Short interspike intervals and double discharges of anconeus motor unit action potentials for the production of dynamic elbow extensions

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Harwood B, Rice CL. Short interspike intervals and double discharges of anconeus motor unit action potentials for the production of dynamic elbow extensions. J Neurophysiol 111: 2039–2046, 2014. First published February 19, 2014; doi:10.1152/jn.00412.2013.—Incidence of double discharges (DDs; >100 Hz) and short interspike intervals (ISIs; >50 to <100 Hz) is reported to vary widely among different muscles and tasks, with a higher incidence in motor unit (MU) trains of fast muscles and for the production of fast contractions in humans. However, it is unclear whether human muscles with a large composition of slower motor units exhibit DDs or short ISIs when activated with maximal synaptic drive, such as those required for maximal velocity dynamic contractions. Thus the purpose of this study was to determine the effect of increasing peak contraction velocity on the incidence of DDs and short ISIs in the anconeus muscle. Seventeen anconeus MUs in 10 young males were recorded across dynamic elbow extensions ranging from low submaximal velocities (16% of maximal velocity) up to maximal velocities. A low incidence of DDs (4%) and short ISIs (29%) was observed among the 583 MU trains recorded. Despite the low incidence in individual MU trains, a majority (71% and 94%, respectively) of MUs exhibited at least one DD or short ISI. The number of short ISIs shared no variance with MU recruitment threshold ($R^2 = 0.02$), but their distribution was skewed toward higher peak velocities ($G = -1.26$) and a main effect of peak elbow extension velocity was observed ($P < 0.05$). Although a greater number of short ISIs was observed with increasing velocity, the low incidence of DDs and short ISIs in the anconeus muscle is likely related to the function of the anconeus as a stabilizer rather than voluntary elbow extensor torque and velocity production.

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VOLUNTARY TORQUE PRODUCTION in muscles that control joint movements occurs in response primarily to increases in two primary motor unit (MU) mechanisms: recruitment and discharge rate (Heckman and Enoka 2012). However, in addition to these fundamental properties, other MU mechanisms function to amplify and optimize the resultant mechanical output of the neuromuscular system (Garland and Griffin 1999; Semmler 2002; Semmler et al. 2004). One mechanism is the modification of interdischarge interval temporal variability in a MU train to which the muscle is very responsive (Binder-Macleod and Kesar 2005). Double discharges (DDs) or short interspike (ISI) intervals early in an MU train of action potentials have been shown to greatly increase the torque output (up to 20%) and the rate of torque development (up to 50%) in animal (Binder-Macleod and Barrhied 1992) and human muscle (Binder-Macleod and Kesar 2005; Garland and Griffin 1999) without relying on a sustained increase in the average rate of MU discharge. Studies using percutaneous electrical stimulation report the optimal ISI range for generation of maximal tetanic tension is 5–10 ms (Stein and Parmiggiani 1979; Zajac and Young 1980a). Accordingly, recent studies of voluntary force production have defined DD as the consecutive discharge of two action potentials belonging to the same MU at ISIs of less than 5 ms (>200 Hz) (Van Cutsem et al. 1998; Van Cutsem and Duchateau 2005) or less than 10 ms (>100 Hz) (Christie and Kamen 2006; Mrówczyński et al. 2011), whereas ISIs of less than 20 ms (>50 Hz) but greater than 10 ms (<100 Hz) are referred to as short ISIs (Griffin et al. 1998). Either of these events is often observed at, or near, the beginning of a train of MU action potentials. Many studies have investigated the incidence of DDs or short ISIs (Binder-Macleod and Kesar 2005; Garland and Griffin 1999), but few have explored the functional consequences of these short ISIs during voluntary contractions in humans (Christie and Kamen 2006; Desmedt and Godaux 1978, 1979; Van Cutsem et al. 1998; Van Cutsem and Duchateau 2005). Of these studies, most have been limited to isometric contractions (Garland and Griffin 1999).

The timing of MU DDs and short ISIs during voluntary contractions is believed to be closely related to their proposed function (Binder-Macleod and Kesar 2005; Desmedt and Godaux 1978; Mrówczyński et al. 2011). These functions include absorbing the resting slack of the muscle to enable linear isometric force production, increasing series elastic stiffness for greater force transmission (Binder-Macleod and Kesar 2005; Parmiggiani and Stein 1981; Wilson and Larimer 1968), or rapid summation of MU twitch tensions to increase the rate of isometric torque production (Desmedt and Godaux 1978; Mrówczyński et al. 2011; Van Cutsem et al. 1998). Although DDs have been observed periodically in long trains of MU action potentials (Bawa and Calancie 1983; Kudina and Alexeeva 1992; Westad et al. 2004) and at termination of isometric force production (Kudina and Alexeeva 1992; Kudina and Churikova 1990; Stephenson and Maluf 2010), they are more often found at or near minimal firing rates (Bawa and Calancie 1983; Calvin and Schwindt 1972) when MUs are first recruited during low isometric torque contractions (Bawa and Calancie 1983; Denslow 1948; Kudina 1974; Kudina and Churikova 1990), or preceding fast ballistic isometric contractions (Bawa and Calancie 1983; Desmedt and Godaux 1977). Similarly, short ISIs have been noted preceding moderately fast (<250°/s) dynamic contractions in 97% of triceps brachii MUs recorded (Griffin et al. 1998). Furthermore, increases in peak shortening velocity have been demonstrated in muscles stim-
ulated initially with high-frequency stimulation indicating a role for DDs and short ISIs in maximizing contraction velocity during initial shortening (MacIntosh et al. 2008).

Another important factor related to the incidence of DDs or short ISIs in humans is motor unit type. Although equivocal (Garland and Griffin 1999), more often DDs and short ISIs (<20 ms ISI) are observed in higher threshold motor units in humans (Griffin et al. 1998; Kudina 1974), which presumably innervate predominantly type II muscle fibers with faster contractile properties. The force-frequency relationships of slow and fast muscle fibers have been shown to differ in animal preparations (Fitts et al. 1998), between fast and slow whole human muscles (Bellemare et al. 1983), and between fast and slow motor units of a single muscle (Thomas et al. 1991). Generally, slower muscles reach tetanic fusion or peak forces at lower stimulation frequencies than faster muscles. Therefore, muscles with slower twitch contractile properties and a greater type I fiber composition likely do not require the high rates of activation potentially provided by a DD to reach a maximal level of torque development and, ultimately, maximal shortening velocities. Rather, torque production in slower muscles may experience similar relative changes in mechanical output when activated with short ISIs (<20 ms) to those observed when faster muscles are subjected to DDs (ISI < 10 ms). Studies of the cat hindlimb muscles, which range from slow to fast, have shown that the incidence of DDs varies widely (8–95%) among motor neurons during slow locomotion (Hoffer et al. 1987; Zajac and Young 1980b). To date, no study has investigated the effect of DDs or short ISIs on peak shortening contraction velocity in either slow or fast human skeletal muscles. Thus the purpose of the present study was to determine the effect of increasing resultant peak shortening contraction velocity on the incidence of MUDDs and short ISIs in a muscle with a large composition of slow motor units. On the basis of previous investigations of human MU behavior, we hypothesized that in the anconeus muscle, during its contribution to elbow extensor movements, 1) few MUDDs would occur but short ISIs would be more prevalent as peak elbow extension velocity was increased, and 2) MUDDs and short ISIs would occur more frequently during the first ISI (initiation of force production) compared with all subsequent ISIs of a recruited MU train.

METHODS

Instantaneous MU discharge rates and ISIs of the anconeus and elbow extension torque, position, and velocity were recorded during dynamic contractions of varying peak velocities in 10 young men (26 ± 2 yr, 177.3 ± 8.5 cm, 77.7 ± 7.0 kg) free from orthopedic, neuromuscular, and cardiorespiratory limitations. Informed written consent was obtained from all subjects prior to participation, and all procedures were approved according to the policies and guidelines of the local Research Ethics Board for human participants and conforming to the Declaration of Helsinki.

One to three visits (~1.5 h/visit) were required to ensure an adequate quantity and quality of MU recordings. Elbow extension torque, position, and velocity measures were obtained using a Biodex System 3 multi-joint dynamometer (Biodex Medical Systems, Shirley, NY) with the subject’s left shoulder joint flexed 90° and the arm abducted 20°. The subject’s arm rested on a support positioned ~10 cm proximal to the olecranon process of the ulna, and the forearm was secured in the semiprone position to a custom-built support attached to the Biodex lever arm.

The protocol has been described in detail previously (Harwood et al. 2011; Harwood and Rice 2012). Briefly, the protocol began with three (~5 s) isometric elbow extension maximal voluntary contractions (MVCs) at 60° elbow flexion (0° = full extension), of which the highest value was taken as the representative MVC and used to determine the load (25% MVC) of the subsequent dynamic contractions. Dynamic contractions were defined as those in which a predetermined load was held relatively constant and the velocity was allowed to vary throughout the range of motion (ROM). Five loaded (25% MVC) maximal velocity elbow extensions (V\text{max25}) were performed over a 120° ROM (starting from 120° elbow flexion to 0° elbow extension). Torque and velocity output were displayed on a computer screen for visual feedback during MVCs and V\text{max25}, respectively, and verbal encouragement was provided during each maximal effort. Four target peak velocities (25, 50, 75, and 100% V\text{max25}) were calculated for each subject individually from the highest V\text{max25} recorded. Four sets of at least five loaded (25% MVC) elbow extensions were performed at each of the four target peak velocities in a randomized order. Subjects were instructed to equal the peak velocity of each submaximal elbow extension performed to a horizontal cursor displayed on the computer screen that corresponded to one of the three submaximal target velocities. Additional elbow extensions were performed when subjects failed to match the target peak velocities. Therefore, the number of contractions performed often exceeded the number of contractions required for completion of the protocol. As a result, each subject performed a brief MVC (~5 s) to verify fatigue was not induced in response to the protocol. Each submaximal elbow extension was separated by an ~30-s rest, whereas MVCs and V\text{max25} were separated by at least a 2-min rest. Additional rest was allotted at the request of the subject.

Single MU action potential trains of the anconeus were recorded with custom-made insulated stainless steel fine-wire electrodes (100 μm; California Fine Wire, Grover Beach, CA). Two hooked-tip fine wires (length 15–30 cm) were passed through a 27.5-gauge hypodermic needle (Becton Dickinson, Franklin Lakes, NJ) and inserted into the belly of the anconeus ~2–4 cm distal to the space between the olecranon process of the ulna and the lateral epicondyle of the humerus. To maximize the number of single MU trains recorded throughout a protocol, two needles were inserted and withdrawn immediately, leaving the two bipolar pairs of fine wires embedded in the muscle. A common ground electrode for the fine-wire electrode pairs was placed over the styloid process of the radius and secured with surgical tape.

Intramuscular electromyography (EMG) of the anconeus was pre-amplified (100–1,000 times), high-pass filtered (10 Hz; Neurolog, Welwyn City, UK), and digitized using an analog-to-digital converter [Cambridge Electronics Design (CED), Cambridge, UK] at a rate of 15 kHz. Torque, position, and velocity data were sampled at 100 Hz. All data were stored offline for analysis, where intramuscular EMG signals were high-pass filtered at 100 Hz to remove any movement artifact.

Data analyses. Torque, position, and peak elbow extension velocity were determined using a custom software package (Spike 2 version 7.0; CED) for all dynamic contractions included in the data analysis. Average rate of torque development (RTD) was determined, beginning with a 5% MVC departure from baseline torque to the attainment of the requisite load, and normalized to MVC. Peak velocity was expressed relative to V\text{max25}. For each contraction in which a MU discharged either a DD or short ISI, the absolute constant error [(peak velocity − target velocity)/target velocity] × 100%] was calculated. Average absolute constant errors were computed for the full range of elbow extension velocities and for each of the target velocities.

Single MUs were identified using a template matching algorithm (Spike 2 version 7.0), which amassed waveforms of sequential action potentials sharing similar temporal and spatial characteristics. The ultimate determinant in deciding whether an action potential belonged within a train of MU action potentials was visual inspection by an
experienced investigator (BH). Motor unit discharge times (ms) were determined for each MU action potential from which ISIs and subsequently instantaneous MU discharge rates were calculated between each successive MU action potential (Spike version 7.0). The inclusion criteria for MUs to be included in the statistical analysis required that each MU fired at least five consecutive action potentials, 2) was active during both the initiation phase (torque development) and movement phase of each elbow extension, and 3) was consistently present during each set of dynamic contractions.

An instantaneous MU discharge rate was recorded for each ISI sequentially until peak velocity was attained, and an average MU discharge rate was calculated for each MU train. Double discharges (>100 Hz) and short ISIs (>50 to <100 Hz) were not included in the calculation of average MU discharge rate. The number of instantaneous MU discharge rates recorded for a single MU train ranged from 4 to 24, for which 24 represented the last functional discharge (preceding peak contraction velocity) of the slowest firing single MU recorded. Double discharges (>100 Hz, or <10 ms) and short ISIs (>50 to <100 Hz, or 10 to <20 ms) were identified within each MU train meeting the inclusion criteria for a dynamic contraction. Two separate analyses were performed for DDs and short ISIs. The first involved determining the incidence and number of DDs and short ISIs over the first 4 to 24 ISIs, which was dependent on the length of each MU action potential train. The second focused on the incidence of DDs and short ISIs for the 1st ISI, because the discharge of short ISIs during the 1st ISI has been identified as a potential mechanism by which RTD may be increased (Bawa and Calancie 1983; Van Cutsem et al. 1998). Recruitment thresholds of MUs were also determined for MU action potential trains meeting the inclusion criteria for both analyses as the relative force (%MVC) at which the first MU action potential discharged.

Statistical analysis. To investigate the difference between the expected and observed frequencies of DDs and short ISIs, $\chi^2$ tests were performed across all elbow extension velocities and for each range of peak elbow extension velocity separately. Separate frequency histograms were generated for DDs and short ISIs relative to peak elbow extension velocity and MU recruitment threshold. Skewness ($G$) was determined for each histogram, where a value of zero indicates a symmetrical distribution, a positive value indicates a leftward skewed distribution, and a negative value indicates a rightward skewed distribution.

Analytical statistics were performed for short ISIs over the first 24 ISIs because only one MU recorded elicited more than one DD over the first 24 ISIs and the incidence of short ISIs and DDs during the 1st ISI is a binary variable. Shapiro-Wilks tests of normality determined that the number of short ISIs over the first 24 ISIs was not normally distributed relative to peak elbow extension velocity ($P < 0.05$) or MU recruitment threshold ($P < 0.05$). Therefore, Kruskal-Wallis ANOVAs were used to determine whether a main effect of peak elbow extension velocity or MU recruitment threshold was present. Because of unequal variances between the average incidence of DDs and short ISIs for the four peak elbow extension velocity ranges (<25, 25 to <50, 50 to <75, and ≥75% $V_{\text{max}25}$) and MU recruitment threshold ranges (<10, 10 to <15, 15 to <20, and ≥20% MVC), Welch’s t-tests were used to test whether there was a difference between any two ranges on determination of a main effect. Regression analyses were performed, and coefficients of determination ($R^2$) were calculated to demonstrate the amount of shared variance between the number of short ISIs and MU recruitment threshold, between the number of short ISIs and RTD, and between the number of short ISIs and peak contraction velocity.

RESULTS

A total of 583 MU trains were recorded from 17 distinct MUs active throughout the whole protocol in 10 subjects (1–3 MUs per subject). Representative data from one MU for which a short ISI was recorded at 75% $V_{\text{max}25}$ (left) but not 25% $V_{\text{max}25}$ (right) is shown in Fig. 1. The distribution, average recruitment thresholds, and discharge rates of the recorded MUs in addition to contractile properties of the elbow extensions from which these MUs were recorded are presented in Table 1. The average absolute constant error for contractions across the full range of velocities was 9.3 ± 8.1%, wherein the ability of subjects to equal the target velocity was greater at higher velocities (15.6 ± 8.5% at 25% $V_{\text{max}25}$ vs. 3.9 ± 4.4% at 100% $V_{\text{max}25}$). Of the 17 MUs recorded, 12 MUs (71%) exhibited DDs and 16 (94%) exhibited short ISIs. The number of short ISIs over the first 24 ISIs was 171, of which 88 (15% of MU action potential trains) were recorded during the 1st ISI. The number of DDs recorded over the first 24 ISIs was 21. Similarly, the number of DDs recorded for the 1st ISI was 20,
which corresponded to ~4% of the total MU action potential trains recorded. A detailed description of the incidence of DDs (>100 Hz) and short ISIs (>50 to <100 Hz) in each MU is provided in Table 2. χ² tests showed that the observed frequency of both DDs and short ISIs was less than the expected frequency for the full range of elbow extension velocities investigated and within each velocity range (Table 3). The distribution of these data relative to each target velocity range and MU recruitment threshold for all ISIs and for the 1st ISI is presented in Figs. 2 and 3, respectively. The distributions of peak contraction velocities at which DDs and short ISIs were recorded were skewed toward higher velocities (G = −0.33 and 0.51, respectively), and the distribution of MU recruitment thresholds at which short ISIs were recorded was skewed toward lower MU recruitment thresholds (G = 0.84) when all 24 ISIs were considered (Fig. 2, A and B). However, the distribution of MU recruitment thresholds in which DDs were observed was normally distributed (G = −0.09) about a mean and standard deviation of 11.3 ± 7.2% MVC (0.2–5.6% MVC, Fig. 2B). When only the 1st ISI was considered, the peak contraction velocities in which a DD or short ISI were observed were skewed (G = −0.29 and −1.26, respectively) toward higher velocities (Fig. 3A). However, DDs were only observed in higher threshold MUs (>10% MVC) during the 1st ISI, and the distribution of short ISIs during the 1st ISI was bimodal with a greater number of short ISIs being recorded in both the highest and lowest MU recruitment threshold ranges (Fig. 3B).

Regression analyses demonstrated no shared variance between MU recruitment threshold and the number of short ISIs recorded (R² = 0.02, P = 0.14) when all ISIs were considered. However, a greater number of short ISIs was recorded during contractions that exhibited higher RTDs (R² = 0.24, P < 0.05) and greater peak velocities (R² = 0.14, P < 0.05). Moreover, the Kruskal-Wallis ANOVA revealed a main effect of target velocity for short ISIs [χ²(3) = 10.42, P < 0.05]. Welch’s t-tests demonstrated fewer short ISIs at <25, 25 to <50, and 50 to <75% Vmax25 than at ≥75% Vmax25 (P < 0.05, Δ = 1.25–0.86) and fewer short ISIs at <25 and 25 to <50% Vmax25 than at 50 to <75% Vmax25 (P < 0.05, Δ = 0.52 and 1.86, respectively; Fig. 2A).

### DISCUSSION

Anconeus MUs tracked during the production of a range of elbow extension velocities (16–100% Vmax25) in the present study exhibited very few DDs (4% of MU action potential...
trains, 1.2 ± 1.1) and short ISIs (29% of MU action potential trains, 10.1 ± 12.3) across the first 24 ISIs of the MU trains recorded. Even fewer short ISIs (15% of MU action potential trains, 5.2 ± 5.1) were observed when only the 1st ISI interval of MU action potential train was considered (Table 2). Despite the relatively low incidence of DDs and short ISIs within any individual MU action potential train in this study, overall 71% and 94% of the recorded anconeus MUs exhibited at least one DD or short ISI, respectively. The number of MUs discharging short ISIs or DDs is reported to range widely (0 – 97%) across human studies during mainly isometric tasks and is believed to be more frequent in fast-contracting muscles (Garland and Griffin 1999). However, MU studies of the slow soleus and intercostal muscles (Johnson et al. 1973; Mizuno and Secher 1989) and the relatively faster biceps brachii (Denslow 1948; Kukulka and Clamann 1981) have reported low numbers of DDs (0 – 23% of MUs) (Kudina and Alexeeva 1992; Kukulka and Clamann 1981; Whitelaw and Watson 1992), indicating that the relationship between contractile properties of the skeletal muscle and incidence of DDs is equivocal. In general, the results of the present study provide support for low incidence of DDs in slow human skeletal muscle.

The anconeus muscle provided an attractive model to investigate the incidence of DDs and short ISIs during the production of maximal velocity contractions because of its common innervation with the main elbow extensor, the triceps brachii (Fornalski et al. 2003, Hwang et al. 2004). Together they function to extend the elbow and have similar relative changes in fascicle length as a function of elbow joint range of motion (Buchanan et al. 1986; Harwood et al. 2010; Murray et al. 2000; Pereira 2013). Furthermore, the anconeus is activated throughout all contractile intensities and velocities of elbow

Table 3. \( \chi^2 \) values of double discharges and short ISIs at each elbow extension velocity range

<table>
<thead>
<tr>
<th>Elbow Extension Velocity, %V_{max}\text{25}</th>
<th>&lt;25</th>
<th>25 to &lt;50</th>
<th>50 to &lt;75</th>
<th>\geq 75</th>
<th>Sum</th>
</tr>
</thead>
<tbody>
<tr>
<td>ISI&lt;10</td>
<td>N/A</td>
<td>\chi^2 (1, N = 3) = 176.2</td>
<td>\chi^2 (1, N = 7) = 165.0</td>
<td>\chi^2 (1, N = 10) = 113.7</td>
<td>\chi^2 (1, N = 20) = 570.5</td>
</tr>
<tr>
<td>ISI&gt;10&lt;20</td>
<td>\chi^2 (1, N = 6) = 94.23</td>
<td>\chi^2 (1, N = 13) = 139.6</td>
<td>\chi^2 (1, N = 25) = 105.0</td>
<td>\chi^2 (1, N = 44) = 26.3</td>
<td>\chi^2 (1, N = 88) = 343.8</td>
</tr>
</tbody>
</table>

N/A, no \( \chi^2 \) value calculated due to no ISI<10 recorded at <25\% V_{max}\text{25}.

Fig. 2. Incidence of short ISIs (gray) and double discharges (black) relative to 4 peak elbow extension velocity ranges (A) and 4 motor unit recruitment threshold ranges (B) over the first 24 ISIs. MVC, maximal voluntary contraction.

Fig. 3. Incidence of short ISIs (gray) and double discharges (black) relative to 4 peak elbow extension velocity ranges (A) and 4 motor unit recruitment threshold ranges (B) for the 1st ISI.
On the basis of these shared properties of the anconeus and triceps brachii, it is assumed that a similar level of synaptic drive activated these muscles at the various elbow extension velocities investigated. However, the anconeus possesses fewer MUs (Stevens et al., in press) than other upper limb muscles tested (Power et al. 2012), even those of a similar size (Boe et al. 2005), and the range of anconeus MU recruitment thresholds is low (Harwood and Rice 2012; Le Bozec and Maton 1987) compared with other large force-producing muscles (Griffin et al. 1998; Seki and Narusawa 1996). Indeed, these features may have lessened the probability that the number of DDs or short ISIs would differ among anconeus MUs of different recruitment thresholds. Furthermore, during high-velocity contractions, the MU recruitment threshold range of the anconeus is compressed (Harwood and Rice 2012), contributing to the lower probability that differences between high- and low-threshold MUs would be detected. Despite these factors, intramuscular EMG signals in the anconeus exhibit high signal clarity compared with the larger triceps brachii muscles, suggesting that the number of high- and low-threshold MUs would be detected. Some (Bawa and Calancie 1983) have proposed that short DDs (4%) and short ISIs (15%) observed during the 1st ISI of anconeus MU action potential trains relative to other upper limb muscles investigated (Kukulka and Clamann 1981) is likely related to the proposed functions of DDs. Double discharges have been shown to either facilitate high rates of torque development (Desmedt and Godaux 1978; Van Cutsem et al. 1998) or to lessen the slack of elastic elements in the muscle (Binder-Macleod and Kesar 2005) and to increase series elastic stiffness for greater force transmission (Parmigiani and Stein 1981). The anconeus is responsible for less than 15% of the elbow extension torque (Zhang and Nuber 2000), and therefore it is unlikely the resultant rate of torque development is influenced greatly by the anconeus, especially considering its contractile speed (Le Bozec and Maton 1987), size (Hwang et al. 2004; Pereira 2013), and mechanical arrangement for elbow extension torque (Pereira 2013). It is also unlikely that a great deal of slack accumulates in the anconeus. The superficial anconeus tendon spans ~70% of the muscle length, but the length of the tendon in series with anconeus muscle fibers is very short compared with that of other muscles (Keener et al. 2010; Pereira 2013). Moreover, the anconeus is active at all elbow joint angles (Le Bozec et al. 1980a), and thus slackening of its elastic elements would likely only accumulate in a hyperextended position when the anconeus is inactive. Thus a role for DDs in reducing series elastic slack in the anconeus would be unnecessary and seems highly unlikely.

Some (Bawa and Calancie 1983) have proposed that short ISIs preceding ballistic (high rate of force development) iso- metric contractions require “massive synaptic inputs” to discharge action potentials in the “secondary firing range” (Calvin and Schwindt 1972; Granit et al. 1966) to achieve requisite rates of torque development. Synaptic drive to the anconeus motor neuron pool was likely high in the present study because average MU discharge rates at 75% and 100% Vmax25 (28.7 and 39.0 Hz, respectively) were higher than during isometric MVC (23.8 Hz) in the anconeus in an identical protocol (Harwood et al. 2011). Furthermore, muscle-dependent motor cortical excitability and spinal reflex studies have shown excitability to be higher during shortening than during isometric contractions (Duchateau and Enoka 2008; Duclay et al. 2011). Despite a high level of synaptic drive, low percentages of DDs and short ISIs were observed during the 1st ISI of anconeus MU action potential trains (4% and 15% of action potential trains, respectively), yet the number of anconeus MUs (94%) for which at least one short ISI was recorded in the 1st ISI was similar to the number of triceps brachii MUs (97%) exhibiting short ISIs during similar, but less intense, contractions (Griffin et al. 1998). However, it must be noted that resampling bias as a consequence of recording single MUs across repeated contractions in this study and that of Griffin et al. (1998) likely increased the probability that a MU would fire at least one short ISI. In view of this limitation, these findings indicate that regardless of the architectural, histochemical, and electrophysiological differences among muscles, a high level of synaptic drive is likely sufficient to elicit DDs in a majority of MUs. It was hypothesized that fewer DDs would be observed in the anconeus due to potential diminished responsiveness to high-frequency stimulation as indicated by the force-frequency relationships of human skeletal muscle exhibiting slower contractile speeds and greater type I fiber composition. The incidence of DDs in anconeus MU action potential trains was observed to be much less (~20%) than that reported for two other upper limb muscles, the adductor pollicis and biceps brachii (Kukulka and Clamann 1981). The type I fiber composition and contractile speed of these two upper limb muscles studied differed greatly, with the anconeus [67% type I, 80-ms
half-relaxation time (HRT) situated between the adductor pollicis (~80% type I, 131-ms HRT) and biceps brachii (~45% type I, 67-ms HRT) (Dalton et al. 2010; Johnson et al. 1973; Le Bozec and Maton 1987; Round et al. 1984). Moreover, the contractile speed and type I fiber composition of the anconeus and triceps brachii vary greatly (Le Bozec and Maton 1987), yet a similar number of MUs exhibited short ISIs (94% vs. 97%) in these two elbow extensors (Griffin et al. 1998). Thus it is unlikely differences in fiber composition or contractile speed account for the lack of DDs in anconeus MU action potential trains.

Finally, the function of the anconeus is such that high rates of torque development may not be useful or advantageous. The anconeus also assumes the role of humeroulnar stabilization (Pereira 2013) in addition to elbow extension (Buchanan et al. 1986; Murray et al. 2000). Simulations of isometric force production show that steadiness at low forces is highly dependent on muscle twitch contractile properties, the size of the motor unit population, recruitment range of the motor unit pool (Dideriksen et al. 2012), and discharge behavior of motor units (Yao et al. 2000). Generally, optimal force steadiness at low contractile forces is attained from the activation of a low number of motor units with long twitch contraction times (Dideriksen et al. 2012). The anconeus muscle has slow twitch contractile properties (Le Bozec and Maton 1987) and a low number of motor units (Stevens et al., in press). Moreover, the pattern of activation of the elbow extensors shows that anconeus muscle activation precedes that of the triceps brachii during shortening, especially at low forces (Le Bozec et al. 1980b). At MU activation immediately preceding the 1st ISI, when elbow extension force was low, a low incidence of anconeus DDs and short ISIs likely assumed a primary role of humeroulnar stabilization during initiation of fast elbow extension.

In summary, very few DDs (4%) are elicited in action potential trains of the anconeus MUs for the production of dynamic contractions. Although short ISIs in these MU action potential trains increased as a function of target velocity, the incidence was not related to MU recruitment threshold and was comparable to those previously reported for both fast- and slow-contracting muscles. Together, the results of this study indicate that the increase in the number of short ISIs with target velocity is likely related more to the level of synaptic drive and not functionally linked to an increase in the rate of torque development or a reduction in series elastic slack as has been proposed in other muscles. Rather, the low incidence of anconeus DDs may facilitate its stabilizer role at the initiation of fast elbow extensions.

GRANTS

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

B.H. and C.L.R. conceived and designed the research; B.H. performed experiments; B.H. analyzed data; B.H. and C.L.R. interpreted results of experiments; B.H. and C.L.R. prepared figures; B.H. drafted manuscript; B.H. and C.L.R. edited and revised manuscript; B.H. and C.L.R. approved final version of manuscript.

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