, respectively. This was done for each measured FR interval across MU trains, and these relationships from the composite of MU trains are summarized in Figs. 2–3

Elbow extension movement

Real-time feedback of elbow joint velocity on a computer monitor was provided (Fig. 1). Elbow extension movement was commonly loaded with 20% of isometric MVC torque normalized for each participant, with the dynamometer in the unconstrained-velocity (i.e., isotonic-like) configuration. This low-load baseline of elbow joint torque

acted as common tension against each movement and was used to normalize contraction initiation across movement speeds and participants. After familiarization and practice, each participant exerted elbow extension MVC limb movements with peak velocity defined as their maximum movement velocity (V_{max}), and consisted multiple (6–9) attempts. The range of motion for each movement was 120 deg, starting at 40 and extended to 160 deg along the

sagittal plane. Four velocity ranges (0–25, 25–50, 50–75 and 75–100% of V_{\max}) were calculated relative to each participant's V_{\max} that were used during targeted velocity movements (Fig. 1, panel A). The velocity for each targeted movement was self-initiated and in a self-defined order. Each set consisted of the four different targeted movement velocities and sets were repeated 6–12 times for each participant. To minimize any effects of fatigue, rest periods of 3–5 min were provided between contraction sets. On-line examination of the quality of the intramuscular EMG signals helped to determine when sufficient representative recordings were captured for off-line analysis for each condition and participant. This often-required repositioning and reinsertion of electrodes in a different region of the muscle belly between contraction sets.

Data analysis. Intramuscular EMG signals were high pass filtered (IIR, second order, 1 kHz), and individual MU potential waveforms were sorted using the wavemark algorithm requiring manually inspection and correction based on template-matching (spike2 software, version 7.20). For inclusion, each distinct waveform, attributed to a single MU train was required to have consistent, and repeatable waveform shape within each contraction (Harwood et al. 2011; Harwood and Rice 2012, 2014). Furthermore, the amplitude of a distinct MU waveform slowly changed across successive MU potentials (Fig. 1, panels A and B), however, the shape remained relatively constant (see overlays, Fig. 1, panel D). Within each contraction, inter-spike-interval (ISI) time in seconds was calculated from pairs of successive MU potentials and the frequency was calculated. Across different contractions, electrode displacement resulted in different and new MU potential waveforms being recorded, therefore MU trains were analysed as unpaired between each contraction.

Alignment of firing rate intervals to measured elbow joint kinematics

For each contraction, MU potentials measured within each MU train were locked to the corresponding time coordinate of the contraction time course in Spike2 software. These coordinates were then used to link the measured kinematic parameters of elbow extension that occurred at the same time points (see blue arrow, Fig. 1, panel D). As the sampling rate was 1 kHz for each kinematic parameter, MU potentials were linked with calibrated torque, angular velocity, and position displacement of the elbow joint with a resolution of 1 ms. In addition, the rate of torque development (RTD), angular acceleration, and instantaneous power (product of torque and velocity) were calculated relative to the time point of the first MU potential at firing recruitment threshold for each MU train. Data from spike2 were exported, with statistical analysis and figures written in R (version 3.6).

Principal component analysis (PCA)

The aggregated dataset comprised both elbow joint kinematic (RTD, torque, acceleration, velocity, position) and non-kinematic parameters (participant, muscle, participant's sex, testing session, targeted velocity, and MU train). Parameters were scaled to a standard normal distribution and centred prior to PCA using the package 'ggfortify' (Tang et al. 2016).

Mixed effects linear regression

Additive linear regression from the packages 'lme4' (Bates et al. 2015) and 'lmerTest' (Kuznetsova et al. 2017; Luke 2017) was used to estimate the statistical dependence of FRs from the aggregated dataset. To minimize the leverage effect on linear regression by the few high frequency FRs that are physiologically relevant (i.e., doublets), FRs were transformed by the natural logarithm. The model was fit with fixed effects that included elbow joint kinematic parameters, participants' sex, and muscle (anconeus or triceps brachii), and random intercept effects that were non-kinematic including the participant (Tenen et al. 2014), MU train and the targeted velocity.

Correlation

Between FRs and kinematic parameters, probability distribution estimates of Pearson's correlations were calculated using bootstrap simulation from the package 'boot' (Davison and Hinkley 1997; Canty and Ripley 2019). As distributions were unimodal, we used bootstrapping as a nonparametric approach with data normalized per participant (Efron 1979; Wagstaff et al. 2009). Furthermore, bootstrap resampling was stratified by participant and consisted of $1 \cdot 10^5$ iterations per probability distribution estimate (Fig. 3). When subset by participant, correlations were stratified by targeted velocity. Statistical significance was determined by the range of bootstrapped Pearson's r coefficients not crossing zero. To quantify indirect relationships between FRs and kinematic parameters, multiple correlation was calculated based on the product of statistically significant stepwise correlations throughout contraction time course.

Results

During voluntary elbow extensions at four different targeted movement velocities along a fixed plane, 856 MU trains were measured from intramuscular EMG recordings during separate agonist muscle shortening contractions (Table 1). The effect of contraction lag between targeted limb movement comparisons was accounted for

Table 1 Motor unit trains during muscle shortening contraction

Parameter		
Isometric MVC (Nm)	65 ± 18 (37–90)	
Movement MVC (deg·s ⁻¹)	200 ± 28 (150–263)	
Muscle	Anconeus	Triceps brachii
Participants (<i>n</i>)	15	6
Sex (male: female)	11: 4	2: 4
Total MU trains (#)	628	228
MU trains (#)/participant	42 ± 19	38 ± 14
MU trains (#)/targeted velocity		
0–25% <i>V</i> _{max}	166	72
25–50	153	69
50–75	128	26
75–100	181	61
Median FR (Hz)/targeted velocity		
0–25% <i>V</i> _{max}	15 (12–18)	17 (13–21)
25–50	16 (12–21)	20 (15–26)
50–75	20 (14–26)	24 (18–35)
75–100	26 (19–36)	31 (23–42)

The aggregated dataset comprised 11,022 FR intervals from 856 MU trains that were measured from 15 participants. Single MU recordings were in two agonist muscles during voluntary shortening contraction, that resulted in elbow extension movement. Values are mean ± standard deviation, and for FRs the median (1s–3rd inter-quartile range). Successful recordings of MU trains occurred in 15 participants for the anconeus and 6 participants for the lateral head of the triceps brachii muscle

by instantaneously linking each FR interval to limb kinematic parameters (see Fig. 1, panel D). From PCA of the aggregated dataset, the proportion of cumulative variance explained from included parameters was > 90% by the eighth principal component rotation (Supplement Table 1). With the explained variance in principal components one (27%) and two (19%), attributed to the largest eigenvectors of elbow extension torque and velocity, respectively.

From the aggregated dataset, the response of FRs analysed by linear regression (adjusted R^2 63%), resulted in kinematic parameters of elbow extension RTD (t value 24.3, $p < 0.001$) and torque (t value 16.4, $p < 0.001$) having the strongest estimated statistical difference to effect FRs, as compared to acceleration (t value – 6.2, $p < 0.001$), velocity (t value – 12.8, $p < 0.001$) and position (t value – 5.4, $p < 0.001$). From non-kinematic parameters, the difference between the anconeus and triceps brachii muscles had no significant effect on FRs (t value – 0.14, $p = 0.88$), but a sex-related effect (t value – 4.0, $p = 0.002$) indicated that FRs were ~ 8 Hz higher in females as compared to males based on the slope constant.

The relationship between FRs and limb kinematic parameters across targeted velocities was explored through

bootstrap correlation (Figs. 2 and 3) in the anconeus (panels A–F) and lateral head of the triceps brachii muscles (panels G–L). In both muscles, the strength of correlations were similar for the same associations, with the variability and shifts of data points having similar patterns between the different targeted movement velocities (25, 50, 75 and 100% of V_{\max}). Correlations are depicted in a female participant (Fig. 2) and from the aggregated dataset of all participants (Fig. 3).

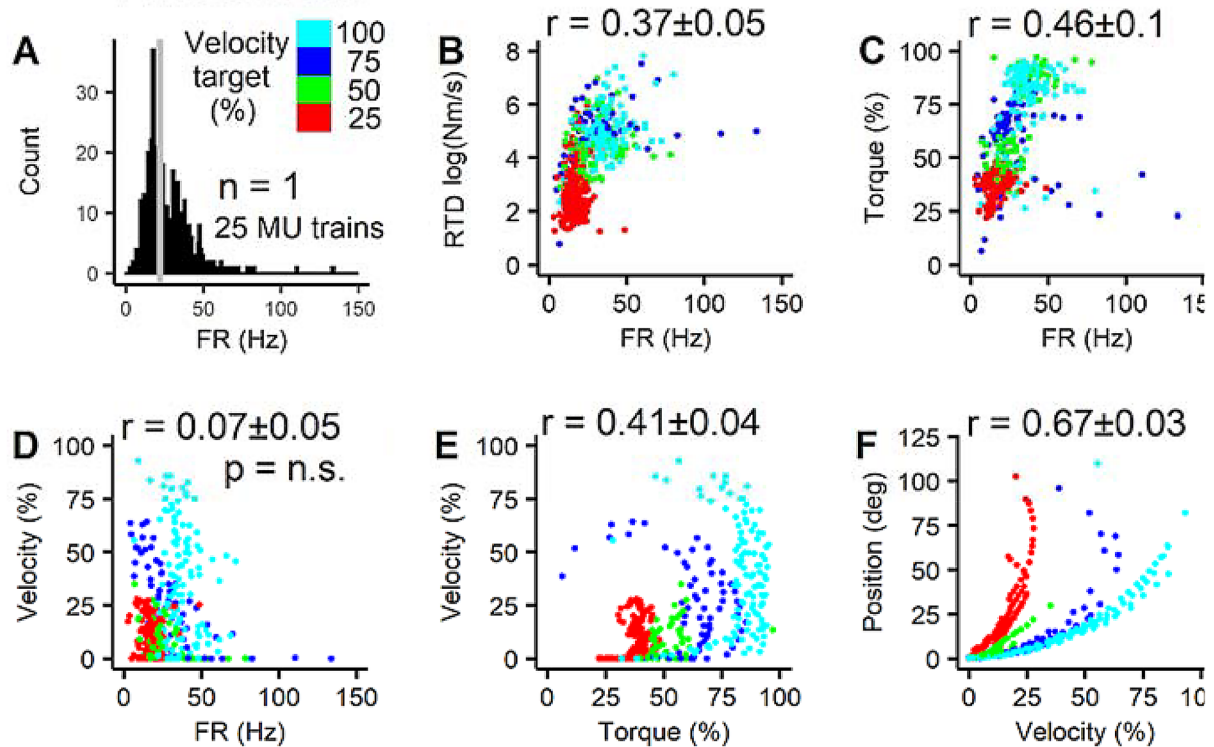
The relationship between FRs with elbow extension RTD and torque was significantly correlated (Figs. 2 and 3, panels B, C, H and I), however, the relationship between FRs and elbow extension velocity was not significantly correlated (Fig. 3, panels D and J). Through correlation, this indicated that FRs were more directly related to torque parameters but were less directly related to elbow extension velocity. Instead, FRs were indirectly related to elbow extension velocity through a stepwise ordering of correlations between FRs and torque (Figs. 2 and 3, panels C and I), and torque with velocity (Figs. 2 and 3, panels E and K).

From raw data tracings during limb movement (Fig. 1, panel D), the stepwise ordering is observed from the succession of peak values throughout contraction time course from FRs to torque to velocity and to position, which were all significantly correlated when compared in a stepwise ordering (Figs. 2 and 3). However, if FRs were compared to a non-ordered kinematic parameter, such as between FRs and elbow extension velocity (that was confounded by torque), the correlation was non-significant (Fig. 3, panels D and J). Therefore, it was unlikely that FRs were directly related to limb velocity or position, but that higher movement velocity was attributed to higher preceding magnitudes of elbow extension torque (i.e., acceleration) and FRs (Figs. 2 and 3, panels E and K). However, at the single MU level, this indirect relationship between FRs and limb velocity, quantified through multiple correlation between FR to torque and torque to velocity, had a low predictive value in both the anconeus and triceps brachii muscles ($R^2 = \sim 0.17$).

Discussion

In this study, FRs measured from recordings of single MU trains during agonist muscles shortening contraction were instantaneously related to elbow extension kinematics throughout movement. Each voluntary effort was self-initiated (Chen et al. 1998), and graded by contraction intensity through different targeted velocity movements (Harwood et al. 2011). To account for the effects of contraction time course across associations, each FR interval was time-locked and instantaneously linked to separated kinematic parameters with a time resolution of 1 ms, that was well below the biological delay attributed to EMD during shortening

Anconeus



Triceps brachii

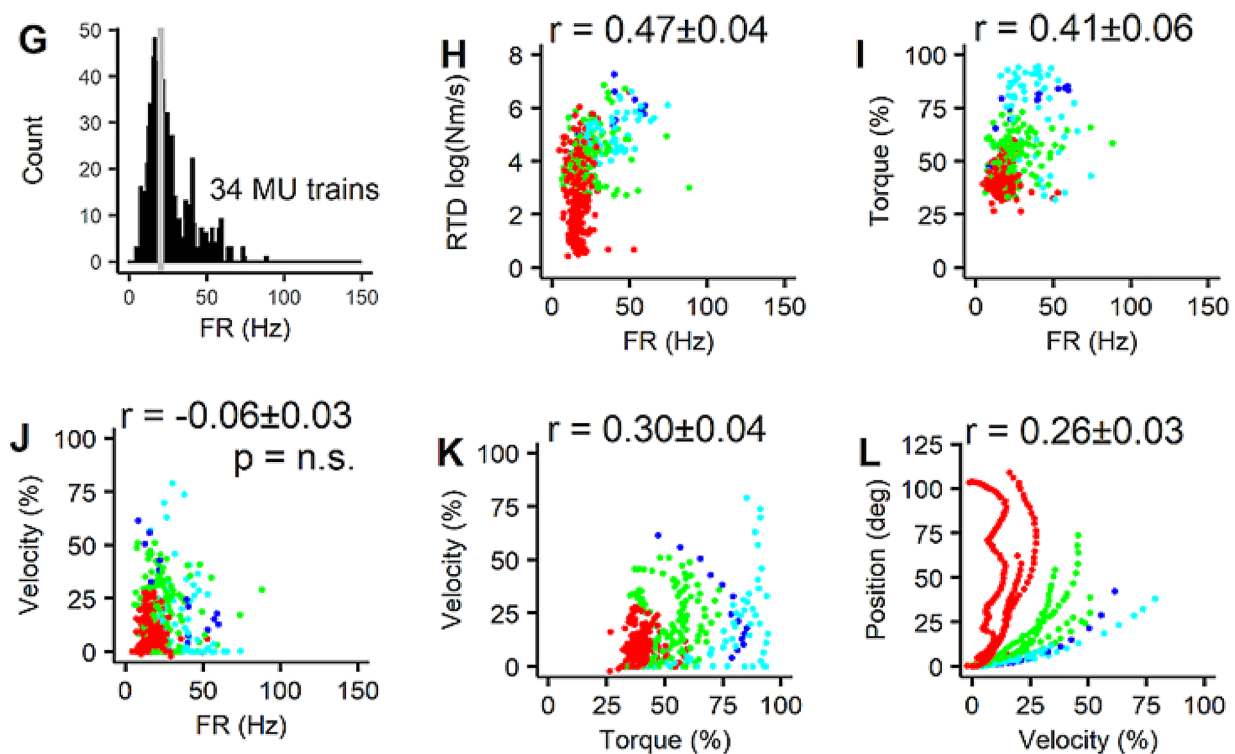


Fig. 2 Data from a female participant (21 years old). Scatterplots depict the relationship between FRs from agonist muscle shortening contraction in the anconeus (A–F) and lateral head of the triceps brachii muscles (G–L) with elbow extension kinematic parameters. Each dot represents an instantaneous association of a FR interval from single MU EMG activity across measured elbow joint kinematic parameters, with the effect of contraction time course accounted for, with 497 FR intervals in the anconeus and 790 FR intervals in the triceps brachii. Elbow extension torque, velocity, and position are relative to the participant's maximum. Elbow extension rate RTD is depicted in the log scale. Histograms representing summary frequency of FR intervals for each muscle with the grey vertical as the median statistic for the anconeus (median 22 Hz) and triceps brachii (median 21 Hz). For each scatterplot, the mean \pm standard deviation of correlation values (r) were calculated from the simulated probability distribution of bootstrap correlations stratified by targeted velocity

contraction elbow extension movements that is 26 ± 11 ms (Norman and Komi 1979). From the aggregated dataset that included both non-kinematic (i.e., participant, sex, etc.) and kinematic parameters, our results show that RTD and torque were most likely to have a significant effect on FRs, as compared to acceleration, velocity, and position. Through correlation (Figs. 2 and 3), FRs were directly related to elbow extension torque, but not directly related to elbow extension velocity. Instead, through multiple correlation between stepwise relationships of the kinematic progression (Fig. 3), FRs were indirectly related to elbow extension velocity ($R^2 = 0.17$) and position ($R^2 = 0.04$ – 0.08), however these relationships had relatively lower predictive values.

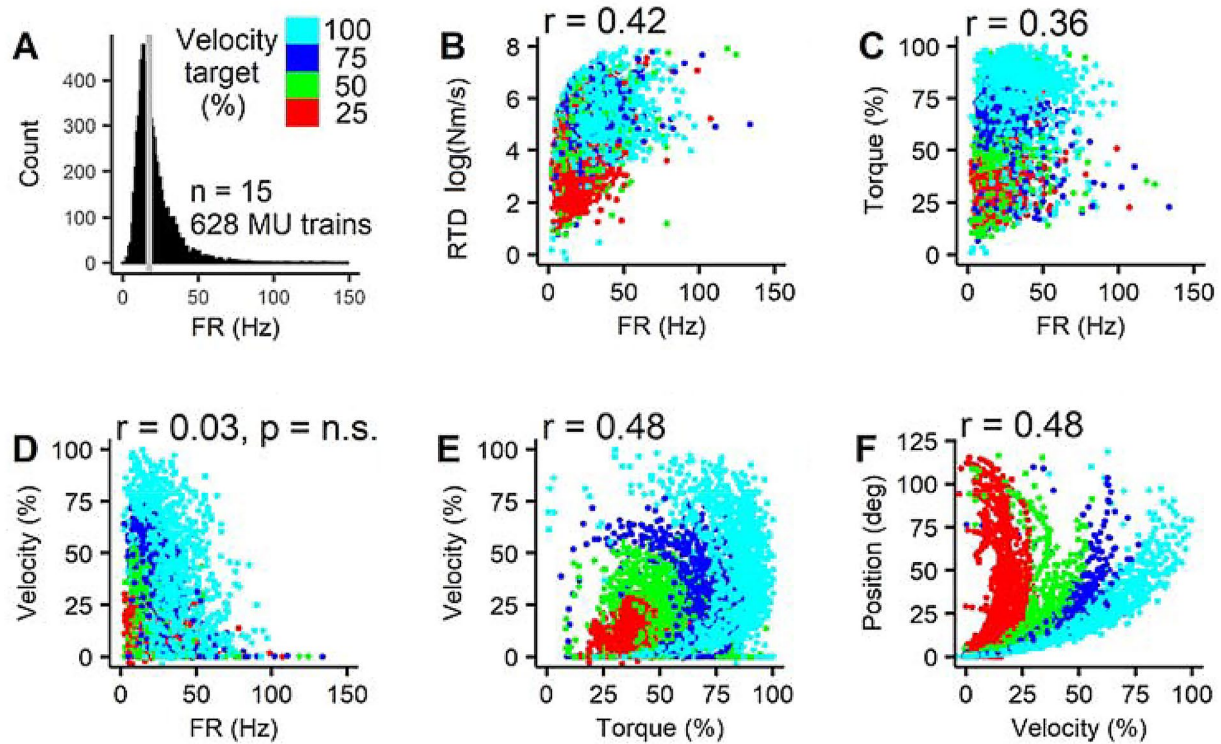
At the single MU level during voluntary shortening contraction, the weak indirect relationship between FRs and limb movement velocity (Fig. 3), suggests that limb velocity is predicted but never directly controlled by FRs, and this observation is important to consider in experiments that relate the timing of MU firings to movement speeds. Kinematic parameters of the limb lag throughout contraction time course (Partridge 1966; Cavanagh and Komi 1979; Norman and Komi 1979; Binder-Macleod and Lee 1996; Baldissera et al. 1998). Such lag was evident in the disassociation of FR to movement velocity (Fig. 3, panels D and J) suggesting that voluntary limb movement relies on the coordination of synaptic inputs between cortical (Churchland and Shenoy 2007; Churchland et al. 2012) and sensory sources (Weiler et al. 2019) that can predict and correct MU activity throughout an effect of contraction lag.

In naturalistic movements that have unconstrained-velocities, the velocity tracings are bell-shaped (Hallett et al. 1975; Garland et al. 1996; Harris and Wolpert 1998; Harwood et al. 2011), and a general principle exists across anatomical structures, as both eye and limb movement velocity tracings have been explained by a single model (Van Gisbergen et al. 1981; Harris and Wolpert 1998). However, in limb movement we show that resulted movement velocity occurs from an indirect relationship to FRs (Fig. 3), with the underlying

relation between movement speed and FRs. From this we infer that anatomical characteristics can determine the tension and consequent torques in a muscle. From MU recordings of extra-ocular muscles in non-human primates, FRs are directly related to eye movement velocity and are described to function as a 1:1 ratio (Robinson 1970), because tension was instantaneous and occurred without a significant effect of lag (Robinson 1970; Van Gisbergen et al. 1981). From single extra-ocular MU recordings, the time-delay between a stimulated input and force response is ~ 5 ms (Goldberg et al. 1998), with eye displacement controlled by few MUs that generate minimal forces under a high input frequency range (Goldberg et al. 1998). In contrast, elbow extension movement operated within a lower FR range (Table 1), and had no instantaneous relationship between FRs and elbow extension velocity (Figs. 2, 3), and this difference was attributed to contraction lag, due to the limb moment of inertia and the torque measuring device requiring the generation of relatively larger forces. For example, during limb movement, kinematic parameters of torque, velocity, and position relative to FRs, lag throughout contraction time course (Fig. 1, panel D), and in agreement with a reduced preparation (Partridge 1966), with the limb expectedly gaining momentum throughout contraction duration. As compared to limb movement, minimal contraction lag (i.e., EMD) may not significantly impact motor control in smaller and lighter anatomical arrangements that have lower relative mass (i.e., eyes, fingers, toes, etc.), and this may implicate how voluntary descending (Lawrence and Kuypers 1968; Economo et al. 2018) or sensory feedback controls (Weiler et al. 2019) are anatomically dependent. An extremity with lower relative mass would have a closer relationship between force and acceleration (based on Newton's second law, $\text{force} = \text{mass} \times \text{acceleration}$) to be controlled by motor unit inputs, like during eye movements (Robinson 1970; Goldberg et al. 1998) or presumably during finger movements. For example, fingers are evolved to have low mass that can perform dexterous interaction with the environment, therefore, if the fingers have less contraction lag, FRs would be expected to have a more direct relationship to finger movement velocity, and may explain how finger movement velocity is correlated to specific representations in sensory-motor cortex (Ejaz et al. 2015). Whereas, an extremity with higher relative mass (i.e., upper limb), would have a greater disparity between force and acceleration during faster movements (Fig. 3) and may rely more on corrective short-latency sensory feedbacks to aid in movement precision (Weiler et al. 2019).

During shortening contractions that result in limb movement (Fig. 3), current results of an indirect relationship between FRs and movement velocity are in some agreement with other reports during isometric contraction that infer ballistic movement speed (Desmedt and Godaux 1979).

Anconeus



Triceps brachii

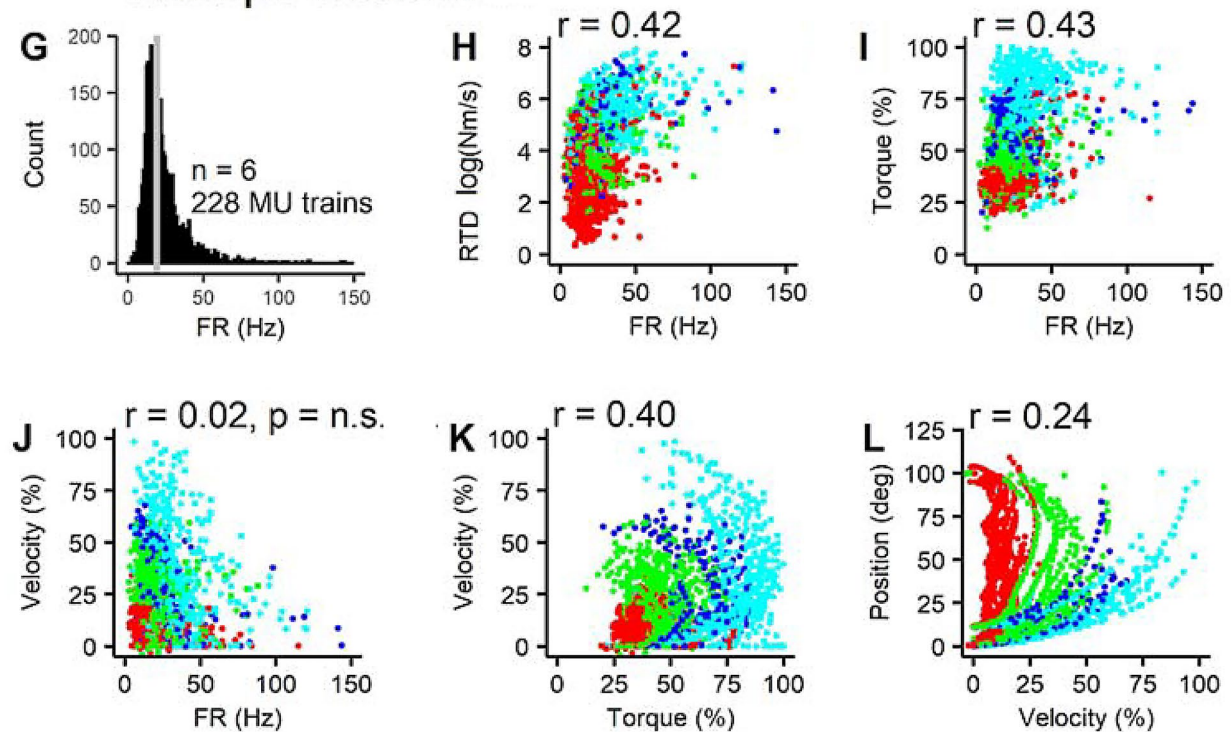


Fig. 3 Aggregated data from all participants. Scatterplots depict the relationship between FRs from agonist muscle shortening contraction in the anconeus (A–F) and lateral head of the triceps brachii muscles (G–L) with elbow extension kinematic parameters. Each dot represents an instantaneous association of a FR interval from single MU EMG activity across measured elbow joint kinematic parameters, with the effect of contraction time course accounted for, with 7640 FR intervals in the anconeus and 3382 FR intervals in the triceps brachii. Elbow extension torque, velocity, and position are in percentages relative to each participant's maximum. Elbow extension RTD is depicted in the log scale. For the number of MU trains for each targeted velocity condition refer to Table 1. Histograms representing summary frequency of FR intervals for each muscle with the grey vertical as the median statistic for the anconeus (median 17 Hz) and triceps brachii (median 19 Hz). For each scatterplot, the mean correlation value (r) was calculated from the simulated probability distribution of bootstrap correlations stratified by participant, and the standard deviation of the bootstrap distribution was between $r=0.01$ – 0.02 , see Supplement Table 2 for estimate values and ranges

However, this remains a tenuous comparison between isometric and shortening contraction, as differences are found across cortical motor neurons (Churchland and Shenoy 2007; Churchland et al. 2012), lower motor neuron intrinsic excitability (Hyngstrom et al. 2007), averaged MU FRs (Desmedt and Godaux 1979; Gydikov et al. 1986; Howell et al. 1995; Garland et al. 1996; Harwood et al. 2011; Harwood and Rice 2012, 2014; Kallio et al. 2013), and with length-dependent and altered calcium sensitivity at the muscle fibre (Ford et al. 1977; Balnave and Allen 1996; Edman 2014). During shortening contraction, the patterns in Fig. 3 were representative of each participant (Fig. 2) in both the anconeus and lateral head of the triceps brachii muscle. Although quantifying power has been used widely to describe muscle work during movement (Hill 1922), we found it was less informative when related to instantaneous FRs during limb movement (Supplement Fig. 1, panel A), as FRs were correlated to torque, but not velocity (Fig. 3). Furthermore, additional associations were calculated that did not follow an ordered kinematic progression, and to highlight some FR relationships that were spurious and weakly correlated to kinematic parameters that had greater contraction lag (Supplement Fig. 1).

In humans, we have no direct way to quantify descending synaptic inputs to the MU pool, but similar to other reports in humans (Desmedt and Godaux 1979; Gydikov et al. 1986; Garland et al. 1996; Harwood et al. 2011, 2012; Harwood and Rice 2014) FR increases dependent on targeted movement velocity (Table 1) was representative of increasing gradations of likely descending excitatory drive to the MU pool (Lawrence and Kuypers 1968; Harwood et al. 2011). From reduced preparations in the cat, another factor that may have explained the disassociation between FRs and limb movement velocity during elbow joint rotation, was that the intrinsic state of lower motor neuron excitability. This likely would have been lower during movement through antagonist

muscle stretch reflex inhibition (Hyngstrom et al. 2007; Johnson and Heckman 2014), and has only been observed during decerebrate conditions.

The FR ranges in this muscle group (Table 1 and Fig. 3) were in agreement with prior observations (Del Valle and Thomas 2005; Dalton et al. 2010; Harwood et al. 2011, 2012, 2013; Harwood and Rice 2014). However, based on linear regression, we found that higher FRs measured in the triceps brachii were also explained by a sex-related effect, and this requires further investigation, because during isometric contraction there is no reported difference in FRs between sexes in the first dorsal interosseous muscle (Parra et al. 2020). Despite similar FR responses to voluntary contraction between muscles (Figs. 2 and 3), the anconeus additionally acts to stabilize the elbow joint (Le Bozec and Maton 1982, 1987; Coriolano et al. 2009; Miguel-Andres et al. 2017) but undergoes relative fascicle length changes like the triceps brachii (Stevens et al. 2014), which is the primary agonist muscle (Le Bozec and Maton 1987; Harwood et al. 2013). From ramp isometric contractions, MUs in both the anconeus and triceps brachii muscles have FR increases, but differ in MU recruitment thresholds (Harwood et al. 2013). Although the effect of the muscle on FRs was non-significant from linear regression, it remains important to consider how anatomical differences within muscle synergists may affect the relationship between FRs and movement velocity. For example, as the anconeus muscle stabilizes the elbow joint and is active just prior to the triceps brachii during voluntary elbow extension (Le Bozec et al. 1980; Maton et al. 1980; Le Bozec and Maton 1987; Harwood et al. 2013), this would likely contribute towards a small EMD increase (on the order of ms) in the anconeus as compared to the triceps brachii muscles.

We were limited in our ability to classify recorded MU EMG activity by MU type or size and we did not measure the effect of ordered MU recruitment within participants. However, faster movement speeds would be expected to have compressed timing of MU recruitment thresholds towards contraction onset (Desmedt and Godaux 1979; Harwood and Rice 2012). We relied on a relatively small sample of MU trains per participants to what are likely active during shortening contraction at high movement velocity, and sampled a larger proportion of the MU pool in the anconeus than the triceps brachii, as MU number estimates in the anconeus are approximately four-fold lower compared to other upper limb muscles tested (Boe et al., 2006; Stevens et al. 2013). Across targeted velocity movements, MU trains were likely resampled within participants during lower contraction intensities (Rich et al. 1998), and therefore we relied on stratifying MU data per participant (Tenan et al. 2014) and statistically accounted for the participant and resampled MU trains using linear regression and bootstrapping. Because bootstrap correlation can be used as a nonparametric approach

(Efron 1979; Wagstaff et al. 2009), we did not adjust for nonlinear components in scatterplot relationships (Figs. 2 and 3), but instead used a higher number of bootstrap iterations to increase confidence in the resulted correlation and error estimates (Supplement Table 2). Relating elbow joint kinematics as a proxy to contractile mechanics at the level of the muscle is indirect, which at the muscle fibre and sarcomere are shown to have force–velocity, force–length and length-dependent differences during shortening contraction preparations in response to injected current inputs (Ford et al. 1977; Edman 1979, 2014; Balnave and Allen 1996; Brown et al. 1999; Brown and Loeb 2000). Furthermore, as movement occurred with a 20% of MVC torque load, this may have contributed to greater contraction lag between FR and velocity that would be minimized during lower loads (i.e., faster movements). However, as the torque load was relatively low and easily overcome by participants, this was unlikely to change the main conclusions. More general limitations were in only studying a stereotypic movement behaviour that occurred along a single joint and plane of movement, however, velocity tracings were comparable to goal-direct arm movements in other reports (Hallett et al. 1975; Desmedt and Godaux 1979; Garland et al. 1996; Harris and Wolpert 1998). Likewise, we did not measure single MU EMG activity in antagonist muscles (Hallett et al. 1975) or in other supporting muscles that stabilize the upper limb apart from the elbow, but are likely important during more complex movement tasks (Weiler et al. 2019).

In summary, during limb movement, agonist muscle FRs were more directly related to the kinematic parameter of torque, but not velocity or position due to contraction lag. Instead, FRs were indirectly related to velocity and position through a stepwise ordering of the kinematic progression (multiple correlation of FR to torque to velocity and to position). In highlighting the importance of contraction lag between FRs and kinematic steps, this increased buffering time in the limb may serve as a beneficial component between cortical and sensory neural computations, as reducing noise variance (Harris and Wolpert 1998) or permitting redundant variance (Todorov and Jordan 2002) are likely represented at the single MU level. Understanding how characterized patterns (Fig. 3) may be different during more complex movement behaviour with comparisons between muscles that actively shorten (agonist) versus actively and passively lengthen (antagonist) are important next steps to understand how voluntary neuromuscular controls coordinate muscle tension and force throughout limb movements.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00221-021-06168-8>.

Acknowledgements We thank all participants for their volunteered contribution.

Funding This work was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) to E. A. Kirk (CGS-D) and C. L. Rice (No. 180970).

Availability of data and material Datasets described in this paper can be accessed by correspondence with the authors on reasonable request.

Code availability All analyses were supported from open source software packages in R, specific code described in the current study can be accessed by correspondence with the authors.

Declarations

Conflict of interest The authors have no competing interests.

Ethical approval In agreement with the latest revision of the Declaration of Helsinki, the local University's full research ethics board for human experimentation approved all procedures (no. 107505).

Consent to participate Each participant gave their informed consent.

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