

Motor unit properties from three synergistic muscles during ramp isometric elbow extensions

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Abstract Many tasks require synergistic activation of muscles that possess different architectural, mechanical, and neural control properties. However, investigations of the motor unit (MU) mechanisms which modulate force are mostly restricted to individual muscles and low forces. To explore the pattern of MU recruitment and discharge behavior among three elbow extensors (lateral and long heads of the triceps brachii, and anconeus) during ramp isometric contractions, recruitment thresholds of 77 MUs in five young men were determined and corresponding MU discharge rates were tracked in 1-s epochs over forces ranging from 0 to 75 % of maximal voluntary isometric force (MVC). Across all forces, MUs in the lateral head discharged at higher rates than those in the anconeus ($p < 0.001$, $\Delta = 0.23$). When all MUs were considered, recruitment thresholds in the long head of the triceps brachii were higher than the lateral head ($p < 0.05$, $\Delta = 0.70$)

with a trend ($p = 0.08$, $\Delta = 0.48$) for higher recruitment thresholds in the long head compared with the anconeus. Together, these data indicate a potential mechanical disadvantage of the long head of the triceps brachii at 0° shoulder flexion. However, among low-threshold MUs (<10 % MVC), recruitment thresholds were lower in the anconeus than in both heads of the triceps brachii consistent with the expected twitch contractile and fiber type differences among these muscles. These findings illustrate the importance of considering synergistic relations among muscles used for a coordinated task, and the sensitivity of synergies to muscle architectural, mechanical, and possibly specific synaptic input factors.

Keywords Recruitment threshold · Discharge rate · Anconeus · Triceps brachii

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Introduction

Force production is accomplished primarily through the modulation of motor unit (MU) recruitment and rate coding in an integrative process. MUs are generally recruited in an orderly and near-linear fashion in relation to the size of the motor neuron cell body (Duchateau and Enoka 2011; Henneman et al. 1965), beginning with smaller motor neurons and proceeding to larger ones. The relative influence of MU recruitment and rate coding varies with muscle and task, and to understand the interplay between these two force-grading mechanisms, slightly different control paradigms have been proposed. In some paradigms, MUs which are recruited at low forces, or low recruitment thresholds, discharge at higher rates relative to subsequently recruited higher threshold MUs (De Luca and Contessa 2012; De Luca et al. 1982). Others have reported that MUs recruited

at higher thresholds achieve the highest discharge rates for ramp isometric contractions (Monster 1979; Monster and Chan 1977). It is likely that these control paradigms are more complex or less predictable when the combined forces of multiple muscles acting synergistically, which possess varying architectural properties, force vectors, and length-dependent mechanical properties, are activated collectively to perform a common task (Dalton et al. 2010; English et al. 1993; ter Haar Romeny et al. 1984).

The elbow extensors, comprised of the long, lateral, and medial heads of the triceps brachii and the anconeus, have different muscle fiber compositions (Le Bozec and Maton 1987), muscle architectures (i.e., fascicle lengths and pennation angles), length-dependent mechanical properties (Murray et al. 2000; van Groenigen and Erkelens 1994), and varying force distribution profiles (Buchanan et al. 1986; Murray et al. 2000). For example, the three heads of the triceps brachii have similar fiber type composition (~33 % type I), which is approximately equal and opposite to that of the fourth elbow extensor, the anconeus (60–67 % type I) (Le Bozec and Maton 1987). Moreover, twitch contraction duration is ~25 % longer in the anconeus than the lateral head of the triceps brachii (Le Bozec and Maton 1987). Despite the considerable morphological and functional differences among these muscles, all four elbow extensors are innervated by the same nerve root supply (radial, C7–C8) (Fornalski et al. 2003).

Investigations of surface-detected EMG (Buchanan et al. 1986, 1989) at low [<30 % of maximal voluntary isometric contraction (MVC)] isometric elbow extension forces showed all four elbow extensor muscles active at various EMG amplitudes (30–100 % of maximal EMG at ~30 % MVC or ~20 N m) (Harwood et al. 2011). Other studies using surface-detected EMG (Bilodeau et al. 1992; Le Bozec and Maton 1982; Le Bozec et al. 1980) have demonstrated either a plateau in anconeus muscle activation at <30 % MVC elbow extension (Le Bozec and Maton 1982; Le Bozec et al. 1980) or reported increases in anconeus EMG amplitude up to 80 % MVC elbow extension (Bilodeau et al. 1992). However, with the shoulder abducted 90° and the elbow flexed 90° , Le Bozec et al. (1980) observed lesser increases in surface-detected EMG relative to increasing force up to 80 % MVC in the long head of the triceps brachii and anconeus compared with the medial and lateral heads of the triceps brachii, which both behaved similarly. In that same study, the medial and lateral heads of the triceps brachii, and the anconeus were active from the onset of force production, whereas the activation of the long head occurred predominantly at higher force levels (Le Bozec et al. 1980). Several factors affect the surface-detected EMG–force relationship and the interpretation of these data [i.e., cross talk contamination (Le Bozec and Maton 1987), fascicle strain rates (Rau et al. 2004;

Solomonow et al. 1990), and MU control strategies (Disselhorst-Klug et al. 2009)], especially during contractions that may induce neuromuscular fatigue (Dideriksen et al. 2010; Dideriksen et al. 2011). Recording single MU properties from indwelling electrodes can overcome many of these limitations and may help resolve some of these incomplete and disparate reports.

Most reports of isometric elbow extensor MU properties (Del Valle and Thomas 2004; Garland et al. 1997; Griffin et al. 2001; Ivanova et al. 1997; Klein et al. 2001, 2002; Le Bozec and Maton 1982, 1987; Thomas and Del Valle 2001), except three (Dalton et al. 2010; van Groenigen and Erkelens 1994), have focused solely on the lateral head of the triceps brachii. None has evaluated systematically single MU properties of multiple elbow extensor muscles concurrently during higher force levels (>30 % MVC). It is important that MU properties of synergistic muscles responsible for a common task be considered both individually and as a group because various potentially contributing factors (both anatomic and neural) may shape the emergent integrative pattern of MU recruitment and discharge behavior differently. Thus, the purpose here was to investigate MU recruitment and discharge behavior of the lateral and long heads of the triceps brachii, and anconeus in relation to isometric force production at low to high contraction intensities (up to 75 % of MVC). We hypothesized based on previous studies cited above that the order of whole muscle activation during increasing isometric contraction intensities (90° elbow extension and 0° shoulder angle), as indicated by average MU recruitment thresholds of each muscle, would be the anconeus, the lateral head of triceps brachii, and finally, the long head of triceps brachii. In line with this activation order, and based on the force distribution data (Buchanan et al. 1986; Murray et al. 2000), we also hypothesized that recruitment of anconeus MUs would continue above 30 % MVC despite one previous study indicating the contrary (Le Bozec et al. 1980). Lastly, in view of the twitch contractile speed differences between the anconeus and the triceps brachii (Le Bozec and Maton 1987) and EMG–force relationships of the elbow extensors from one study (Bilodeau et al. 1992), we expected that MU discharge rates of the anconeus and long head of the triceps brachii would be lower compared with those of the lateral head of the triceps brachii.

Methods

Five young men (26.3 ± 1.9 years, 184.3 ± 6.2 cm, 86.6 ± 8.0 kg) free from orthopedic, neuromuscular, and cardiorespiratory limitations participated in the present study. Subjects provided informed written consent prior to participation, and all procedures were approved according

to the policies and guidelines of the local Research Ethics Board for human participants and conformed to the Declaration of Helsinki.

Elbow extension force was recorded using a custom built dynamometer fastened to an examination plinth on which subjects laid supine (Klein et al. 2002). The nondominant (left) arm rested in a padded elbow support attached to the horizontal platform of the dynamometer. The arm was abducted slightly ($<10^\circ$) and positioned at 0° and 90° of flexion at the shoulder and elbow joints, respectively. The medial surface of the wrist rested against a firmly padded C-shaped metal support mounted to a linear calibrated force transducer (SST-770-100A, AST Technologies, Haliburton, Ontario, Canada) so that the forearm was in the semi-prone position. Straps secured the wrist to the support and the arm to the horizontal support. Force feedback at a gain relative to each individual's MVC was displayed on a flat-screen monitor suspended from the ceiling at a distance of 1 m from the face.

Single MU potentials were recorded using custom-made bipolar intramuscular EMG electrodes inserted into the lateral and long heads of the triceps brachii, and the anconeus. Each pair of fine wire stainless steel electrodes (100 μm , California Fine Wire, Grover Beach, California, USA) was threaded through separate 27.5 gauge hypodermic needles (Becton–Dickinson, Franklin Lakes, NJ, USA) for insertion. Intramuscular electrode pairs were inserted (~ 2 cm depth) via the hypodermic needle parallel to the muscle fascicles of (1) the lateral head of the triceps brachii above the mid-shaft of the postero-lateral humerus, (2) the long head of the triceps brachii mid-shaft above the postero-medial humerus, and (3) the anconeus ~ 1 – 2 cm distal to the midpoint between the lateral epicondyle of the humerus and the olecranon process of the ulna. Three visits (~ 1.5 h per visit) were required to ensure an adequate quantity and quality of single MU recordings. Intramuscular EMG was high-pass filtered (10 Hz), pre-amplified (100–1000 \times , Neurolog, Welwyn City, England), and digitized with an analog-to-digital converter (Cambridge Electronics Design, Cambridge, UK) at a rate of 10 kHz. Force was sampled at 100 Hz, and all data were stored offline for analysis. Offline, intramuscular EMG was high-pass filtered at 100 Hz to remove any remaining motion artifact.

Single twitches of the elbow extensors were evoked using a constant voltage stimulator (DS7AH; Digitimer, Ltd., Welwyn Garden City, Hertfordshire, UK) at a pulse width of 100 μs through two custom-made aluminum foil stimulation pads (ranging from 5×6 cm to 5×12 cm depending on arm size) coated in electrode gel and firmly secured transversely over the muscle belly of the triceps brachii. The anode was positioned ~ 10 cm proximal to the olecranon process of the ulna and the cathode ~ 10 cm distal to the axilla. Current intensity of the stimulator

(80–160 mA) was increased until no additional twitch force was generated and then increased by 15 % to ensure supramaximal stimulation.

Experimental protocol

Initially, three single twitches were elicited at supramaximal stimulation intensity at 1-s intervals to determine the resting twitch tension amplitude prior to determining maximal isometric force. Next, three brief (~ 5 s) isometric elbow extension MVCs were performed with supramaximal twitch stimuli delivered immediately preceding (resting twitch), during the plateau in MVC force (interpolated twitch), and immediately following a return to baseline force levels (post-MVC twitch). Two minutes rest was allotted between each MVC effort. Voluntary activation (VA) was calculated using the twitch interpolation technique [VA (%) = $1 - (\text{interpolated twitch} / \text{control twitch}) \times 100$ %], where the control twitch is the post-MVC twitch.

Following the MVCs, three horizontal cursors at 25, 50, and 75 % MVC were placed on the screen with the top and bottom of the monitor adjusted to 100 % MVC and 5 % MVC, respectively. The x -axis frame was constant at 5 s. Subjects were asked to increase elbow extension force at a rate of 5 % MVC s^{-1} paced by the experimenter's verbal enumeration and a metronome. Upon achievement of the target force, subjects held the force steady for 5 s before returning to baseline at a rate of 5 % MVC s^{-1} . Three ramp isometric contractions at each target force were performed in a randomized fashion with 2 min of rest between low (25 % MVC) and moderate (50 % MVC) contractions, and 5 min of rest following each 75 % MVC ramp isometric contraction. Following completion of the targeted ramp isometric contractions, a final MVC attempt was performed to assess whether a reduction in maximal force generating capacity occurred as a result of the protocol. Neuromuscular fatigue in the present study was defined as "any reduction in the force generating capacity of the total neuromuscular system regardless of the force required in any given situation" (Bigland-Ritchie and Woods 1984).

Data analyses

Off-line data analyses were performed using a custom software package (Spike 2 version 7.0, CED, Cambridge, UK). Voluntary activation was calculated for each subject from the baseline MVCs preceding the ramp isometric contractions, and maximal force was determined for a 1-s period during the plateau of the pre- and post-protocol MVC. The highest force recorded from the three pre-protocol MVCs was considered as maximal force. Group means were calculated for pre-protocol VA, and for MVCs both pre- and post-protocol.

Single MUs were identified using a template matching algorithm (Spike 2 version 7.0, CED, Cambridge, UK) that considers temporal and spatial waveform characteristics of sequential action potentials. However, the ultimate determinant of whether a MU action potential belonged to a single MU was made by visual inspection by the same experienced investigator. Inclusion criteria for statistical analysis required that MUs fired consecutively for at least 3 s following recruitment. To avoid the augmentation of average discharge rates by doublet or nonphysiological firing patterns, interspike intervals of <10 ms or >150 ms were not included in the analysis.

Motor unit discharge times (s) and instantaneous MU discharge rates (Hz) were determined for each MU action potential. Average discharge rates of individual MUs were calculated for each 1-s epoch of the ramp increase in isometric force up to the target force or for as long as the MU could be tracked. Only 10 MUs were tracked at relative forces above 55 % MVC, and therefore, average discharge rates determined for 1-s epochs at relative forces below 55 % MVC only were considered in the statistical analysis. The relative force at which each MU discharged its first action potential was considered the MU recruitment threshold and was expressed relative to MVC (% MVC). For each MU, an average recruitment threshold was calculated from those ramp isometric contractions in which the MU met the inclusion criteria noted above.

Statistical analysis

All statistical analyses were performed using SPSS 20 (IBM, Armonk, NY, USA). Descriptive statistics were calculated for all variables. For the dependent variable MU recruitment threshold, frequency histograms were generated at bin widths of 10 % MVC intervals up to 30 % MVC for each elbow extensor, and a stacked percent histogram consolidating these data on a relative basis was created. All MU recruitment thresholds exceeding 30 % MVC were grouped in a single bin (≥ 30 % MVC). Histograms revealed a MU recruitment threshold identification bias (Fig. 1), whereby many more MUs were recruited at low (<10 % MVC) forces likely due to reduced signal clarity at higher relative forces. Shapiro–Wilk tests of normality confirmed that these data were nonnormally distributed ($p < 0.05$). Accordingly, an a priori comparison was performed using Kruskal–Wallis tests for the <10 % MVC and ≥ 10 % MVC ranges independently to determine whether MU recruitment threshold differences among the elbow extensors were confined to low or moderate relative forces. An independent samples Kruskal–Wallis test was also performed to explore the effect of muscle on MU recruitment thresholds across the full range of recorded forces. In the event of a main

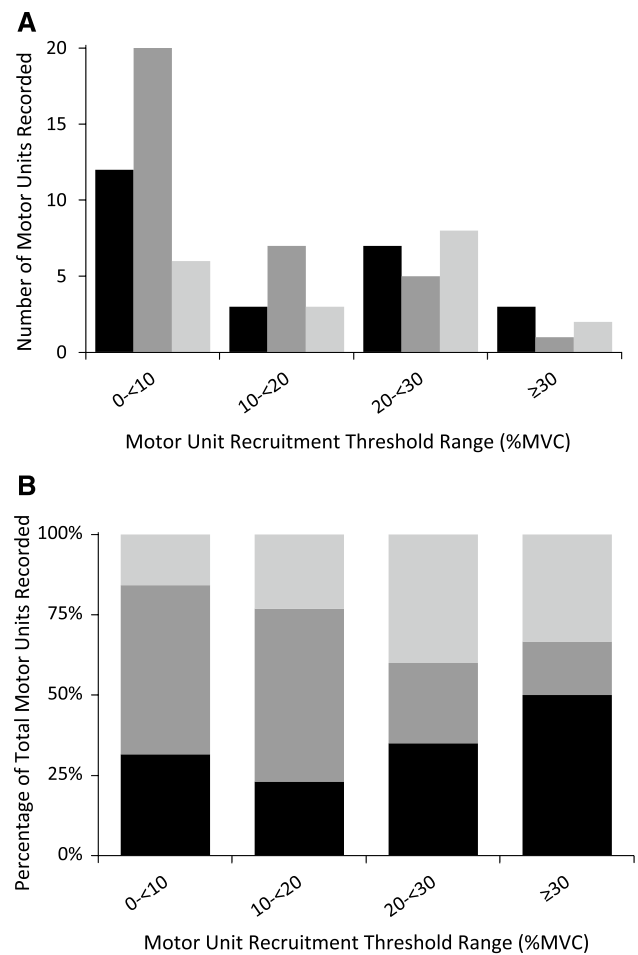


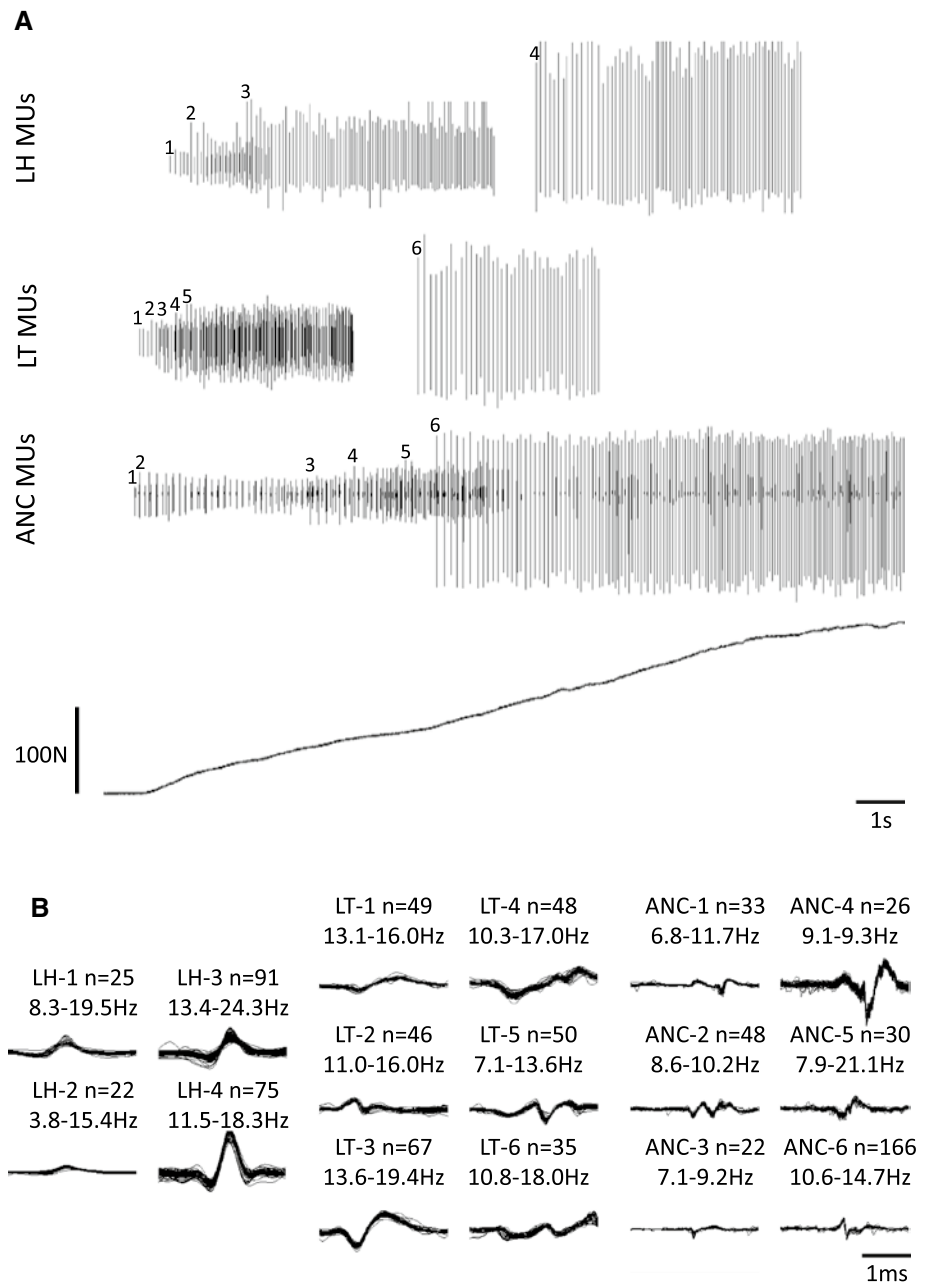
Fig. 1 Frequency (a) and stacked percent (b) histograms of the anconeus (black), lateral (dark gray), and long (light gray) heads of the triceps brachii relative to five elbow extension force ranges. **a** Each bar represents the number of MUs recruited from a respective muscle for a given elbow extension force range. **b** Each bar represents the percentage of MUs recruited from a respective muscle relative to the total number of MUs recruited for that range in all muscles investigated for a given elbow extension force range

effect, Mann–Whitney U tests were performed to investigate differences among the anconeus, lateral head of the triceps brachii, and long head of the triceps brachii, and Glass's Δ (Δ) effect sizes were determined for all pairwise comparisons.

Motor unit discharge rates were investigated using a mixed model analysis with initial MU discharge rate (first 1-s) as a covariate. Bonferroni-corrected post hoc comparisons were used to explore differences among the three muscles investigated, and effect sizes (Glass's Δ) were calculated for each comparison.

Three separate regression analyses were also performed, and coefficients of determination (R^2) were calculated. The first regression was between elbow extension force and average MU discharge rates at 1-s intervals in

Fig. 2 Representative MU data and MU action potential templates of the elbow extensors as a function of increasing force. **a** Sorted single MU action potentials of the long (LH, *top* MU panel), and lateral (LT, *middle* MU panel) heads of the triceps brachii, and anconeus (ANC, *bottom* MU panel) are expressed relative to elbow extension force (*bottom panel*). **b** Overlay of single MU action potentials from those highlighted in panel (a). The number (*n*) of MU action potentials discharged per MU and minimal to maximal range of recorded average MU discharge rates over 1-s intervals from low to higher contraction intensities are noted above each template. Numbers above single MU action potentials in the *top*, *middle*, and *bottom* panel represent the recruitment thresholds of the corresponding MUs from (b). N, Newtons; s, seconds; ms, milliseconds



each of the three muscles investigated. Next, the amount of shared variance between recruitment thresholds and initial (first 1-s) discharge rates of each MU was determined. Lastly, regression analysis was performed between MU recruitment thresholds and peak discharge rate of only those MUs that were tracked continuously from recruitment to target force (Fig. 2, e.g., ANC-6). Peak discharge rate was defined as the average MU discharge rate recorded at target force. Finally, a paired *t* test was used to determine whether maximal force differed between pre- and post-protocol MVCs. The alpha level was set at 0.05. All values in the text are presented as means ± standard deviations.

Results

Average elbow extensor MVC force of the five subjects was 239.6 ± 54.8 N at 95.6 ± 5.2 % VA and did not differ from MVC force recorded post-protocol (231.2 ± 46.5 , $p = 0.25$). Representative data showing discharge patterns of multiple MUs from the long and lateral heads of the triceps brachii, and the anconeus in one subject, and the corresponding overlaid action potentials of these MUs, during a ramp isometric contraction to ~75 % MVC, are depicted in Fig. 2. Average MU recruitment thresholds and average MU discharge rates at 1-s intervals were recorded from a total of 77 MUs acquired from the lateral ($N = 33$) and long

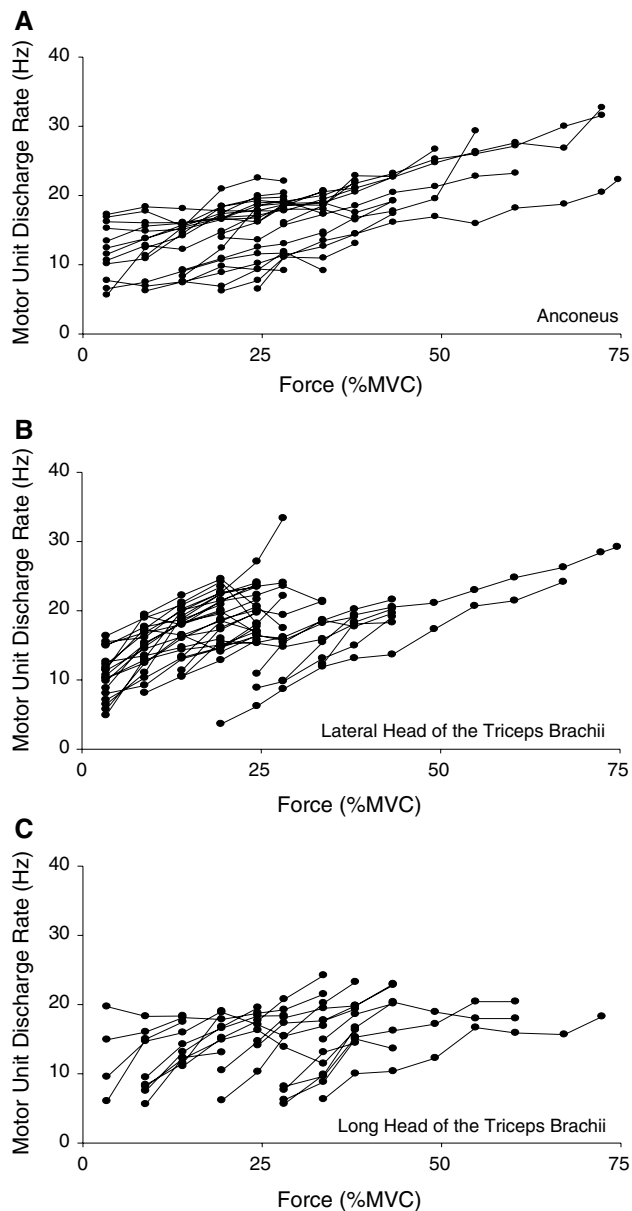


Fig. 3 Discharge rates of individual MUs ($N = 77$) from all three muscles relative to elbow extension force in **a** the anconeus ($N = 25$), **b** the lateral head of triceps brachii ($N = 33$), and **c** the long head of the triceps brachii ($N = 19$)

($N = 19$) heads of the triceps brachii, and the anconeus ($N = 25$) in the five subjects. The majority of MUs were recorded at force levels below 55 % MVC (Fig. 1); however, 10 MUs spread among all three muscles were tracked at forces above 55 % MVC (Fig. 3).

A main effect for muscle was observed for MU recruitment threshold ($p = 0.05$). Motor unit recruitment thresholds were higher in the long head (19.2 ± 11.8 % MVC) compared with the lateral head (10.9 ± 9.3 % MVC) of the triceps brachii ($p < 0.05$, $\Delta = 0.70$), and there was a trend

with a moderate effect size for lower recruitment thresholds of anconeus MUs (13.5 ± 12.2 % MVC) compared with those of the long head of the triceps brachii ($p = 0.08$, $\Delta = 0.48$). MU recruitment thresholds did not differ between the anconeus and lateral head of the triceps brachii ($p = 0.78$, $\Delta = 0.28$). When the three elbow extensors were compared within the two ranges selected a priori, a main effect for muscle ($p < 0.05$) was observed for the <10 % MVC range, but not for the >10 % MVC range ($p = 0.22$). Mann–Whitney U tests of the three elbow extensors for the <10 % MVC range determined MU recruitment thresholds were lower in the anconeus (2.0 ± 2.5 % MVC) compared with both the lateral (4.5 ± 3.3 % MVC, $p < 0.05$, $\Delta = 0.79$) and long (5.8 ± 3.4 % MVC, $p < 0.05$, $\Delta = 1.14$) heads of the triceps brachii. No differences were observed between MU recruitment thresholds of the lateral and long heads of the triceps brachii within the same range ($p = 0.61$, $\Delta = 0.37$).

Mixed model analysis of MU discharge rates identified a main effect for muscle ($p < 0.001$). Post hoc analyses showed MU discharge rates across the recorded isometric forces were ~ 10 % higher in the lateral head of the triceps brachii (16.7 ± 4.9 Hz) than the anconeus (14.9 ± 4.8 Hz) ($p < 0.001$, $\Delta = 0.18$) (Fig. 3). No difference was observed for MU discharge rates between the anconeus and the long head (15.2 ± 4.1 Hz) of the triceps brachii ($p = 0.30$, $\Delta = 0.16$) or between the lateral and long heads of the triceps brachii ($p = 0.27$, $\Delta = 0.35$) (Fig. 3).

Average MU discharge rate over the first 1-s interval for all muscles was 11.0 ± 3.9 Hz (range 3.6–19.7 Hz) and shared no variance ($R^2 = 0.01$, $p = 0.17$) with the recruitment threshold of each respective MU. Average MU discharge rates of the anconeus ($R^2 = 0.37$, $p < 0.05$) demonstrated the greatest amount of shared variance with elbow extensor force followed by the lateral ($R^2 = 0.16$, $p < 0.05$) and long ($R^2 = 0.12$, $p < 0.05$) heads of the triceps brachii. In a subset of MUs, in which discharge rates could be tracked from recruitment to the target force (17, anconeus; 11, lateral head of triceps brachii; and 7, long head of triceps brachii), peak discharge rates recorded shared no variance ($R^2 = 0.02$, $p = 0.22$) with MU recruitment threshold. The majority of these MUs were tracked to 25 % MVC (18), but others tracked to 50 % (11) and 75 % (6) were also included in this regression analysis.

Discussion

The present findings show diverse modulation of MU properties of three of the four elbow extensor muscles in relation to increasing force for the common goal of isometric extension. The hypothesized activation order of muscles, as reflected by their corresponding MU thresholds (Buchanan

et al. 1986; Le Bozec and Maton 1982, 1987; Le Bozec et al. 1980; Murray et al. 2000), was partially supported by the results of the present study. Over the range of elbow extension forces recorded here (up to 75 % MVC), the anconeus and lateral head of the triceps brachii recruited their respective MUs at lower forces than the long head of the triceps brachii, but no MU recruitment threshold differences were observed between the anconeus and lateral head of the triceps brachii. However, at low relative forces (<10 % MVC), average MU recruitment thresholds indicated that these muscles were activated in an order consistent with the reported fiber composition and twitch contractile properties of the elbow extensors (Le Bozec and Maton 1987) with the slow anconeus activated at lower relative forces compared with the fast lateral and long heads of the triceps brachii. Although the anconeus exhibited low average MU recruitment thresholds, it continued to recruit MUs at forces above 30 % MVC, which exceeded the plateau in muscle activity observed previously in one study using surface EMG (Le Bozec et al. 1980). Average MU discharge rates of the anconeus were lower compared with those of the lateral head of the triceps brachii, but did not differ significantly from those of the long head of the triceps brachii, indicating perhaps a role of muscle architecture and length-dependent mechanical advantages in synergistic elbow extensor MU activity. Collectively, these findings illustrate the value of considering MU properties of multiple muscles contributing to a common task and possible limitations that need to be recognized when only one contributing muscle is tested.

Modulation of MU discharge rate is an important mechanism for the gradation of force and varies depending on the muscle investigated (Seki et al. 1991) and activation history (Klein et al. 2002). In the present study, MU discharge rates of the long head of the triceps brachii (15.2 ± 4.1 Hz), which exhibited the highest MU recruitment thresholds (19.2 ± 11.8 % MVC), did not differ from those in the anconeus (14.9 ± 4.8 Hz). The anconeus exhibited lower MU recruitment thresholds (13.5 ± 12.2 % MVC) than the long head of the triceps brachii across the range of forces recorded here, and the lowest average thresholds of the three muscles investigated in MUs recruited below 10 % MVC. In a subset of MUs tracked from recruitment to the designated target force, MU recruitment thresholds shared no variance with the peak discharge rate recorded at target force ($R^2 = 0.02$, $p = 0.22$). These results are in contrast to the pattern of discharge proposed by stereotyped paradigms of MU behavior (De Luca et al. 1982; De Luca and Contessa 2012) in which higher threshold MUs achieve the lowest discharge rates. Interestingly, these paradigms (De Luca et al. 1982; De Luca and Contessa 2012) also show a strong positive relationship between MU recruitment threshold and initial MU discharge rate. Yet, in the present

study, there was effectively no shared variance between MU recruitment threshold and average MU discharge over the first 1-s interval ($R^2 < 0.01$, $p = 0.17$). This finding is similar to that observed in other earlier studies of isometric force production (Monster 1979; Monster and Chan 1977) in which higher threshold MUs were found to discharge at higher rates than low-threshold MUs. Furthermore, the discharge rates of six higher threshold MUs (21.3–40.2 % MVC) tracked at forces above 55 % MVC (Fig. 3a) were shown to exceed those of lower threshold MUs recorded at the same relative elbow extension force. Therefore, our results extend previous reports (Monster 1979; Monster and Chan 1977; Srinivasan et al. 2007; ter Haar Romeny et al. 1984) that show MU behavior is dependent upon the task and the muscle performing that task. These results indicate also that synergistic relations among MUs, and ultimately muscles, are potent modifiers of MU behavior.

Previous studies investigating elbow extensor (Le Bozec and Maton 1987) and plantar flexor (Bellemare et al. 1983; Dalton et al. 2009) properties have reported that muscles with a greater type I muscle fiber composition and slower contractile speeds, such as the anconeus, discharge MU action potentials at lower rates, compared with faster contracting muscles containing a greater type II fiber composition (triceps brachii), even when activation results in a similar contractile action. This relationship is supported in the present study by the observation of higher discharge rates (~10 %) in the lateral head of the triceps brachii compared with the anconeus. However, similar discharge rates in the anconeus and long head of the triceps brachii indicate the presence of an additional factor, muscle architecture, influencing MU activity of the long head of the triceps brachii. According to previous work, the long and lateral heads of the triceps brachii, which possess similar architectural and functional properties (Srinivasan et al. 2007; Terzis et al. 2003), should exhibit similar patterns of MU recruitment and discharge behavior during a common task (Clamann 1993; De Luca et al. 1982; Henneman et al. 1965; Seki et al. 1991). The observed discrepancies in the present study were likely the result of a greater mechanical advantage of the lateral head in the 0° shoulder flexion position compared with the long head of the triceps brachii (Davidson and Rice 2010; van Groenigen and Erkelens 1994). MU discharge rates are generally higher and recruitment thresholds lower at shorter fascicle lengths (Duchateau and Enoka 2008). Therefore, the long head of the triceps brachii, which is relatively shortened in the shoulder and elbow positions (0° and 90°, respectively) investigated here, would require greater levels of MU activity than the lateral head of the triceps brachii to produce an equivalent force. However, despite similar MU discharge rates, MU recruitment thresholds were higher in the long head than the lateral head of the triceps brachii.

It is likely that this pattern of activation served to limit the relatively costly MU unit activity associated with a short muscle length, thereby optimizing the efficiency by which the elbow extension task is performed. Muscle length has been shown previously to affect MU recruitment thresholds in the plantar flexors, wherein muscles in a shortened position (gastrocnemii) exhibit higher MU recruitment thresholds than those at longer lengths (Kennedy and Cresswell 2001; Nishimura and Nakajima 2002). Thus, it appears similar processes that govern the medial gastrocnemius at shortened muscle lengths (Kennedy and Cresswell 2001; Nishimura and Nakajima 2002), which may include either presynaptic inhibition or muscle spindle disfacilitation, may also be responsible in the present study for higher MU recruitment thresholds and lower MU discharge rates in the relatively shortened position of the long head of the triceps brachii.

Progressive MU recruitment related to motor neuron size is the other main neuromuscular factor responsible for roughly linear gradations in force in a variety of human muscles (Clamann 1993). Although many (Dalton et al. 2010; Del Valle and Thomas 2004; Garland et al. 1997; Griffin et al. 2001; Ivanova et al. 1997; Klein et al. 2001, 2002; Le Bozec and Maton 1987; Thomas and Del Valle 2001) have recorded MU discharge rates primarily from the lateral head of the triceps brachii, fewer (Griffin et al. 1998; Harwood and Rice 2012; Ivanova et al. 1997; Maton and Bouisset 1975; Miller et al. 1996) have recorded MU recruitment thresholds. In the lateral head of the triceps brachii, MU recruitment thresholds have been recorded up to ~50 % MVC (Griffin et al. 1998). However, MUs have not been recorded from multiple elbow extensors simultaneously during isometric contractions at >20 % MVC. According to Henneman's Size Principle (Henneman et al. 1965), MUs with larger cell bodies (high-threshold, fast-type MUs) are recruited at higher relative forces compared with those having smaller cell bodies (low-threshold, slow-type MUs). In view of the twitch contractile and fiber composition differences among the elbow extensors (Le Bozec and Maton 1987), it is reasonable to expect that the anconeus would exhibit lower average MU recruitment thresholds compared with either the long or lateral heads of the triceps brachii. Results of the present study are equivocal with respect to this hypothesis, wherein MU recruitment thresholds of the anconeus and lateral head of the triceps brachii did not differ when considered across the range of elbow extension forces studied, but were both lower than the long head of the triceps brachii.

However, when MU recruitment thresholds were compared among the three elbow extensors at <10 % MVC, differences consistent with the hypothesis that the anconeus would exhibit lower MU recruitment thresholds than the two heads of the triceps brachii were evident. Indeed, at

<10 % MVC, recruitment thresholds of anconeus MUs were lower than the lateral and long heads of the triceps brachii. At force levels of >10 % MVC, the number of MUs recorded, and the range over which MU action potentials could be discerned, differed among muscles (Fig. 2a). More MUs were identified in the lateral head of the triceps brachii at lower relative forces (Fig. 1a) when the density of the EMG signal was low. The unique properties of the anconeus resulted in a relatively low EMG signal density over the greater range of elbow extension forces. As a consequence, the average MU recruitment threshold of the lateral head of the triceps brachii may have been biased toward lower forces, whereas the average MU recruitment threshold of the anconeus was likely more representative of its full MU recruitment threshold range.

A specific advantage of the present model was the ability to record MU action potentials of three elbow extensors concurrently up to moderate forces (~55 % MVC), which revealed additional MU recruitment of the anconeus above the previously suggested plateau in muscle activity at 30 % MVC (Le Bozec et al. 1980) (Fig. 1a, b). However, the selectivity of intramuscular EMG recordings (Merletti and Farina 2009) presents the possibility that additional MUs outside the detection area may have been recruited at forces higher than those observed in the present study. One surface-detected EMG study of the elbow extensors showed EMG amplitude of the anconeus increasing linearly up to 80 % MVC (Bilodeau et al. 1992), which may in part be due to MU discharge rate increases (up to 75 % in the present study), but is more likely due to further MU recruitment (Christie et al. 2009). Thus, despite its high type I fiber composition (Hwang et al. 2004; Le Bozec and Maton 1987), slow twitch contractile speeds (Le Bozec and Maton 1987), smaller size (Hwang et al. 2004), and low average MU recruitment thresholds, the unique qualities of the anconeus for recording single MUs (Harwood et al. 2011; Harwood and Rice 2012) indicate that this muscle is a useful model for investigation of MU properties in technically challenging situations.

More importantly, recording MUs from multiple muscles concurrently for the common goal of isometric elbow extension up to moderate forces (~55 % MVC) identified varying patterns of MU recruitment that support the concept of orderly recruitment (Henneman et al. 1965), but indicate also that muscle synergies may operate according to a unique neural strategy that shares only some aspects of earlier MU force gradation models (De Luca et al. 1982; Monster 1979; Monster and Chan 1977). These data indicate that the human neuromuscular system is likely organized in a manner that precludes activation of muscles possessing a mechanical disadvantage possibly through either inhibitory synaptic connections or disfacilitation of excitatory synapses (Kennedy and Cresswell 2001). This pattern of activation likely serves

to improve the efficiency of these muscles collectively for performance of a common task by reducing the amount of voluntary drive required for a given force.

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