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Task-Dependent Properties of the Human Anconeus Muscle

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A thesis submitted in partial fulfillment of the requirements for the degree in Doctor of Philosophy

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TASK-DEPENDENT PROPERTIES OF THE HUMAN ANCONEUS MUSCLE

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by

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The thesis by

Brad Harwood

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Task-dependent properties of the human anconeus muscle

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Abstract

Recording motor unit (MU) action potentials during fast muscle contractions, specifically during movement, presents unique challenges that constrain the investigation of the upper limits of human MU performance. The anconeus muscle exhibits many advantageous characteristics that suggest it is an appealing model for the study of MU behaviour in challenging experiment paradigms. Thus, the purpose was to determine the MU recruitment and discharge properties associated with the generation of movement up to maximal angular velocities of elbow extension and to determine the effect of submaximal fatiguing movements on these MU properties. Due to the synergistic nature of the anconeus in the elbow extensor muscle group, a secondary purpose was to determine whether MUs of the muscles comprising the elbow extensor group behave differently during the production of high forces.

Discharge rates and recruitment thresholds were tracked in 24 and 17 MUs, respectively. It was revealed that anconeus MUs increase discharge rates over two distinct linear ranges possessing different input-output gain relationships relative to elbow extension velocity. Anconeus MUs exhibited variable responses to increased resultant velocity when recruitment thresholds were considered. These variable responses, that were more common in higher threshold MUs, indicated that a compression of the MU recruitment range of the anconeus occurred as elbow extension velocity increased.

Using the same recording techniques, fatigue-related changes in discharge rates and recruitment thresholds of 12 MUs were determined throughout a protocol comprised of fast, maximal, static muscle contractions, and submaximal and periodic maximal movements. Results of this study demonstrated that MU properties are graded differently in response to submaximal fatiguing movements depending on the intensity of the movement, but that contraction type did not affect the relative changes in these MU properties.

Lastly, MUs in three elbow extensors including the anconeus were tracked during constant joint angle force production to near maximal intensities. Differences between the elbow extensors were observed for MU discharge rates and recruitment thresholds with increasing force. These findings support an integrated model of earlier established MU control strategies for the elbow extensors and show anconeus MU recruitment occurs over a greater range than previously believed.

Keywords

Motor unit, Discharge rate, Recruitment threshold, Elbow extensor, Anconeus, Contraction Velocity, Task, Fatigue, Synergists

Co-Authorship Statement

This thesis contains material from published manuscripts (Chapters 2 and 3). On all manuscripts, Brad Harwood was the first author and Charles L. Rice was a co-author. Andrew W. Davidson was a co-author of Chapter 2, In Ho Choi was a co-author of Chapter 4, and Brian H. Dalton and Geoffrey A. Power were co-authors of Chapter 5. All experimental data presented in this thesis were collected, analyzed, and interpreted by Brad Harwood.

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I was incredibly fortunate to have the opportunity to work for two amazing individuals. My first advisor, Dr. Jennifer Jakobi, prepared me well for my doctoral work. I credit her with teaching me the technique which allowed me to perform the studies I did, with providing the foundational skills required to publish, and more importantly, with treating me as a friend first, a peer second, and finally a colleague. It would be difficult to surpass the influence Dr. Jakobi made in my life, but Dr. Charles Rice is a formidable challenger. From the first day I stepped foot in Dr. Rice's lab, I felt welcomed and valued for my skills. In my opinion, the atmosphere that he has created is unparalleled in its ability to promote success. His patient, genuinely concerned approach to mentoring was exactly the experience I was looking for. His dedication to the growth of his students' careers was evident right from the beginning and never faded. I am truly impressed by Dr. Charles Rice and I will certainly model my future approach to graduate student mentoring on his example.

The support I received through my journey at the University of Western Ontario did not stop at the laboratory. I believe the Kinesiology Graduate Office staff to be the finest administrators, counselors, and friends a student could hope to have. Jennifer Plaskett and Jacqui Saunders were always available to help guide me through the graduate process, to resolve any issue I might have, and to share a short conversation with. Both Jenn and Jacqui invest themselves personally in every student's success and I thank them for their investment in me.

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LIST OF ABBREVIATIONS

MU – Motor unit

EMG - Electromyography

MVC - Maximal voluntary isometric contraction

ROM – Range of motion

ANOVA – Analysis of variance

SD – Standard deviation

HSD – Honest significant difference

PIC – Persistent inward current

RMS – Root mean square

V_{max25} – Maximal peak velocity at 25%MVC

EMG_{RMS} – Root mean square of surface-detected EMG

V_{max40} – Maximal peak velocity at 40%MVC

VA – Voluntary activation

EMG_{ANC} – Intramuscular global EMG of the anconeus muscle

EMG_{LT} – Intramuscular global EMG of the lateral head of the triceps brachii

EMG_{LH} – Intramuscular global EMG of the long head of the triceps brachii

TTF – Time to task failure

GLOSSARY OF TERMS

Velocity-dependent contraction – Originally inappropriately termed ‘isotonic’ contractions, velocity-dependent contractions are those in which the imposed load remains relatively constant and the velocity is allowed to vary throughout the joint range of motion

Motor neuron pool – A collection of motor neuron cell bodies in the ventral horn of the spinal cord that innervate a given muscle or muscle group

Motor unit – A single motor neuron and all the muscle fibers it innervates

Motor unit recruitment threshold – The relative force or torque at which a motor unit is activated indicated by the first discharge of a single motor unit action potential

Motor unit discharge rate – The number of single motor unit action potentials that are fired per second

Time to task failure – The duration of time elapsed before a subject is unable to perform the experimenter-defined task (i.e. a decline in elbow extension velocity 10% below a target of 60% of maximal velocity)

Neuromuscular Fatigue – Any exercise-induced reduction in force or power regardless of whether the task can be performed

Isometric – A static muscular contraction in which the joint range of motion is constant

Isokinetic – A dynamic muscular contraction in which the velocity is constant

Power – The product of force and velocity expressed in Watts (W)

Torque – Also termed ‘moment’ is the product of the lever arm length, the magnitude of force vector, and the sine of the angle between the force vector and the lever arm vector, and is expressed in Newton·meters (Nm)

Chapter 1 : General introduction

1 The production of movement

The production of movement requires the generation of enough force to overcome a load (inertial or imposed) at a rate that ultimately determines the resultant peak velocity and power of a dynamic contraction. Modulation of these resultant mechanical outputs is dependent upon many factors (electrophysiological, mechanical, architectural, etc.) along the corticospinal pathway originating at, or above the motor cortex, and culminating in contraction of the target muscle to move a load over a distance (i.e. range of motion), essentially performing work. Investigations of reduced animal preparations have elucidated many of these neuromodulatory influences, however the necessity to perform human studies *in vivo* has rendered the investigation of dynamic contractions and their neuromodulatory influences less accessible.

1.1 Basic organization of the corticospinal pathway and the final common pathway

The derivation of force production commences in the primary motor cortex in self-initiated movements ~100ms prior to muscle activation (12), which is indicated by the onset of electromyography (EMG). Motor cortical potentials then propagate along the corticospinal tract, the primary bundle of nerves responsible for conduction of voluntary motor commands. Once at the spinal cord, potentials are transmitted along the remainder of the corticospinal tract to the level of the spinal cord without interference, where they synapse with motoneurons belonging to the target muscles. At the spinal cord level, an abundance of neuromodulatory inputs, in addition to the corticospinal input converge upon the motoneurons (Figure 1). These additional inputs originate from a number of locations (reticulospinal, rubrospinal, etc.) (7) and result in different postsynaptic effects (excitatory or inhibitory) (39), which act on the motoneuron pool at different synaptic strengths (7).

Each input is received via the dendritic processes of individual motoneuron cell bodies. Potentials of various amplitudes (graded potentials) arise as a consequence of these inputs and summate in motoneuron cell body. In order to propagate an action potential along the motoneuron axon to the target muscle, the sum of these graded potentials must depolarize the cell ~20-30mV from the resting potential of ~-70mV to ~-50mV, which is termed the threshold potential for initiation of an action potential and occurs at a structure at the base of the axon termed the axon hillock. At this point, the origin and strength of the incoming signals is irrelevant as these parameters culminate in a signal defined by the frequency of action potentials in the time domain, rather than the amplitude domain. These action potentials arrive at the terminus of the axon and activate a signaling cascade that results in electrical potentials being converted into a chemical signal expressed by the release of the excitatory neurotransmitter acetylcholine from vesicles (storage sacs) at the neuromuscular junction into the synaptic cleft. Acetylcholine binds to postsynaptic receptors on the sarcolemma opening ligand-gated channels and allowing an influx of cations that depolarize the post-synaptic cell membrane once again bringing the resting membrane potential of the target cells (muscle fibers) closer to the threshold for action potential generation. These neuromuscular connections are generally concentrated in a single area termed the motor point approximately mid-muscle length, however, the number of motor points is muscle dependent (63). Action potentials propagate in both directions from the motor point along the sarcolemma initiating the excitation-contraction coupling signaling cascade, which entails the release of calcium from the sarcoplasmic reticulum into the sarcoplasm and reveals the binding sites for the myosin cross-bridges on the actin molecule allowing the shortening of sarcomeres according to the Sliding Filament Theory (41).

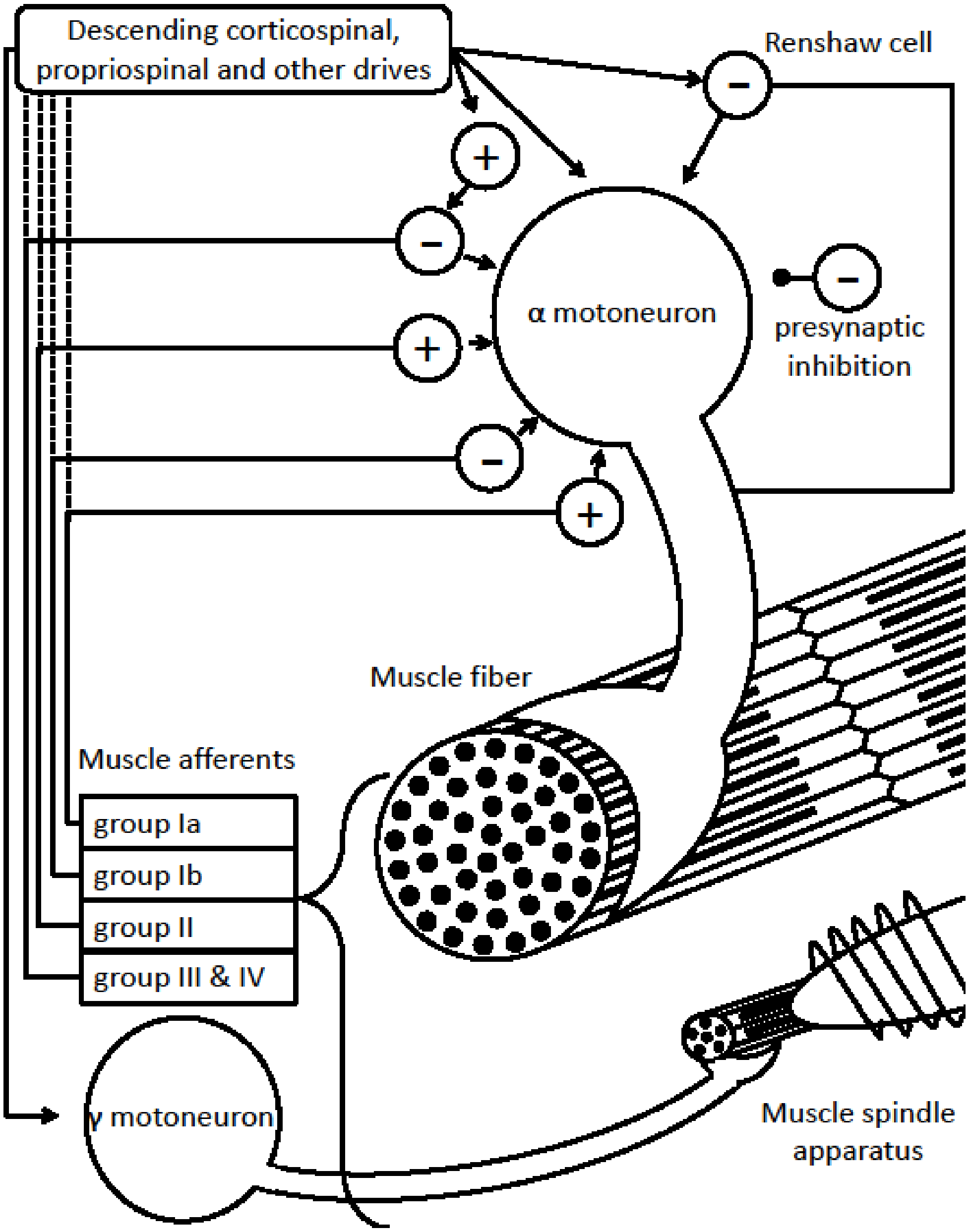

Figure 1. Supraspinal and spinal inputs onto the α motoneuron. Arrows indicate the target of the various inputs displayed. Circles represent synapses with the plus sign signifying an excitatory input and the minus sign signifying an inhibitory input. Dotted lines reflect additional afferent pathways that travel from muscle afferents to the supraspinal centers. The left brace signifies that all the muscle afferents manifest from receptors in the muscle or in the muscle spindle apparatus.

The processes that transpire between the motoneuron dendrites and the individual muscle fibers occur in an integrated structure of nervous and muscle tissues, the basic functional unit of the neuromuscular system, termed the motor unit (MU) (Figure 2). A MU is comprised of a single motoneuron and all the muscle fibers it connects to, and because MU behavior reflects the convergence of many synaptic inputs it is considered the final common pathway (54).

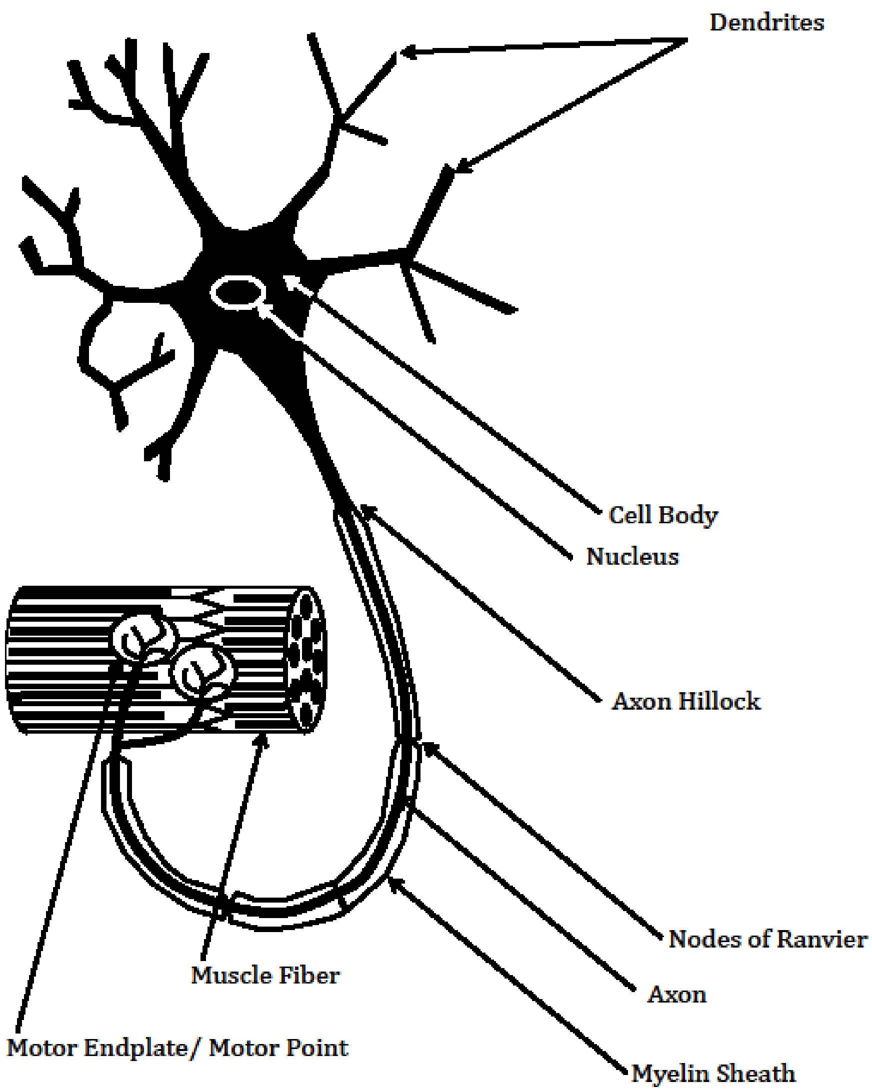

Figure 2. Diagram of a motor unit

1.2 Motor control through modification of MU input-output relationships

Virtually all voluntary motor control requires the coordinated activation and modulation of MU properties of a number of muscles to produce a mechanical output appropriate for completion of a task. Any deviation from these optimal control parameters, whether it is due to lack of familiarity with the task or in response to a physiological change in the neuromuscular system (i.e. fatigue), results in error between the intended and actual output of the system. The quantification of these control parameters is of great interest in understanding what final common input to the contractile apparatus (i.e. muscle fibers) is associated with the production of outputs ranging from those representative of optimal control parameters (i.e. elite performance) to those associated with a failure of the neuromuscular system (i.e. clinical populations, fatigue, etc.).

The seminal work of Adrian and Bronk (1) in 1929 introduced the two primary mechanisms of muscle force gradation, MU recruitment and discharge rate, which were expressed as the relative force at which a MU became active (MU recruitment threshold), and the frequency at which a MU discharged action potentials (MU discharge rate), respectively. Over the years following this original discovery, many have investigated the modulation of these MU control properties for the production of a variety of tasks, in a variety of muscle groups, and following numerous physiological changes (22). Despite significant advancements in our understanding of MU control properties, many questions remain (22, 25). One such question is how MUs are activated and how their discharge rate is modulated in order to produce high velocity dynamic contractions. Due to the technical limitations associated with recording single MU action potentials at high velocities during movement (discussed below), an overwhelming majority of studies have focused on the gradation of isometric (constant joint angle) force via MU properties (22). Generally, increases in force are achieved by increasing the number of active MUs in an orderly manner relative to the size of the motoneuron cell body (small to large diameter) (40); and once activated, increasing the frequency at which MUs discharge action potentials as a function of force until some upper limit is reached.

1.3 The elbow extensor muscle group

At a systems level, individual MU activation and discharge properties manifest as a net muscle force. However, most activities involve several agonist, synergist and antagonist muscles, often possessing very different characteristics from each other and thus modifying the appropriate or desired agonist output. The elbow extensor muscle group, which is comprised of the long, lateral, and medial heads of the triceps brachii, and the anconeus, is a good example of coordinated force production. Of the four elbow extensor muscles, the long head of the triceps brachii crosses both the glenohumeral and elbow joints, which is in contrast to the other three muscles which only cross the elbow joint (Figure 3). Despite common innervation by the radial nerve, the fiber composition, architectural properties, and force distributions of these synergists differ (9, 50-53, 59, 74) (Figure 3). Most studies of the elbow extensor MU properties have investigated the lateral head of the triceps brachii (16-18, 31, 32, 36, 43, 47, 48, 69) or did not specify which head of the triceps brachii was investigated (49). Very few (51, 72) have recorded MU action potentials from multiple elbow extensors concurrently. Le Bozec and Maton (51) recorded fiber composition, twitch properties, and both integrated surface-detected EMG and MU discharge rates up to 30%MVC. The slower, more type I (65%) anconeus possessed lower MU firing rates in this range and integrated surface-detected EMG suggested the anconeus may be fully recruited at low forces (<30%MVC) (51). van Groeningen and Erkelens (72) determined MU recruitment threshold for the long, lateral, and medial heads of the triceps brachii (~35% type I) during low (20%MVC) isometric, and slow (2°/s) elbow extension over a limited range of joint motion (20°). Results showed similar recruitment thresholds of the three heads of the triceps brachii for isometric contractions, but determined MUs in the long head of the triceps brachii were recruited at lower relative forces in contractions that resulted in movement compared to those performed isometrically.

Although these studies provide some insight into the synergistic activities of the constituent muscles of the elbow extensor group, the relatively low target forces and extremely low (2°/s) movement velocities utilized in these studies leave a considerably portion of the force and velocity gradation spectrum undefined.

Although the same general principles of MU control apply to the production of movement (21), the demand to produce the requisite high rates of torque development to move at maximal velocities likely necessitates the use of unique motor control strategies (60, 61). In addition, the voluntary motor command specific to the production of fast goal-directed movements must account for length- and tension-dependent passive muscle properties of both the contractile apparati and myotendinous structures. This is needed to complement the variety of excitatory and inhibitory afferent and efferent inputs in a manner specific to the electrophysiological characteristics (i.e. input conductance, rheobase, etc.) of the target motoneuron pool(s) so that the ensuing MU activity results in the desired mechanical outcome.

Studies of fast isometric (ballistic) contractions (19-21, 56, 57, 64, 71, 73) have demonstrated MU recruitment at lower relative forces and higher MU discharge rates in comparison to slow isometric contractions. While these studies provide an indication of the changes likely associated with movement, cortical excitability and MU properties differ for shortening contractions compared with isometric contractions (23, 24, 62). Furthermore, maximal velocity shortening contractions likely receive higher levels of synaptic input compared with slow dynamic or isometric contractions, and utilize the upper limit of MU discharge rate and lower limit of MU recruitment threshold. To determine the MU control strategies associated with production of dynamic contractions up to maximal velocities, a unique muscle model was investigated.

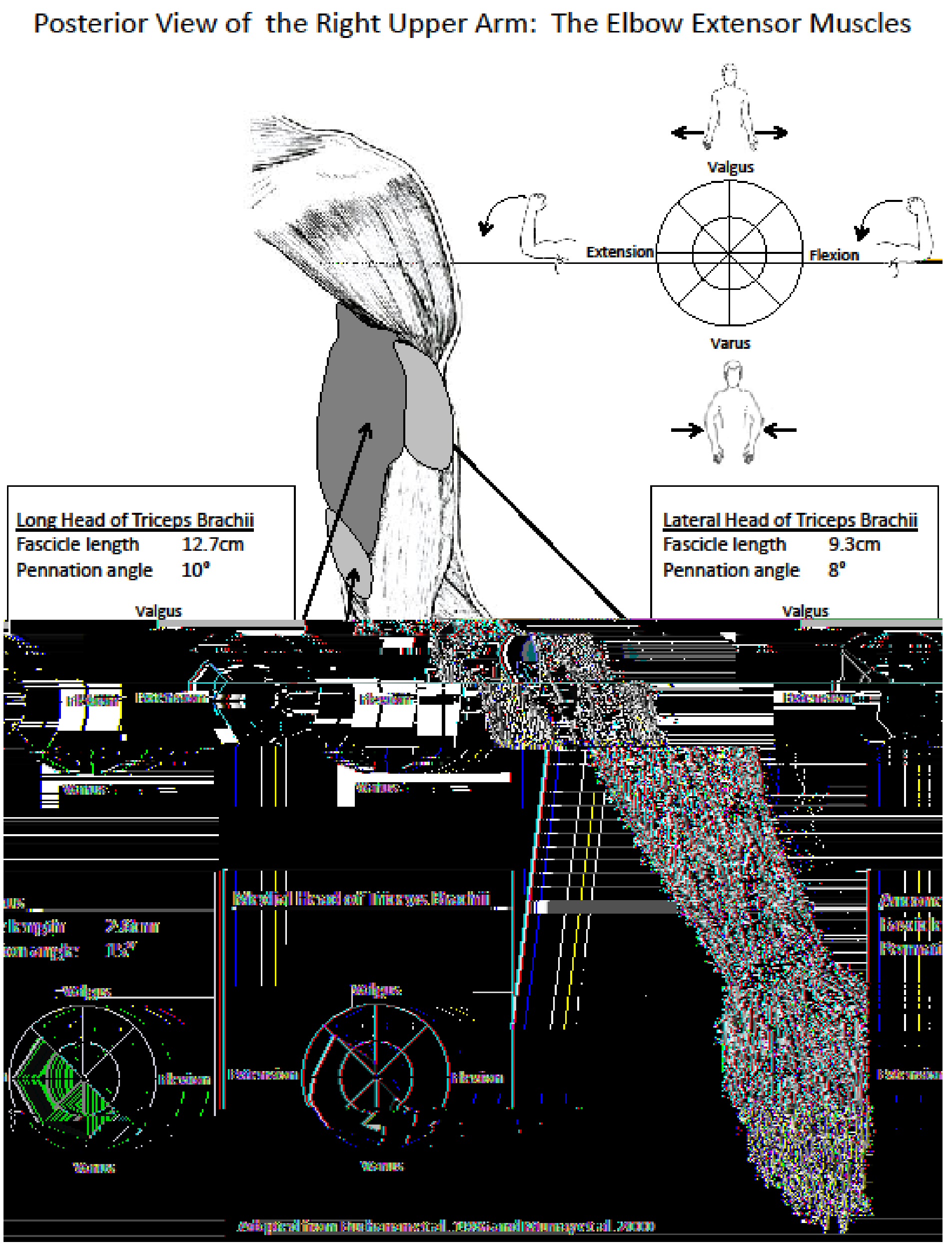

Figure 3. Anatomy and torque distribution profiles of the human elbow extensors. Polar plots display the EMG associated with torque produced in four planes, extension, valgus, flexion, and varus, which are depicted in the upper right corner. The outer circumference of each polar plot represents the maximal EMG value recorded for each muscle.

1.4 The anconeus model

The anconeus muscle represents an appealing model for the study of MU control strategies in view of its advantageous architectural and muscle activation properties (2, 9, 42, 50-53, 59, 70, 74) summarized in Figure 3. A major limitation of the recording electromyography (EMG), and more specifically single MU action potentials, of fast ballistic isometric contractions and during joint movement is that the surface or intramuscular electrodes may be displaced as a consequence of large and rapid changes in muscle fiber fascicle length (27). Due to the relatively small size and short fascicle lengths of the anconeus amongst the elbow extensor group, it experiences less shortening per joint range of motion in comparison to the long, lateral, and medial heads of the triceps brachii (9, 59). The small size of the anconeus also implies it possesses fewer MUs compared with the other larger elbow extensors (37). Furthermore, there is evidence to suggest the anconeus is active throughout elbow extension at all angles, forces and velocities (50, 52, 53), and that activation precedes the other elbow extensor synergists. Together, these characteristics of the anconeus indicate it may be suitable for recording single MUs, determining accurate MU recruitment thresholds void of synergist contamination, and tracking MU discharge behaviour in a variety of tasks including rapid joint movements.

1.5 Changes in MU behavior with neuromuscular fatigue

Another advantage of the anconeus model, related to the potential to record single MU action potentials during fast dynamic contractions, is the possibility to track MU behavior in response to a physiological perturbation, such as fatigue. However, fatigue may represent an array of stress-related (psychological, physiological, or mechanical) manifestations, which renders it an inappropriate term to characterize, with specificity, the exercise-associated changes that occur in corticospinal pathways and associated muscle fibers (8). Thus, a more focused and practical term is neuromuscular fatigue, defined as any exercise-induced reduction in force or power independent of task sustenance (6). Despite the relatively narrow scope of this definition, neuromuscular fatigue is highly dependent upon subject characteristics (i.e. age, sex, etc.), the fatigue task employed (isometric vs. isokinetic, maximal vs. submaximal, etc.), and the task or measure used for assessment. As a consequence, equivocacy is a central feature of neuromuscular fatigue literature; one which is addressed by conscientious control of the many potential confounding variables.

For fatiguing submaximal isometric contractions, whether sustained or performed intermittently, MU recruitment progressively increases, MU recruitment thresholds are reduced (3, 4, 11, 13, 28, 44, 66), and MU discharge rates decline (11, 26, 30, 33, 34, 67), or are unchanged (14, 18, 28, 44, 66). Similar fatigue-related MU behavior is also observed for submaximal dynamic shortening elbow extensions (36, 58). However, when maximal voluntary isometric contractions (MVCs) are sustained or performed intermittently, MU discharge rates decline (3, 5, 55, 65, 66). Although no systematic study has determined whether MU recruitment thresholds decrease with increasing target force, there is considerable evidence from studies of ballistic isometric contractions (20, 21) that MU recruitment thresholds are lower for higher rates of torque development, for which the highest rates of torque development are observed for MVCs. Due to the aforementioned technical limitations of recording single MU action potentials during movement and at high velocities, MU recruitment thresholds or discharge rates of these contractions in response to neuromuscular fatigue have yet to be investigated.

1.6 Purposes and hypotheses

Thus, collectively the purpose of this thesis is to determine the MU recruitment and discharge properties associated with the generation of movement up to maximal velocities and to determine the response of these MU properties to submaximal fatiguing movements. A secondary purpose of this thesis is to determine whether differences between the muscles comprising the elbow extensor group exist for isometric contractions up to maximal forces. Chapter 2 describes the relationship between MU discharge rates of the anconeus muscle and peak elbow extension velocity and provides compelling support from movements for reduced animal (10, 35, 45, 46) and human (29, 38) models of the MU input-output relationships . In Chapter 3, a similar protocol to Chapter 2 is used to determine the relationship between MU recruitment thresholds of the anconeus and elbow extension velocity, which offers evidence that MU recruitment grades mechanical output in a linear fashion (15). The MU recruitment thresholds and discharge rates of both submaximal and maximal velocity dynamic contractions are investigated in response to submaximal velocity fatiguing contractions in Chapter 4. These data represent the first observations of the MU discharge rate changes of maximal velocity contractions throughout a fatiguing protocol and highlight the task-dependent nature of neuromuscular fatigue with respect to both the fatigue task employed and the assessment of fatigue-related changes. Lastly in Chapter 5, the MU recruitment and discharge properties of the muscles comprising the elbow extensor group are investigated in isometric contractions up to maximal forces to determine whether the findings from the previous studies in the anconeus are representative of the entire muscle group, or if they are unique to the anconeus muscle. As suggested in previous studies (51-53, 72), it appears there are muscle-dependent differences within the elbow extensor group, however, the findings of the current study challenge the limited operating range of the anconeus muscle and suggest it may play a role throughout the entire force gradation spectrum.

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Chapter 2 : Motor unit discharge rates of the anconeus muscle during high-velocity elbow extensions[1]

2 Introduction

Production of an accurate and economical movement requires the consideration of a number of target parameters [torque, shortening velocity, range of motion (ROM)]. The net synaptic input to activate a requisite number of motor units (MUs) at an appropriate discharge rate to achieve these desired parameters is provided by descending neural inputs from supraspinal centers, in addition to a number of excitatory and inhibitory afferent inputs that converge onto the motoneuron pool in the spinal cord (16).

The electrophysiological properties of MUs provide a model for studying the final spinal output of human motoneurons by means of electromyographic (EMG) recordings. However, technical challenges limit the utility of EMG recordings during active length changes of muscle, and as a result, knowledge of MU discharge rates during freely moving actions has been confined largely to EMG recordings made during relatively slow dynamic, or steady-state isometric contractions (18, 19). Attempts to describe the behavior of single MUs in concert with changes in muscle fascicle length have been studied during ballistic isometric contractions (15, 40, 47, 61, 62) and during slow isokinetic (constant velocity) contractions (3, 11, 14, 45, 53-55, 57). Although these paradigms have identified task-related differences in MU output, the applicability of these results to unconstrained high-velocity shortening contractions is not well understood.

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Harwood B, Davidson AW, and Rice CL. Motor unit discharge rates of the anconeus muscle during high-velocity elbow extensions. *Experimental brain research* 208: 103-113, 2011.

Less often, single MU activity has been studied during slow (2–72°/s) loaded [5–25%MVC, (24, 35, 60)] and unloaded (35, 58) tasks, and during moderately fast unloaded [150–225°/s, (21)] contractions in which velocity is not constrained (velocity-dependent). In agreement with isometric and slow isokinetic tasks (2, 14, 45, 47), these few studies suggest MU discharge rates increase linearly in relation to the contraction intensity (velocity, work, or acceleration). However, the shortening velocities tested were less than half of maximum and ROMs were 20–80° for muscles crossing the elbow joint (21, 24, 35, 60). For example, Garland et al. (21) reported MU discharge rates at velocities up to 225°/s across 80° ROM for the elbow extensors. However, the ROM for this muscle group is approximately 120°, and in the present study, the maximal velocity during loaded (25% of maximal voluntary contraction (MVC)) elbow extension was observed to reach up to 494°/s. Thus, the range over which rate coding may act, as a function of velocity, is unknown.

Early investigations of anesthetized cat motoneurons in the absence of any neuromodulatory (monoaminergic) influence reported an input–output (current-frequency) relationship fitted by two intersecting linear curves. These are the primary and secondary ranges, which span intensities up to maximum and are dependent upon motor unit type (S, FR, FF), with fast-type motoneurons entering a secondary range at much higher current inputs (9, 23, 37, 38). These investigations have been supported by models of MU discharge that suggest human motoneurons do not fire in a secondary range during steady isometric contraction (5, 20, 50, 56), but may utilize the secondary range of the current-frequency relationship in dynamic conditions (52). Other studies (31, 39) suggest that human motoneurons, in response to synaptic input rather than current injection, fire in a 'preferred' or a 'rate limiting' range in which monoaminergic drive is saturated (27, 31) with no further increase in the gain on the MU discharge rates. However, due to limitations of the techniques used to investigate monoaminergic drive, as represented by persistent inward currents (PICs), data are only available in humans for low threshold (slow type) motoneurons (28). Thus, the phenomenon in which MU discharge rates of low threshold motor units plateau and MU discharge rates of higher-threshold motor units continue to rise, similar to that observed by Monster and Chan (49) and Kanosue et al. (34) isometrically, cannot be ignored. One study (48) of single MU activity in humans during dynamic contraction reports an exponential relationship between the minimal (first) interspike interval of consecutive single MU action potentials belonging to the same MU as a function of work. However, in that study of loaded (1–5 kg) dynamic contractions at high velocities (114–461°/s) in the biceps brachii through 60° of elbow flexion, the changes in interspike intervals were expressed in relation to work, which can vary as a function of either velocity or load (48). Furthermore, only the minimal interspike interval of a single MU train was considered, which usually occurred (87% of records) during the first and second discharges and thus before movement was initiated.

Because interspike intervals tend to be shortest at the beginning of velocity-dependent contractions preceding movement and then decline to a more steady-state level as the movement proceeds (24, 45), it is of interest whether the average MU discharge rate varies exponentially as a function of contraction velocity, and whether this relationship during fast velocity-dependent contractions may represent the presence of MU discharge of fast-type motoneurons in a secondary range. In order to investigate the average MU discharge rates during velocity-dependent contractions up to maximum and through a full range of joint motion, the present study investigated the anconeus muscle. The anconeus is a small (cross-sectional area = 2,002 mm^2), predominantly type I (60–67%) muscle that acts to extend the elbow and serves as an abductor of the ulna during resisted pronation (6, 32, 42, 59) and can contribute up to ~15% of the elbow extensor torque (64). Prior EMG studies of the anconeus suggest it is active at all velocities up to maximum and throughout the full range of elbow extension (41, 43), but that its contribution decreases as isometric elbow extension torque increases (64) and that maximal integrated EMG is realized at low torques and low velocities (41, 43). However, these conclusions were based on global integrated surface EMG in relation to the onset of movement and not the activity of single MUs in relation to the development of torque preceding or during the movement. As a consequence of the small relative changes in muscle fascicle length during elbow extension compared with other muscle groups (1, 25, 53), the anconeus provides an attractive model for investigation of MU discharge rates during fast velocity-dependent contractions throughout the large ROM of the elbow joint. As well, the anconeus, as a small limb muscle, likely has relatively few MUs compared with other muscles. Thus, a preliminary aim of the current study was to explore the utility of recording single MU discharge rates from the anconeus during loaded velocity-dependent contractions. More importantly, the current study sought to investigate the motoneuron output, in the form of MU discharge rate, in response to loaded velocity-dependent contractions from 0°/s to maximal (~500°/s) through a large (120°) elbow joint ROM in which the greatest levels of excitation of natural movements likely occur (52). We hypothesized that, as a result of the high levels of excitation to the motoneuron pool during fast velocity-dependent contractions, average MU discharge rates would increase non-linearly as a function of peak elbow extension velocity similar to the relationship observed for minimal interspike intervals as a function of work (48). We further hypothesized that this relationship would be comprised of positive linear primary and secondary ranges spanning low to moderate submaximal velocities and fast to maximal peak velocities, respectively.

2.1 Methods

Elbow extension torque, position, velocity, and single MU action potentials of the anconeus muscle were recorded in eleven young men (26 ± 2y, 179.1 ± 7.6 cm, 79.9 ± 8.8 kg) free from orthopaedic, 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 conformed to the Declaration of Helsinki.

Subjects visited the laboratory one to three times (~1.5 h/visit). Multiple visits were required to ensure an adequate quantity and quality of MU recordings throughout the entire protocol. Elbow extension torque, position, and velocity measures were obtained using a Biodex System 3 multi-joint dynamometer (Biodex Medical Systems, Shirley, NY, USA) with the shoulder flexed 90°, and the arm abducted 20° and resting on a support positioned ~10 cm proximal to the olecranon process of the ulna (Appendix B). The forearm, in the semi-prone position, was secured to a custom-built support attached to the Biodex lever arm.

A schematic of the experimental protocol is provided in Figure 4. The protocol began with three to five brief (~5 s) isometric elbow extension MVCs at 60° elbow flexion (0° = full extension) of which the highest was taken as the representative MVC. The angle for isometric elbow extension (60°) was chosen because it represented the midpoint between the limits of ROM in this study. However, the elbow extensors exhibit a fairly constant torque–length relationship across the entire ROM (10). Thus, it was expected that the relative torque level at 60° would be similar to those at other joint angles. Subsequently, the highest MVC value was used to determine the load (25%MVC) at which the velocity-dependent contractions would be performed, and to establish target torques for the isometric portion of the protocol. In order to familiarize subjects with the task and to attain the highest velocity, which was used for normalization of velocity-dependent elbow extension and to determine the target velocities, five loaded (25%MVC) maximal velocity elbow extensions (V_{max25}) were performed over 120° ROM (starting from 120° elbow flexion to 0° elbow extension). During all maximal efforts, subjects were encouraged verbally and torque and velocity output were displayed in real time on a computer screen for visual feedback. Horizontal cursors on the screen indicated the target peak velocity for each submaximal velocity-dependent elbow extension (25%V_{max25}, 50%V_{max25}, 75%V_{max25}). Subjects then performed four sets of five loaded elbow extensions at each target velocity (25%V_{max25}, 50%V_{max25}, 75%V_{max25}, V_{max25}) in a random order. Subjects were encouraged to match the peak velocity of each submaximal elbow extension to the horizontal cursor that corresponded to the target peak velocity they were instructed to perform. Failure to achieve the desired peak velocity resulted in the subject repeating the elbow extension at the same target peak velocity following a rest period (30 s). To allow for verification of the tracked MU throughout the protocol and to provide a comparison of a zero velocity condition, three ramped isometric contractions (~10 s) at 25%MVC were performed before each set of velocity-dependent contractions. However, it was not a requirement that MUs be active during the 25%MVC isometric contraction for inclusion in the statistical analysis. Each submaximal elbow extension (isometric or velocity-dependent) was separated by ~30 s rest, whereas MVCs and V_{max25} were separated by 2-min rest. Finally, a post-protocol MVC lasting ~5 s was performed to confirm the absence of fatigue.

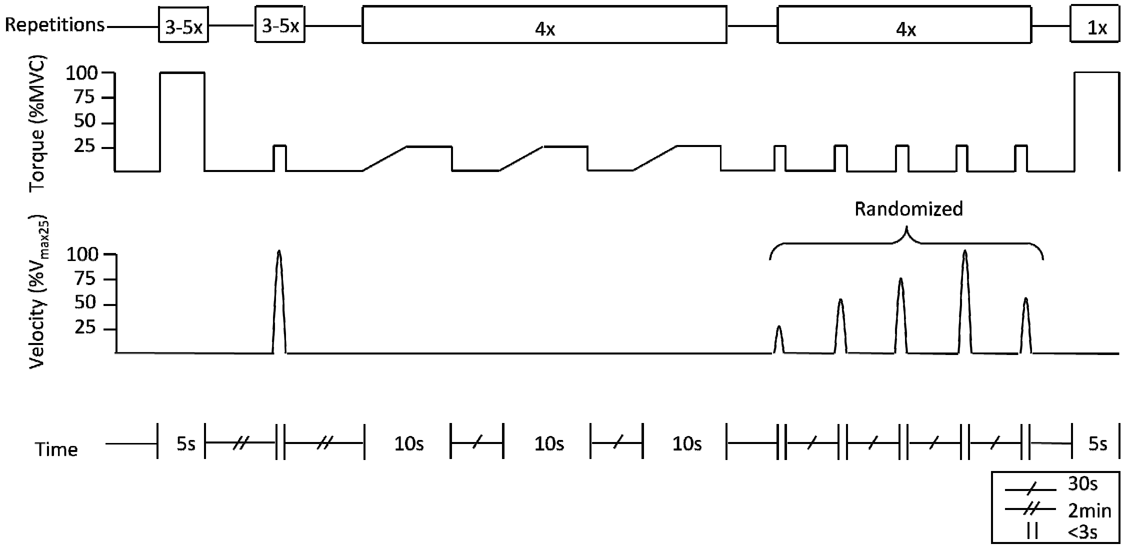

Figure 4. Experimental protocol. From top panel to bottom panel, the number of repeats, elbow extension torque (%MVC) and velocity (%V_{max25}), and duration of each contraction and rest period. All velocity-dependent elbow extensions were preloaded at 25%MVC and the order of the five contractions was randomized across all four sets. As a consequence, subjects always performed one target velocity twice in a single set and may have been required to perform multiple elbow extensions at the same target velocity within a single set as dictated by the randomization. As shown in the 4th panel (time), all velocity-dependent elbow extensions lasted less than 3s, whereas isometric contractions (100%MVC and 25%MVC) lasted 5s and 10s, respectively. Approximately 30s to 2 minutes of rest was allotted after each

contraction. Additional rest was provided at the request of the subject in order to prevent fatigue, with the exception of the post-protocol MVC, which was performed immediately following the final elbow extension.

Surface EMG of the lateral head of the triceps brachii was recorded via self-adhering pediatric electrocardiogram cloth electrodes (H59P 127 Repositionable Monitoring Electrodes; Kendall, Mansfield, Massachusetts). After cleansing the surface of the skin with 70% isopropyl alcohol, a surface electrode pair was placed in line with the fascicles of the lateral head of the triceps brachii at the mid-shaft of the humerus with an interelectrode distance of 2 cm. A ground electrode for the surface EMG channel was placed on the clavicle just proximal to the acromioclavicular joint.

Single MU action potential trains were recorded from the anconeus muscle using custom made insulated stainless steel fine wire electrodes (100 μm, California Fine Wire Company, Grover Beach, CA). The anconeus was located by anatomic landmarks and palpation during elbow movements. The muscle belly can be palpated in a small triangular space between the olecranon process of the ulna and the lateral epicondyle of the humerus. During a low force elbow extension, two hooked tip fine wires (15–30 cm length) were passed through a 27.5 gauge hypodermic needle (Becton–Dickinson and Company, Franklin Lanes, NJ), which was inserted to a depth of ~1 cm into the belly of the anconeus ~2–4 cm distal to the humeral attachment. The needles were withdrawn immediately leaving the two bipolar pairs of fine wires embedded in the muscle. The purpose of using multiple bipolar fine wire arrangements was to maximize the yield of MU trains throughout the protocol. The common ground electrode for the fine wire electrode pairs was placed over the styloid process of the radius and secured with surgical tape. When single MU action potentials of suitable quality and clarity (high signal-to-noise ratio) were found, subjects were asked to perform wrist extension and forearm supination movements to verify the origin of the signal was the anconeus and not from one of the wrist extensors or the supinator muscle. Intramuscular EMG of the anconeus and surface EMG of the triceps brachii were pre-amplified (100–1,000x) and high-pass filtered (10 Hz, Neurolog, Welwyn City, England), which minimized any movement artifact as a consequence of surface electrode displacement during elbow extension. Intramuscular and surface EMG signals were digitized with an analog-to-digital converter (Cambridge Electronics Design, Cambridge, UK) at a rate of 15 and 1 kHz, respectively. Torque, position, and velocity data were sampled at 100 Hz, and all data were stored offline for analysis. Offline, the intramuscular EMG signals were high pass filtered at 100 Hz to remove any additional artifact that resulted from slight shifts in intramuscular electrode position during movement.

2.1.1 Data analyses

The dependent measures of peak velocity, maximal and average torque, and root mean square (RMS) of the triceps brachii EMG were determined using a custom software package (Spike 2 version 7.0, CED, Cambridge, UK). For isometric elbow extensions, the dependent variables were measured during a 3-s plateau at the peak torque of the contraction. For velocity-dependent elbow extensions, RMS of the triceps brachii was taken from the period of time beginning with a rise (2% of maximal RMS) in EMG above baseline and ending at peak velocity. Depending on the velocity, this ranged from ~550 to ~2,100ms.

Motor unit recordings were analyzed using a template matching algorithm (Spike 2 version 7.0, CED, Cambridge, UK) in which individual MU action potential trains were identified using waveform shape by overlaying sequential action potentials with respect to temporal and spatial characteristics (Figure 5). Visual inspection by an experienced investigator was the ultimate determinant in deciding whether a MU action potential belonged within a train of MU potentials. Motor unit discharge times (s) were determined for each MU action potential and mean instantaneous MU discharge rates subsequently calculated (Spike 2 version 7.0, Cambridge, UK). The inclusion criteria for statistical analysis of MU discharge rates during velocity-dependent contractions required that MUs: (1) fire at least five consecutive action potentials, (2) were active during both the initiation phase (torque development) and movement phase of each elbow extension, (3) were consistently present during each set of velocity-dependent contractions (Figure 4). As a consequence of each set consisting of five contractions that varied with respect to their target velocity, it was possible that a MU could be active for each set of the protocol without contributing to the mean instantaneous MU discharge rates at each target velocity. Interspike intervals of less than 10 ms or greater than 150 ms were not included in the analysis of MU discharge rate. The remaining interspike intervals of the MU train were included in the analysis provided they satisfied the inclusion criteria. For isometric contractions, the MU discharge rate was determined for a 1-s plateau in torque during which peak torque occurred. The inclusion criteria for statistical analysis of MU discharge rates during isometric tasks was similar to that of velocity-dependent contractions in that at least five consecutive single MU action potentials were required and no interspike intervals of less than 10 ms or greater than 150 ms were included. For MUs that included an interspike interval of ≤10 ms, indicating a double discharge, the first of the two consecutive potentials comprising the double discharge was excluded so that the remainder of the MU train could be included in the analysis.

From 38 MUs, 978 MU trains were processed and a mean instantaneous MU discharge rate (initiation and movement phase) for each single MU train was recorded for each velocity-dependent elbow extension in which a MU was active and discernible (Figure 5). For MUs satisfying the inclusion criteria, an average MU discharge rate was determined for individual MUs at each target velocity (25%V_{max25}, 50%V_{max25}, 75%V_{max25}, V_{max25}) and target torque (25%MVC, 100%MVC). Average MU discharge rates were comprised of mean instantaneous MU discharge rates recorded during the many repetitions at each target velocity or torque level. The number of mean instantaneous MU discharge rates included in the average MU discharge rate of a MU at any given target velocity or torque varied. The greatest average number of mean instantaneous MU discharge rates included in an average MU discharge rate was at 50%V_{max25} (13), followed by 25%V_{max25} (12), 75%V_{max25} (8), and 100%V_{max25} (5). For isometric contractions, fewer mean instantaneous MU discharge rates were included in an average MU discharge rate

(100%MVC [3], 25%MVC or 0%V_{max25} [3]) because fewer isometric contractions were performed throughout the protocol.

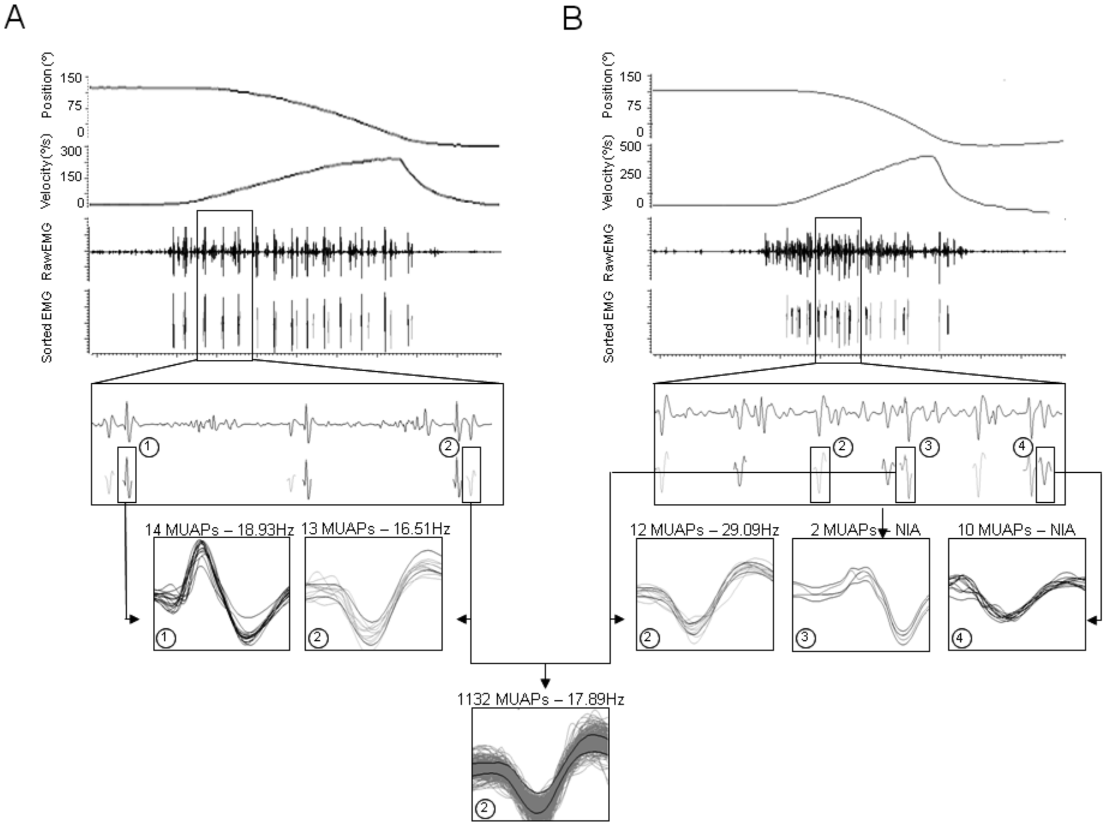

Figure 5. Position, and velocity of elbow extension, and intramuscular EMG and single motor action potentials of the anconeus for: A) a moderate velocity (~50% maximal velocity, 246°/s), and B) a maximal velocity (100% maximal velocity, 492°/s). In both (A) and (B), the top two traces are the position, and velocity profiles, respectively, corresponding to the MU recordings shown below. Approximately 1s of the intramuscular and sorted EMG of the anconeus is highlighted below by the large rectangle. (A) Three single MU action potentials (MUAPs) each are shown for two distinct MUs (1, black; 2, light gray), each encased by a separate rectangle. Below these extended EMG recordings, the overlaid single MUAPs and MU template margins are presented. The overlay includes only the single MUAPs recorded during the elbow extension illustrated above, and two black lines encasing the overlaid potentials represent the margins of shape variability.

Displayed above each box are the number of MUAPs included in the overlay and the MUDR that corresponds to these MUAPs. (B) Two to three single MUAPs are shown for three distinct MUs (2, light gray; 3, dark gray; 4, black), each encased by a separate rectangle. Below the extended recordings, the overlaid single MUAPs and MU template margins are presented. Displayed above each box are the number of MUAPs included in the overlay and the MUDR corresponding to these MUAPs. The acronym NIA indicates a MU was not included in the analysis as a consequence of too few MUAPs to calculate an average MUDR or because it was not consistently observed throughout the duration of protocol. The centered bottom box includes all single MUAPs recorded throughout the duration of the protocol for the MU active at both velocities (2, light gray), with the black lines representing the margins of the template. The total number of MUAPs recorded for this MU and the average discharge rate are listed above the box.

Average MU discharge rates from 24 MUs were included in the final data set used for statistical analysis. In order to express average MU discharge rates as a function of relative velocity or torque (normalized), a MU had to be active at maximal velocity or maximal torque, respectively. In the situation in which a MU was active during maximal velocity or torque, but not active at all submaximal velocities or torques, the average MU discharge rates corresponding to that MU were included but with no values entered for the submaximal velocities or torques for which the MU was not active. As a consequence, 100%V_{max25} contributed the largest number of values (MUs) to the data set (24), followed by 75%V_{max25} and 50%V_{max25} (20), 25%V_{max25} (18), 100%MVC (13), and finally 25%MVC or 0%V_{max25} (9). For each elbow extension that contributed an average MU discharge rate to the data set, the corresponding average torque and peak velocity were also calculated. Peak velocity and average torque values were normalized to maximal values (MVC and V_{max25}) and grouped according to the target elbow extension isometric torque (25, 100%MVC) or velocity (25%, 50%, 75%, 100%V_{max25}) from which they were sampled. In each subject, a single average RMS of the triceps brachii was measured for each target velocity and torque from elbow extensions for which a MU was active. For velocity-dependent contractions, each subject's RMS value was expressed relative to the RMS recorded during 100%V_{max25} in that subject, whereas RMS for isometric contractions was expressed relative to the RMS at 100%MVC.

2.1.2 Statistical analysis

Differences between the pre- and post-MVC and observed contraction velocities were assessed using paired t tests. For group analyses, MU discharge rates were aggregated according to their respective relative target velocities. The dependent variables, MU discharge rate and triceps brachii RMS, were analyzed with SPSS 16.0 (SPSS Inc., Chicago, Illinois) using a one-factor (target velocity) analysis of variance (ANOVA). When significant main effects were obtained, independent t-tests were performed and effect sizes (η^2) calculated. Alpha level was set at $P \leq 0.05$. A two segment piecewise regression analysis was performed with Sigmaplot 11.0 (Systat, San Jose, California) using the variables of relative peak velocity and MU discharge rate. Coefficient of determination (R^2) was first determined for the two segment piecewise regression. Data series (x, y) corresponding to trendlines that described the two linear ranges from the piecewise regression were exported to Microsoft Excel and equations were determined. All values in the text and figures are mean ± standard deviation (SD).

2.2 Results

A total of 800 MU trains from 24 distinct MUs active throughout the protocol in 11 subjects (~2–3 MUs per subject) met the inclusion criteria as outlined in Methods. A sample recording of MU data collected from one subject at 50%V_{max25} and 100%V_{max25} is provided in Figure 5. Torque and velocity ranges corresponding to each of target intensities are provided in Table 1. The average peak velocity for elbow extensions performed at the 25%V_{max25} and 50%V_{max25} deviated 5% or less from the target velocity, whereas the average peak velocity at the 75%V_{max25} target was 10% greater (85%V_{max25}). The amplitude of the pre- and post-MVC did not differ from each other ($P = 0.98$, Table 1).

Table 1. Force and velocity characteristics for elbow extension tasks

	Dynamic			
	Velocity, °/s			
	25%	50%	75%	100%
Mean	130	249	367	453
SD	29	31	31	41
Maximum	191	299	416	494
Minimum	93	189	308	373
	Isometric			
	Torque, Nm			
		Pre	Post	
	25%	100%	100%	
Mean	19	64	64	
SD	4	13	9	
Maximum	25	78	77	
Minimum	12	45	43	

SD, standard deviation

The analyses of variance revealed main effects of target velocity for triceps brachii RMS ($P<0.01$, $\eta^2 = 0.29$) and MU discharge rate ($P<0.001$, $\eta^2 = 0.53$). As a percentage of RMS at V_{max25}, triceps RMS increased linearly before beginning to plateau at the 50%V_{max25} and reaching a steady-state at 75%V_{max25} (Figure 6). Root mean square of the lateral head of the triceps did not differ ($P = 0.80$) between 75%V_{max25} and 100%V_{max25} (Figure 6). As well, no difference for triceps RMS was observed between the 25%MVC and the 25%V_{max25} ($P = 0.90$) or between 25%MVC and 50%V_{max25} ($P = 0.28$) (Figure 6).

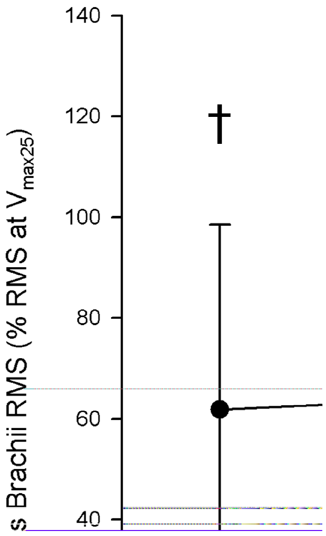

Figure 6. Relative root
velocities. Each point r
regardless of the numb
the triceps brachii is ex
extension velocity was
significantly different f

The variability of the m
the y-axis and x-axis, re
extensions (100%V_{max2}
1.3; 25%V_{max25}, n = 8.0
The mean, SD, and rang
isometric and velocity-

Average MU discharge rates did not differ between 25%V_{max25} and 50%V_{max25} ($P = 0.17$), but differed significantly for all other comparisons (Figure 7b, Table 2). When considering the full range of target velocities (0–100%V_{max25}), a two segment piecewise regression analysis indicated a bilinear fit ($R^2 = 0.47$, $P<0.001$) best represented the positive MU discharge rate/velocity relationship with a transition period occurring at approximately 55%V_{max25} (Figure 7b).

Table 2. Motor unit discharge rates of the anconeus during isometric and dynamic elbow extension

	Dynamic			
	Velocity, °/s			
	25%	50%	75%	100%
N	18	20	20	24
Average MUDR, Hz	19.1†	22.2†	28.7*†	39.0*†
SD MUDR, Hz	5.7	7.9	9.0	13.8
Maximum MUDR, Hz	29.9	42.7	46.9	81.1
Minimum MUDR, Hz	10.4	12.7	16.8	19.0
	Isometric			
	Torque, Nm			
	25%			100%
N	9			13
Average MUDR, Hz	11.8*			23.8†
SD MUDR, Hz	3.2			7.7
Maximum MUDR, Hz	15.9			36.0
Minimum MUDR, Hz	7.6			15.6

N, number of motor units included in average, MUDR, motor unit discharge rate; SD, standard deviation. * Average MUDR significantly different from dynamic 25%, $p<0.05$. † Average MUDR significantly different from isometric 25%, $p<0.05$

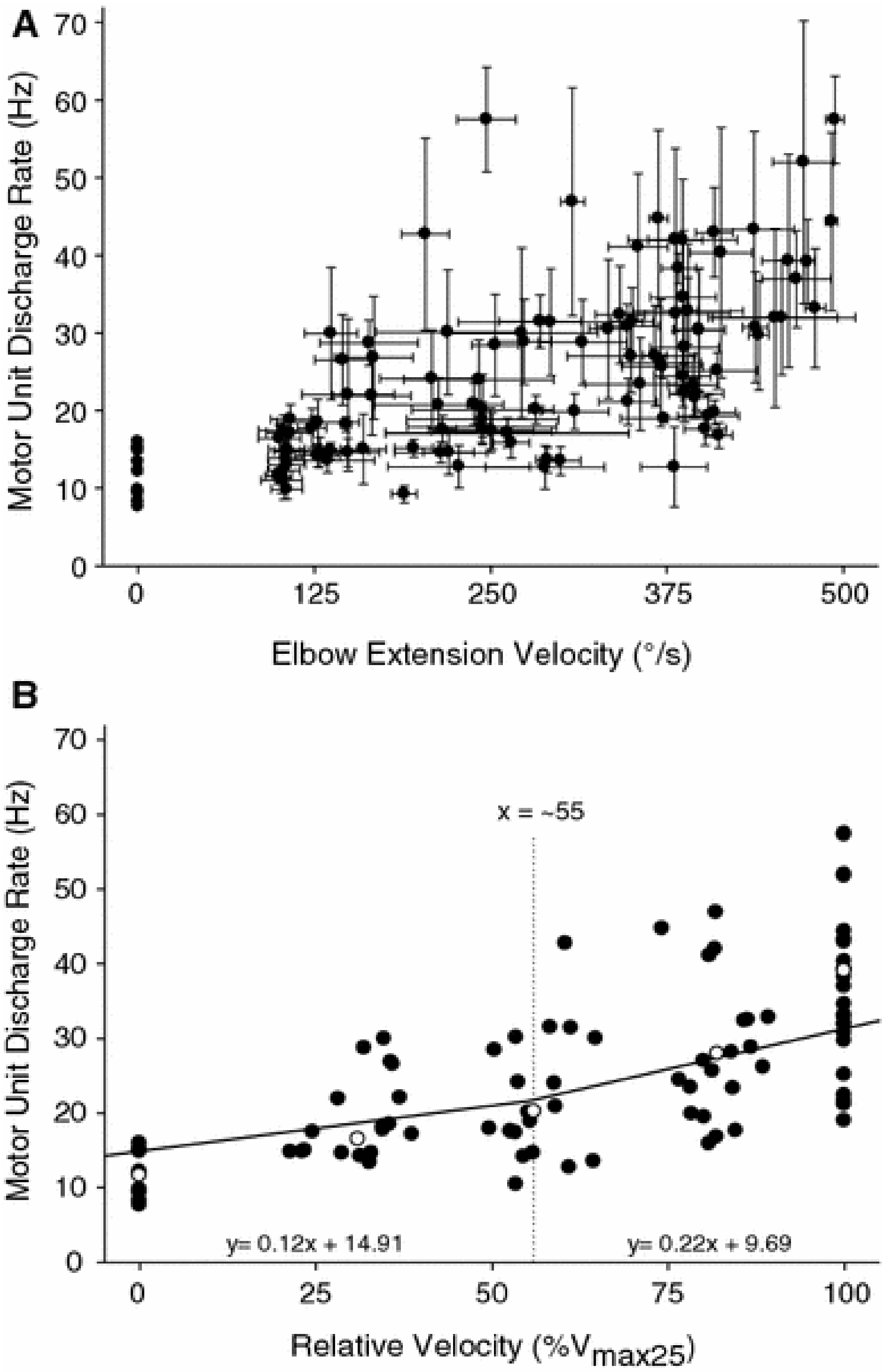

Figure 7. Average MU discharge rates of anconeus MUs proportionate to (A) absolute velocity (°/s), and (B) relative velocity (%V_{max25}). For both (A) and (B), each filled point represents the average MUDR corresponding to the average peak velocity of loaded (25%MVC) contraction for one MU. Accordingly, a maximum of

five points per MU are possible on the figure, although not all MUs were observed at each target velocity and thus may not each contribute the maximum of five points. Furthermore, if a MU was not active at maximal velocity, it was not included in the regression analysis as the MU discharge rate was expressed relative to a percentage of maximal velocity (V_{max25}). (A) Error bars indicate the variability (SD) in MU discharge rates (x error bars) and velocity (y error bars) for the multiple measures taken at each target velocity for a respective MU. (B) Open points represent the average MUDR and velocity for each target velocity. Curve estimation determined a bilinear relationship ($R^2 = 0.47$, $P<0.001$) to be the best fit for these data as represented by the solid trend line. The solid vertical line labeled at 55.47%V_{max25} represents the transition in the bilinear relationship. Equations for each range are located below their corresponding lines.

2.3 Discussion

The neural determinants of torque production and subsequently shortening velocity, at the level of the motoneuron pool, include MU recruitment and MU discharge rate (16, 17). Using the anconeus muscle, MU discharge rates were assessed for elbow extension velocities ranging from 93 to 494°/s, and at elbow extension torques between 12 and 78 Nm (Table 1). Although the intramuscular EMG technique employed precludes any estimation of the total number of active MUs, average MU discharge rates ranged from 19.1 Hz at 25%V_{max25} to 39.0 Hz at 100%V_{max25} for velocity-dependent elbow extensions and were 11.8 Hz and 23.8 Hz at 25%MVC and 100%MVC, respectively (Table 2). Whereas the target torque for isometric contraction and load requirement for shortening during velocity-dependent contractions were constant (25%MVC), average MU discharge rates increased as a function of elbow extension velocity (Table 2) in two positive linear ranges, a primary (0–55%V_{max25}) and secondary (55–100%V_{max25}) range transitioning at approximately 55%V_{max25} (Figure 7b).

A relatively small (2,002 mm^2), short (73 mm), and slow (60–67% type I) elbow extensor (6, 32, 42, 59), the anconeus is estimated to contribute ~15% to the total isometric elbow extension torque (64). The contribution of the anconeus also reportedly decreases as isometric elbow extension torque increases (64). Surface EMG studies support this apparent decrease in contribution to elbow extension torque in that maximal integrated EMG is realized at low torques and low velocities (41, 43). A plateau in the positive linear relationship between work and integrated EMG of the anconeus at low relative torques in an isometric elbow extension was also reported in these studies (41, 43). However, integrated EMG may not reflect accurately changes in all MU properties as it has been demonstrated that the surface EMG signal primarily reflects MU recruitment and is less sensitive to increases in MU discharge rate (12) and may be compromised at high intensities and by movement (36). The results of the present study support these concepts, whereby MU discharge rates of the anconeus continued to increase with greater elbow extension velocity, when there was a plateau in the RMS of the triceps brachii (Figure 6) similar to that observed in the anconeus in previous studies (41, 43).

A caveat of recording single MUs during velocity-dependent contraction is electrode displacement, which may occur either passively as the joint angle changes or actively by the contractile process, or as a consequence of both. A shift in electrode location may alter the spatial and temporal characteristics of the single MU action potential (24), by which single MUs are identified, or result in the non-physiological appearance or disappearance of the single MU recording. To minimize any influence of electrode displacement with a large change in joint angle and high velocity, the anconeus muscle was investigated. It is active throughout elbow extension and its activation precedes that of the triceps brachii (32, 41-43). However, the relative change in fascicle length of the anconeus during elbow extension is ~80% less when compared with the primary elbow extensor, the triceps brachii (25, 51). As a result, it is reasonable to expect less potential displacement of the electrode across large ranges of motion and target velocities. The results of the present study seem to confirm this as the average MU discharge rate of 24 MUs were obtained successfully from velocity-dependent elbow extension across 120° ROM at velocities ranging from 93 to 494°/s (Table 1). More importantly, 18 MUs were tracked through all four velocity-dependent target intensities, with nine of these units active during all isometric and velocity-dependent contractions. Thus, more than a third of the average MU discharge rates used to generate the bilinear fit between MU discharge rate and peak elbow extension velocity (Figure 7b) were contributed by MUs active at all isometric and velocity-dependent target intensities, with three quarters of the total sample of MUs contributing to the average MU discharge rate at all velocity-dependent target intensities.

A bilinear fit best described the relationship ($R^2 = 0.47$) between average MU discharge rates of the anconeus and peak elbow extension velocity. The initial positive linear range supports the concept that linear increases in MU discharge rates occur across low submaximal velocities (21, 24, 35, 60). At the same time, the bilinear fit closely resembles the exponential decline in minimal interspike interval (increased MU discharge rates) with increased work (48) in that a steeper rise in MU discharge rates is realized at fast velocities compared with low submaximal velocities. Although the division of the bilinear fit into two linear components appears to support the anesthetized decerebrate cat model (26) and one human model (63) of MU function, whereby MU discharge rates initially increase linearly within a primary (submaximal) range and upon transcension of a given input, enter a secondary range characterized by a steeper positive slope, studies of persistent inward currents (PICs) in response to synaptic current (39, 41) suggest otherwise. These studies (39, 41) suggest human motoneurons, in response to synaptic input, fire in a ‘preferred’ range, or ‘limiting’ range (27), characterized by a saturation of PICs, abolishing the primary range in slow motoneurons of humans. These observations support early studies of MU discharge rates up to maximal force (42, 49), in which the MU discharge rates of low threshold MUs plateaued at relatively low forces. However, the continued rise of MU discharge rates of higher threshold MUs at a much higher gain compared to the rise of low threshold MUs is inconsistent with PIC saturation. Moreover, the motoneuron input required for high velocity contractions exceeds that of a maximal isometric contraction (52) as evidenced by average MU discharge rates observed in the present study (Table 2).

Average MU discharge rates at 100%MVC were lower than those at 100%V_{max25} ($P<0.001$) and tended ($P = 0.07$) to be lower than MU discharge rates at 75%V_{max25} (Table 2).

Persistent inward currents are potent neuromodulators and they may increase the gain of the current-frequency relationship two- to six-fold (44), which may greatly enhance MU discharge rates (29). It is believed that in slow type motoneurons, PICs are saturated at or below recruitment threshold (30) and firing in the 'preferred range'. Assuming low threshold or slow type motoneurons are firing in the 'preferred' range for all contractions, one possibility is that the synaptic input to the motoneuron pool during slow dynamic contractions is weak enough that the level of monoaminergic drive does not sufficiently drive the fast motoneurons into a secondary range, or that a secondary range is only briefly realized. However, during fast dynamic contractions, the high levels of synaptic input and arousal result in higher levels of neuromodulators (4, 33) likely accelerating the transition to the secondary range, or omission of the primary range altogether, and thus a high gain of the input to output relationship of the fast motoneuron is observed. Support for this hypothesis is provided by the differences between the slopes of the primary and secondary ranges in the present study. The slope of the secondary range (slope = 0.22 Hz/°·s^{-1}) is almost double the slope of the primary range (slope = 0.12 Hz/°·s^{-1}), which coincides with the gain of the primary range (G_1 = 1.5 Hz/nA) and secondary range (G_2 = 3.0 Hz/nA) included in models of motoneuron input/output relationships (26, 27, 63). Consequently, higher MU discharge rates are achieved at the fast velocities compared with slow velocities and the bilinear relationship between relative elbow extension velocity and MU discharge rates may be representative of the primary and secondary ranges of fast type motoneurons observed in the current-frequency relationship.

The significance of exploiting a steeper secondary range of MU discharge for higher velocity contractions likely stems from the effect of MU discharge rate on two important parameters of power generation; rate of torque development and contractile speed. During isovelocity shortening contractions, the inclusion of shorter interspike intervals in constant-frequency trains of electrical stimulation enhances the rate at which torque develops (7, 8). Additional support for this hypothesis comes from studies that show concomitant declines in rate of torque development and MU discharge rate with age (40), and a concurrent increase in rate of tension development and MU discharge rate following 12 weeks of resistance training (62). Interestingly, faster MU discharge rates not only increased rate of torque development, but also were associated with shorter twitch contraction durations (62), suggesting the possibility for faster dynamic contractions. Support for a connection between MU discharge rates and contractile speed is derived from the observation that faster contractile speed is strongly associated with the short afterhyperpolarization of motoneurons (22), which have been linked to fast MU discharge rates (13, 46). Taken together, it is likely that MU discharge rates contribute both to an increase rate of torque development and contractile speed manifesting as faster peak velocities during loaded velocity-dependent contractions.

In summary, the concurrent plateau in surface EMG of the triceps brachii coupled with a bilinear increase in average MU discharge rate with peak contraction velocity of elbow extension suggests differential velocity-dependent changes in the neural determinants of muscle contraction. Motor unit recruitment, which primarily drives the surface EMG signal, is largely complete while MU discharge rates, represented in the intramuscular EMG signal, continue to increase as a function of contraction velocity along the two distinct linear ranges. This finding is of particular interest in the anconeus because based on previous surface EMG investigations, some authors (41, 43, 64) believed the contribution of this muscle to elbow extension, as evidenced by its activation, was confined to low intensities and velocities. Lastly, these data indicate MU discharge rates can be recorded across a full ROM and up to maximal velocities that exceed the limits of current models of MU behaviour during natural human movements.

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Chapter 3 : Changes in motor unit recruitment thresholds of the human anconeus muscle during torque development preceding shortening elbow extensions[2]

3 Introduction

Conceivably, fast human limb movements would benefit from a unique set of activation parameters capable of generating the greatest amount of torque in the shortest possible duration. Modulation of rates of torque development and the subsequently generated movement peak velocities are contingent upon physiological properties of the muscle such as ATPase activity (5), cross-bridge cycle rate (12), and tendon compliance (63). At the level of the motoneuron pool, motor unit (MU) recruitment threshold and MU discharge rate influence the resultant torque development (25). For isometric contractions, many studies report a relationship between MU recruitment thresholds and torque whereby lower MU recruitment thresholds are associated with shorter times to target torque (9, 24, 30, 35, 68, 73). Two scenarios may account for a reduction in average MU recruitment thresholds: 1) the uniform lowering of MU recruitment thresholds across the motoneuron pool (21) or 2) a compression of the MU recruitment threshold range (9, 31). Each scenario results in a decrease in the average relative MU recruitment threshold; however, only a compression of the MU recruitment threshold range could promote greater superposition of MU twitch tensions and faster rates of torque development (31), presumably translating to faster movement velocities (9, 52).

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Harwood B, and Rice CL. Changes in motor unit recruitment thresholds of the human anconeus muscle during torque development preceding shortening elbow extensions. *Journal of neurophysiology* 107: 2876-2884, 2012.

Because of the technical limitations and challenges of recording single MU action potentials, few studies [for review see (26)] have investigated MU activity responsible for generating non-isokinetic dynamic (velocity dependent) contractions (i.e., contraction testing modalities in which velocity is not constrained by the testing device), and the majority of these have studied relatively low joint velocities (~250°/s). The very few (33, 36, 57) who have successfully recorded human single MU action potentials responsible for producing moderate (225°/s) to higher (~500°/s) velocity contractions did not track the behavior of single MUs throughout a series of contractions, or recorded very few MU action potentials for each contraction. Moreover, none of these studies explored the potential relationship between MU recruitment thresholds and the resultant peak contraction velocity.

Recently, Harwood et al. (40) demonstrated the ability to track single MU behavior in the anconeus muscle throughout repeated velocity-dependent elbow extensions over a full range of movement velocities. This model allowed the investigation of MU properties during previously unattainable conditions, specifically maximal velocity contractions. The purpose of the present study was to investigate whether MU recruitment thresholds of the anconeus recorded during the isometric torque production phase prior to fast non-isokinetic shortening elbow extensions are related to the resultant peak elbow extension velocity. On the basis of models of isometric force production (31, 43) and studies of ramp (9, 30, 68, 73) and ballistic (9, 24, 43) isometric contractions, it was hypothesized that MU recruitment thresholds of the anconeus would decrease linearly with an increase in the resultant peak elbow extension velocity.

3.1 Methods

Nine young men (25.8 ±2.4 yr, 177.3±8.5 cm, 77.7±7.0 kg) free from orthopedic, neuromuscular, and cardiorespiratory limitations participated in the 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.

The experimental setup and protocol have been described previously (40). Briefly, elbow extension torque, position, and velocity measures were recorded with a Biodex System 3 multi-joint dynamometer (Biodex Medical Systems, Shirley, NY), while single MU action potentials from the anconeus and surface electromyography (EMG) of the lateral head of the triceps brachii were recorded via fine-wire intramuscular and surface electrodes, respectively. One to three visits (~1.5 h/visit) were required to ensure an adequate quantity and quality of single MU recordings. Subjects were seated in the Biodex dynamometer with their shoulder flexed 90° and arm abducted 20° resting on a support positioned ~10 cm proximal to the olecranon process of the ulna (Appendix B). In the semiprone position, the arm was secured to a custom-built support fastened to the Biodex lever arm.

The protocol (Appendix A) commenced with three brief (~5 s) isometric elbow extension maximal voluntary contractions (MVCs) at 60° elbow flexion (0° = full extension), which represented the midpoint of the elbow extensor range of motion (ROM). The elbow extensors possess a relatively constant torque-length relationship across the entire ROM (14); thus the midpoint (60°) of this ROM was chosen for the isometric portion of the experiment. The highest MVC value was used to establish isometric target torques and to determine the load (25%MVC) for all subsequent velocity-dependent contractions. Next, five loaded (25%MVC) maximal-velocity elbow extensions (V_{max25}) over 120° ROM (120° elbow flexion to 0° elbow extension) were performed, during which subjects were encouraged verbally and provided torque and velocity feedback on a computer screen ~1 m in front of them. After determination of MVC and V_{max25}, a familiarization period was given in which subjects attempted loaded (25%MVC) velocity-dependent contractions at each target velocity (25%, 50%, 75%, 100%V_{max25}) until they and the investigators were confident the task could be performed accurately. After a 5-min rest period, subjects began the velocity-dependent portion of the protocol, which consisted of four sets, each one comprised of five velocity-dependent contractions performed at 25%, 50%, 75%, or 100%V_{max25} in a randomized order. After each set, three ramp isometric contractions to 25%MVC were performed to determine an isometric MU recruitment threshold; however, inclusion in the statistical analysis was not predicated on a MU recruitment threshold being recorded during the ramp isometric contraction. Approximately 30s rest was provided between each velocity-dependent elbow extension, and 2 min was allotted after each MVC and V_{max25}. To determine whether subjects experienced any fatigue, an MVC was performed 30s after the final velocity-dependent elbow extension.

Surface EMG of the lateral head of the triceps brachii was recorded via self-adhering pediatric electrocardiogram cloth electrodes (H59P 127 Repositionable Monitoring Electrodes; Kendall, Mansfield, MA) after the skin surface was cleansed with 70% isopropyl alcohol. A surface electrode pair (interelectrode distance of 2cm) was aligned with the fascicles of the lateral head of the triceps brachii at the midshaft of the humerus, and a ground electrode was positioned on the clavicle just proximal to the acromioclavicular joint. Custom-made insulated stainless steel fine-wire electrodes (100 µm, California Fine Wire, Grover Beach, CA) were used to record single MU action potential trains from the anconeus muscle. Two hooked-tip fine wires (15- to 30-cm length) were passed through a 27.5-gauge hypodermic needle (Becton Dickinson, Franklin Lanes, 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. Two needle insertions were performed and withdrawn immediately, leaving the two bipolar pairs of fine wires embedded in the muscle belly in order to maximize the yield of MU trains per session. The common ground electrode for the fine-wire electrode pairs was placed over the styloid process of the radius and secured with surgical tape. High-pass filtered (10 Hz) intramuscular EMG of the anconeus and band-pass filtered (30–500 Hz) surface EMG of the lateral head of the triceps brachii were preamplified (100 –1000x; Neurolog, Welwyn City, UK) and digitized with an analog-to-digital converter [Cambridge Electronic Design (CED), Cambridge, UK] at a rate of 10 kHz and 1 kHz, respectively. Torque, position, and velocity data were sampled at 100Hz, and all data were stored off-line for analysis. Off-line, the intramuscular EMG signals were high-pass filtered at 100–300Hz to remove any movement artifact.

3.1.1 Data analyses

All off-line data analyses were performed with a custom software package (Spike 2 version 7.0, CED). Peak elbow extension velocity and relative rate of torque development were determined for each elbow extension in which a MU recruitment threshold was obtained. Peak elbow extension velocities for each contraction were normalized to 100%V_{max25}. Relative rate of torque development (%MVC/s) was calculated as the quotient of the increase in relative torque (%MVC) and rise time (s). The torque was defined by the fixed load (25%MVC), so rise time was calculated beginning from the time at which torque increased above baseline to the time at which torque reached 25%MVC. The average root mean square of the lateral head of the triceps brachii EMG (EMG_{RMS}) also was determined for each velocity-dependent elbow extension in which a MU recruitment threshold was obtained. The average EMG_{RMS} was recorded for a period of time beginning with the initial rise in EMG amplitude from baseline to peak elbow extension velocity because the cessation of the initial agonist burst of the triphasic EMG pattern is correlated with peak velocity (4). For each subject, the average EMG_{RMS} was expressed relative to the EMG_{RMS} recorded during the 100%V_{max25} (EMG%V_{max25}). Single-MU analysis was performed with a template-matching algorithm (Spike 2 version 7.0, CED) that identified single MU action potentials using waveform shape by overlaying sequential action potentials with respect to temporal and spatial characteristics. However, the ultimate determinant in deciding whether a MU action potential belonged within a train of potentials was made by visual inspection by an experienced investigator. For both isometric and velocity-dependent elbow extensions, MU discharge times (s) were determined for each MU action potential and MU recruitment threshold was determined as the relative torque at which a MU fired its first action potential. The criteria for inclusion in the statistical analysis required that MUs 1) fired at least five consecutive action potentials, 2) fired continuously after MU recruitment threshold (no interspike intervals >150 ms), 3) were active during both the initiation phase (torque development) and movement phase of each elbow extension, and 4) were consistently present during each set of velocity-dependent contractions. MU recruitment thresholds were expressed relative to the MVC of the subject from which the MU was recorded. Average MU recruitment thresholds for each individual unit were determined from the multiple MU recruitment thresholds recorded during the repeated contractions at each target velocity. These averaged MU recruitment thresholds were determined for the four velocity ranges (0 –25, 25–50, 50 –75, 75–100%V_{max25}). Group averages for the entire pool of MUs were derived for the same four velocity ranges from the average MU recruitment thresholds from each individual MU.

3.1.2 Statistical analysis

Recruitment threshold differences between the four velocity ranges were evaluated for the entire group of MUs rather than on an individual basis. One-factor (velocity) ANOVA was performed with SPSS 17.0 (IBM, Armonk, NY) for the dependent variables relative MU recruitment threshold and relative rate of torque development (%MVC and %MVC/s, respectively) and Tukey honestly significant difference (HSD) post hoc analysis was used to examine differences among velocity ranges with α level set at $P<0.05$. Curve estimation and regression analyses were performed for the dependent variables of relative peak velocity (%V_{max25}) and MU recruitment threshold (%MVC) and relative peak velocity (%V_{max25}) and relative EMG_{RMS} (EMG%V_{max25}). For MU recruitment threshold (%MVC), a single consolidated relative frequency plot comprised of individual relative frequency plots for each resultant peak velocity range (0 –25, 25–50, 50–75, and 75–100%V_{max25}) was generated (see Figure 3A). On the x-axis, four bins were selected based on the distribution of these data (<10, 10–14.99, 15–19.99, and ≥20%MVC), and the relative frequency of occurrence of MUs was expressed as a percentage of the total MUs collected at each resultant velocity range. The 0 –4.99%MVC and 5–

9.99%MVC bins were consolidated to form the <10%MVC bin because of the paucity of data in the 0 –4.99%MVC range, in which the relative frequency of MUs possessing a MU recruitment threshold in the 0 –4.99%MVC range accounted for <10% of the total number of MUs for all resultant target velocity ranges. For each individual MU, linear regression analyses were completed to investigate changes in single MU recruitment thresholds with increasing elbow extension velocity. Pearson product-moment correlation coefficients (r), coefficients of determination (R^2), and least square regression lines were determined for all regression analyses, and ANOVAs were performed for each relationship. Values in the text are means ± SDs.

3.2 Results

Recruitment thresholds for 17 anconeus MUs were tracked across a range (0–100%V_{max25}) of elbow extension velocities in nine subjects (1–3 MUs per subject). Representative MU data from one subject for peak resultant velocities of 25% and 100%V_{max25} are provided in Figure 8. Absolute resultant elbow extension velocities ranged from 64°/s to 500°/s (Table 3). Considerable overlap was observed among absolute peak velocities of each relative velocity range because of the between-subject differences in V_{max25} (Table 3).

Accordingly, the relationships between MU recruitment thresholds and relative resultant peak velocity and between EMG%V_{max25} and relative resultant peak velocity were considered across the entire recorded continuum of resultant elbow extension velocities (~22–100%V_{max25}) rather than binning dependent measures based on target velocity ranges. Linear regression analysis of EMG%V_{max25} and relative resultant peak velocity revealed a moderate amount of shared variance (R^2=0.57) (Figure 9). Average relative rates of torque development also increased with increasing resultant velocity (Table 4), ranging from 33.9%MVC/s at 0–25%V_{max25} for subject 6 to 408.9%MVC/s at 75%V_{max25} for subject 2. Relative MU recruitment thresholds for four relative resultant elbow extension velocity ranges (0 –25, 25–50, 50–75, 75–100%V_{max25}) for each MU are also provided in Table 4.

Table 3. **Relative and absolute elbow extension velocities**

	Relative Velocity Range, %V_{max25}			
	0-25	25-50	50-75	75-100
N	91	193	187	147
	Absolute Velocities, ° s^{-1}			
Mean	100	157*	267*	362*
SD	12	43	46	64
Maximum	124	232	370	500
Minimum	64	80	170	251
	Relative Velocities, %V_{max25}			
Mean	22	37*	62*	87*
SD	2	7	7	8
Maximum	25	50	75	100
Minimum	16	26	51	76

N, number of data, SD, standard deviation, V_{max25}, maximal velocity dynamic elbow extension. * Average velocity significantly different from 0-25%V_{max25}, $p<0.05$.

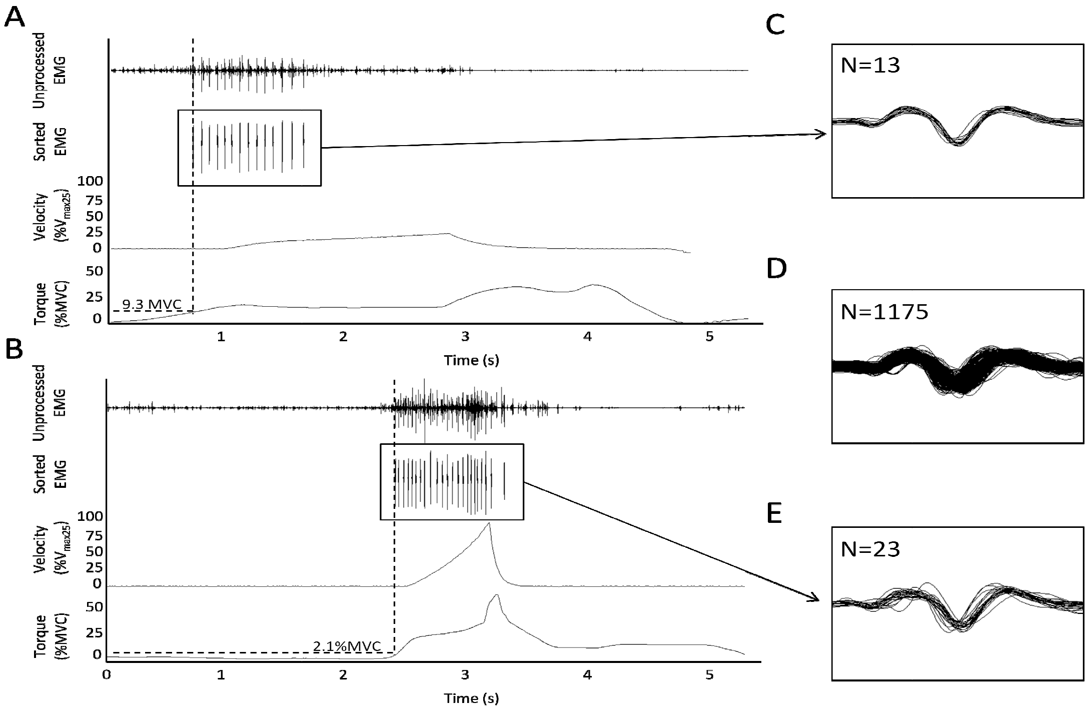


Figure 8. Intramuscular electromyography (EMG) recordings of an anconeus motor unit (MU) for a low (A, ~25%V_{max25}) and high (B, 100%V_{max25}) elbow extension

velocity. For both (A) and (B), from top to bottom panel, unprocessed EMG, single MU action potentials belonging to one MU (sorted EMG), relative velocity, and relative torque are displayed. The vertical dotted line corresponds to the time at which the first MU action potential was recorded, whereas the horizontal line indicates the relative torque corresponding to the recruitment of the MU. Panels (C) and (E) show the overlaid single MU action potentials for each recording in (A) and (B), respectively. The number of single MU action potentials in each overlay is indicated in the upper left corner. The cumulative superposition and total number of single MU action potentials for the representative MU throughout the entire protocol is shown in panel (D).

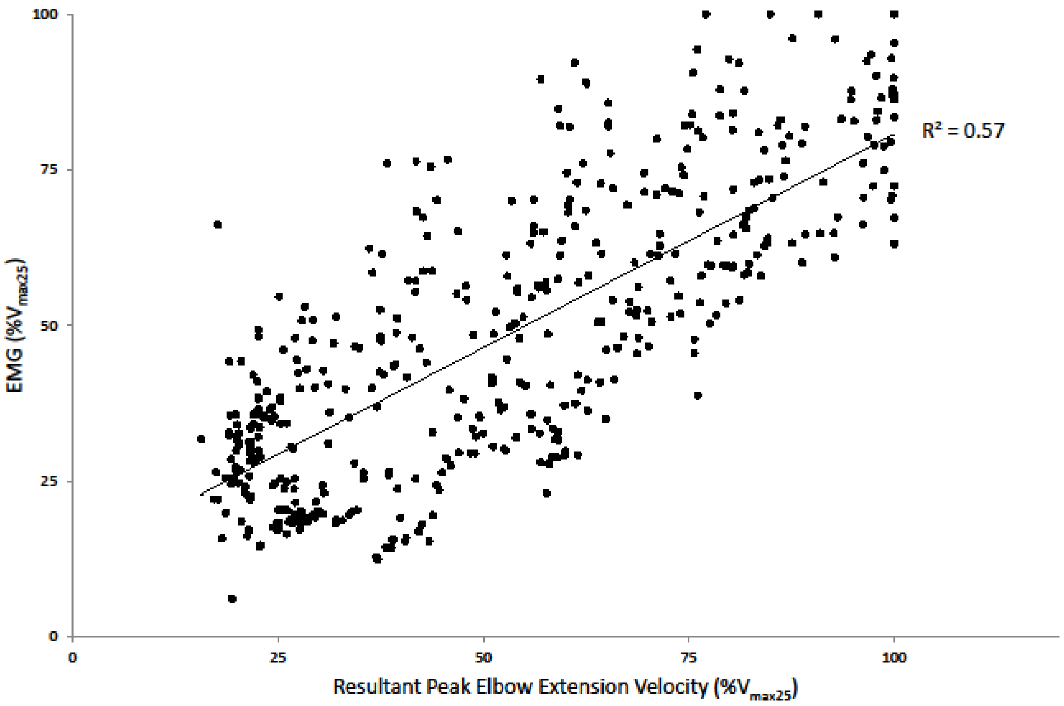


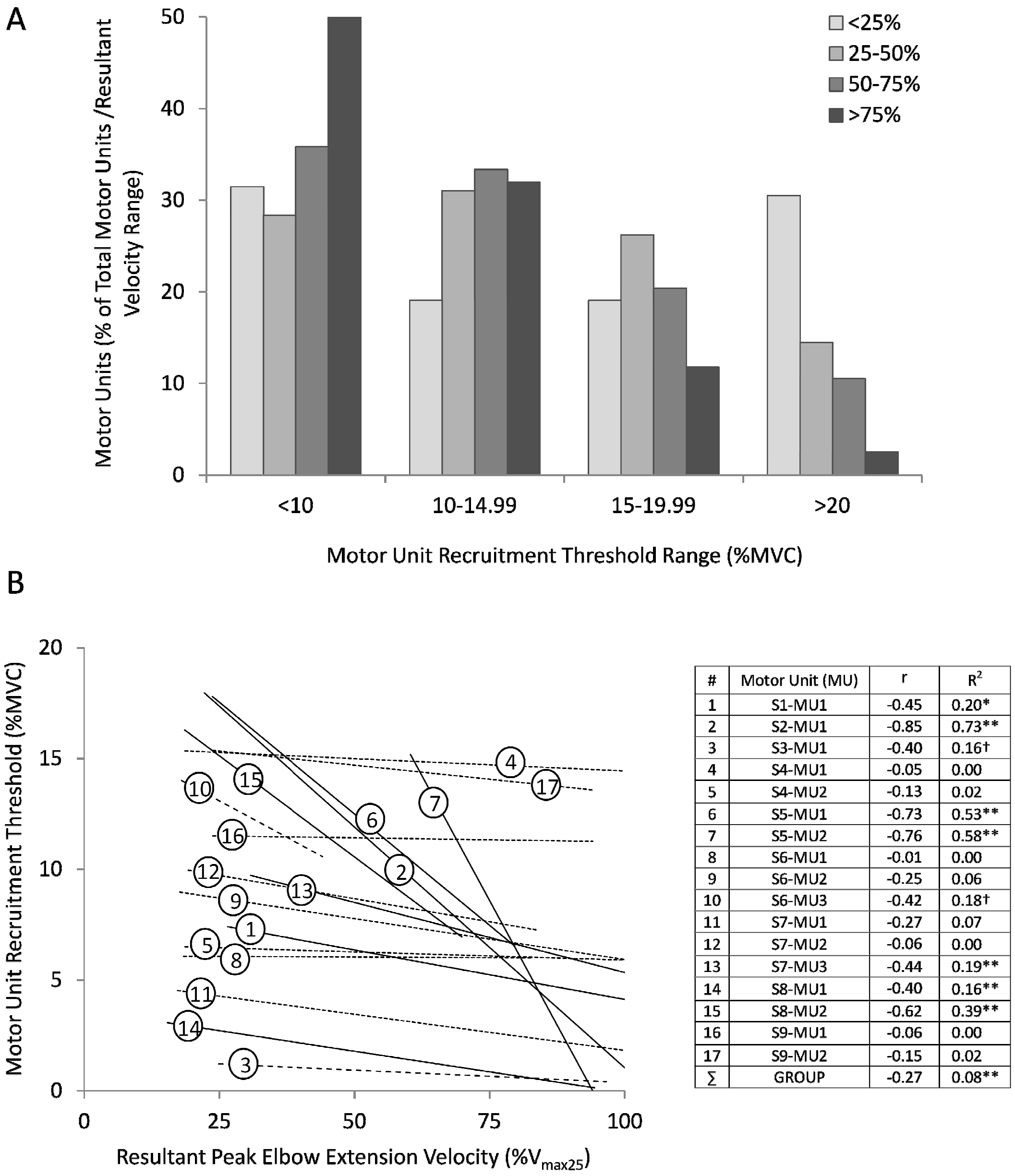
Figure 9. Linear relationship between relative EMG (%V$_{max25}$) of the lateral head of the triceps brachii and relative resultant peak elbow extension velocity (%V$_{max25}$).

Table 4. Average relative motor unit recruitment thresholds and rates of torque development for four relative resultant peak velocity ranges

Subject-MU	$\mu_{0\text{-}25\%Vmax25}$	$\mu_{25\text{-}50\%Vmax25}$	$\mu_{50\text{-}75\%Vmax25}$	$\mu_{75\text{-}100\%Vmax25}$
	Relative Motor Unit Recruitment Threshold, %MVC			
1-1	--	8.2*	5.8	4.4
2-1	17.4*	15.6*	3.9	1.4
3-1	--	1.0	0.9	0.4
4-1	14.7	16.2	16.0	12.3
4-2	6.4	6.1	6.9	5.2
5-1	16.3*	15.4*	12.1*	4.4
5-2	--	--	12.7*	4.0
6-1	4.9	6.1	7.6	2.3
6-2	--	10.0*	9.0*	4.2
6-3	13.2	11.7	--	--
7-1	4.7	4.9	3.1	2.7
7-2	--	5.1*	7.8	9.2
7-3	--	10.3*	8.5	6.1
8-1	2.8*	2.4*	1.4	0.8
8-2	15.6*	12.8*	7.7	--
9-1	12.5	12.5	11.0	11.9
9-2	14.6	14.6	14.8	13.6
Σ	10.7*	9.6*	8.1	5.5
	Relative Rate of Torque Development, %MVC s^{-1}			
1-1	--	97.0*	143.8*	241.7
2-1	54.5*	59.5*	123.6*	408.9
3-1	--	68.9*	110.5*	248.5
4-1	84.6*	108.5*	129.4*	234.0
4-2	77.1*	93.6*	121.3	133.8
5-1	60.5*	114.3*	191.3	221.1
5-2	--	--	186.8*	288.8
6-1	43.1	63.0	73.7	83.3
6-2	--	62.9*	90.6	148.7
6-3	40.1*	50.0	--	--
7-1	43.2	60.4*	100.4	111.7
7-2	--	75.3*	107.5	156.8
7-3	--	59.6*	89.2*	126.1
8-1	42.0*	78.1*	171.8	204.0
8-2	33.9*	80.7*	165.2	--
9-1	--	168.8*	215.3	280.5
9-2	--	167.0*	196.6*	281.6
Σ	53.2*	88.0*	138.6*	210.7

Σ, sum of all motor units, μ, mean, * $p<0.05$, significantly differs with average value at highest velocity range recorded (μ75-100%V_{max25}).

Analysis of variance revealed a main effect ($P<0.05$) of relative resultant peak relative velocity for relative MU recruitment threshold. Post hoc analysis showed that relative MU recruitment threshold was higher at 0–25%V_{max25} and 50–75%V_{max25} compared with 75–100%V_{max25} ($P<0.05$). A weak, but significant, negative relationship ($r=0.27$, $R^2=0.08$, $P<0.001$) between relative MU recruitment thresholds and relative resultant peak velocity was observed when the entire sample of MUs was considered. Regression analyses of individual MUs revealed significant negative relationships ($r=-0.34$ to -0.76, $R^2=0.11$ to 0.58) for 7 of the 17 MUs. Motor unit recruitment thresholds of the additional ten MUs either remained the same (Figure 10B, MUs 4, 5, 8, 9, 11, 12, 16, 17) with increasing velocity or exhibited a trend toward a negative (Figure 10B, MUs 3 and 10, $P=0.06$ and $P=0.07$, respectively) relative MU recruitment threshold-relative resultant peak elbow extension velocity relationship. Relative probability plots for each resultant peak velocity range demonstrated the dependence of MU recruitment threshold decline on the resultant peak velocity. The percentage of MUs for which a recruitment threshold was recruited preceding an elbow extension resulting in a peak velocity of <25%V_{max25} varied from ~20% to ~30% and did not exhibit a pattern with increasing MU recruitment threshold range (Figure 10A). As the resultant velocity range increased, a distinct pattern evolved in which the percentage of MUs recorded decreased with each progression to a higher MU recruitment threshold range (Figure 10A). This observation is clearly evident for MUs reporting a recruitment threshold at >75%V_{max25}, where the percentage of MUs reporting a recruitment threshold below 10%MVC accounted for 50% of the sample, and MUs reporting a recruitment threshold above 20%MVC accounted for less than 5%MVC (Figure 10A).



#	Motor Unit (MU)	r	R^2
1	S1-MU1	-0.45	0.20*
2	S2-MU1	-0.85	0.73**
3	S3-MU1	-0.40	0.16†
4	S4-MU1	-0.05	0.00
5	S4-MU2	-0.13	0.02
6	S5-MU1	-0.73	0.53**
7	S5-MU2	-0.76	0.58**
8	S6-MU1	-0.01	0.00
9	S6-MU2	-0.25	0.06
10	S6-MU3	-0.42	0.18†
11	S7-MU1	-0.27	0.07
12	S7-MU2	-0.06	0.00
13	S7-MU3	-0.44	0.19**
14	S8-MU1	-0.40	0.16**
15	S8-MU2	-0.62	0.39**
16	S9-MU1	-0.06	0.00
17	S9-MU2	-0.15	0.02
∑	GROUP	-0.27	0.08**

Figure 10. Relative frequency and least squares regression lines (LSRLs) for the relationship between MU recruitment threshold (%MVC) and resultant peak elbow extension velocity (%V_{max25}). (A) Relative frequency plots for four velocity ranges (<25, 25-50, 50-75, >75%V_{max25}) with respect to four MU recruitment threshold ranges (<10, 10-14.99, 15-19.99, >20%MVC). (B) Regressions for 7 of 17 MUs were significant with two showing a trend toward significance. Solid LSRLs represent significance ($p<0.05$), whereas dotted LSRLs represent no relationship between

relative MU recruitment threshold and relative resultant peak elbow extension velocity. Long dashed LSRLs indicate a trend ($p<0.08$). Least square regression lines were generated based on individual data points (not shown) corresponding to a MU recruitment threshold and the relative peak velocity of the contraction from which the MU recruitment threshold was recorded. The number attached to each LSRL corresponds to the number in the leftmost column in the table to the right of the figure showing the subject (S) and MU number, Pearson product correlation coefficient (r), coefficient of determination (R^2), and P-value for each linear regression. *$p<0.05$, **$p<0.001$, †$p=0.05$-0.08.

3.3 Discussion

Results of the MU group analysis demonstrated a reduction in relative MU recruitment threshold with an increase in relative resultant peak elbow extension velocity ($r= 0.27$, $R^2=0.08$, $P< 0.001$); however, for more than half of MUs (59%), recruitment thresholds did not change with increasing resultant peak velocity. Support for velocity-dependent modulation of MU recruitment thresholds is evidenced by the relationship between recruitment threshold and velocity for the sample of MUs recorded. However, the variable response to increasing contraction velocities in this same sample of MUs may reflect compression of the recruitment threshold range.

A great deal of our knowledge of MU behavior is the product of studies investigating isometric contractions (25). Generally, during ramp isometric contractions MUs are recruited at a relative torque based on the size of their motoneuron cell body (46) and increase their frequency of discharge of MU action potentials as the relative torque increases (22, 58). Single MU recruitment thresholds are relatively stable regardless of the target force when the rate of torque development remains constant (21, 22). However, with an increase in rate of torque development, such as that observed during an increased speed of ramp contraction (12, 22, 58) or during ballistic isometric contractions (30, 58), MU recruitment thresholds are significantly reduced [for review see (29)]. Models of MU behavior (62), and surface EMG (56) and single-MU studies of the elbow extensors (40) suggest that synaptic input to the motoneuron pool is greater during a shortening compared with an isometric elbow extension, which provides the requisite activation for the generation of the high rates of torque development observed preceding high-velocity dynamic contractions (52). Thus it was hypothesized that a reduction in MU recruitment thresholds as a result of either 1) a uniform MU recruitment threshold decrease across all sampled MUs or, alternatively, 2) a compression of the recruitment threshold range within the MU sample should occur in order to generate high-velocity elbow extensions. The findings of the present study support this hypothesis as evidenced by the significant negative MU recruitment threshold-resultant peak elbow extension velocity relationship of the anconeus (Table 4). However, the variable nature of the MU response, specifically those MUs with higher MU recruitment thresholds, suggests that a compression in the MU recruitment threshold is the most probable mechanism by which a reduction in MU recruitment threshold may occur (Figure 10).

The ability to record the MU action potentials responsible for the ultimate generation of high shortening velocities is unique, and in large part due to the special anatomical and physiological properties of the muscle model investigated. Contributing 15% to the total isometric elbow extension torque (76), the anconeus muscle is a small (2,002 mm^2), short (73 mm), and predominantly type I (60 – 67%) elbow extensor (6, 49, 55, 70). It is likely comprised of relatively few MUs based on the small size (37), which may account for the quality (high signal-to-noise ratio) of single MU recordings observed from this muscle. Despite the small contribution to elbow torque, the anconeus shares the same fundamental innervations as the triceps brachii (radial nerve) and thus displays all typical characteristics of neuromodulation during voluntary movements (49). The anconeus is active throughout the entire elbow extension range of motion and loads tested, and its activation precedes that of the triceps brachii (49, 54-56), suggesting that the relative torque at which anconeus MUs are recruited may be less contaminated by the much greater torque contribution of the triceps brachii (Figure 9) compared with other muscle groups in which synergists are activated simultaneously. Furthermore, surface EMG studies report a plateau in the integrated EMG of the anconeus at low torques and low velocities (54, 56). Considering that the surface EMG signal primarily reflects MU recruitment and is less sensitive to increases in the MU discharge rate (15), MU recruitment in the anconeus likely occurs prior to any potential interference caused by movement artifact as a consequence of the shortening of the much longer triceps brachii. In addition, the relative fascicle length of the anconeus shortens ~80% less during elbow extension than the triceps brachii (39, 59), and, as a result, there is less potential displacement of the intramuscular electrode across large ranges of motion and at high target velocities. As evidenced by the results of the present study and one other study (40), these characteristics present a useful neuromuscular model to study single MU function across a large joint range of motion, for the production of a range of velocities up to maximal velocity, and most importantly, the ability to track successfully MUs throughout repeated contractions.

Ideally, an average MU threshold is derived from a number of repeated contractions in which similar mechanical responses are generated such as can be achieved during constant-rate ramp isometric contractions. However, because of the randomization of target velocities during our protocol, subjects were unable to replicate relative rates of torque development and resultant elbow extension velocities with each new contraction. Because both training (27, 72) and fatigue (1, 13, 23) have the potential to modify MU recruitment thresholds, the fewest repetitions required at each target velocity to yield a suitable number of data points for the generation of an average were performed. Despite considerable variability in resultant peak velocity at each target velocity (Table 3), higher MU recruitment thresholds were observed at 0 –25%V_{max25} and 25–50%V_{max25} compared with 75–100%V_{max25} (Table 4). Moreover, significant negative linear relationships were observed for seven individual MUs (Figure 10B) and for the entire sample of MUs. These relationships support a decrease in MU recruitment threshold relative to increased resultant peak elbow extension velocity. Together with unique properties of the anconeus, the MU tracking method employed in the present study represents a significant improvement upon previous methods employed during ballistic isometric contractions (24, 73) and velocity-dependent contractions (33) by enabling a within-subject comparison of single MU action potentials during the resultant production of a wide range of contractile velocities, but especially those of very high velocities.

3.3.1 Effect of contraction velocity on MU recruitment thresholds

As mentioned above, studies of fast ramp and ballistic isometric contractions have provided a conceptual foundation for the current MU recruitment threshold/resultant peak elbow extension velocity relationship. However, because of the nature of isometric contractions, those studies were insensitive to the unique movement-associated EMG characteristics of the agonist (4, 8, 20, 66), which occur independent of antagonist activity (32). Although many studies have investigated constant-rate shortening dynamic contractions (isokinetic) at low velocities (1.5–15°/s) (2, 16, 17, 48, 64, 67, 69) , few (33, 36, 50) have recorded trains of single MU action potentials responsible for generating nonisokinetic dynamic (velocity dependent) contractions similar to those in the present study. Of these, only three (36, 40, 57) investigated MU properties of high-velocity (~500°/s) contractions in the anconeus and biceps brachii. However, in none of these isokinetic or non-isokinetic studies has the effect of the resultant peak contraction velocity on MU recruitment threshold been evaluated systematically [see review by (28)]. With the anconeus model, single MU action potentials were recorded at joint velocities ranging from 0°/s to 500°/s in 17 MUs and tracked throughout repeated contractions, allowing linear MU recruitment threshold-resultant peak elbow extension velocity regressions to be formed for each individual MU. Together, these regressions support a speed-sensitive (20), or rather a velocity-sensitive, strategy for single-joint movements in which MU recruitment thresholds decreased with increasing resultant peak elbow extension velocity. Further support for a velocity-sensitive strategy is provided by a similar EMG-resultant peak velocity relationship of the lateral head of the triceps brachii in this study (Figure 9). These regressions also support a linear contribution of MU recruitment to the mechanical input-output relationship (18), which differs from the input-output relationship of MU discharge rate whereby the mechanical response (torque, velocity, etc.) is modulated across multiple linear ranges, each with a distinct input-output relationship gain (7, 31, 40).

3.3.2 Neuromodulation and velocity-dependent MU recruitment thresholds

Tracking single MU recruitment thresholds may also provide some insight into the mechanisms responsible for the differential velocity-dependent responses of MUs belonging to the same motoneuron pool. Differential MU behavior is not a novel concept, and indeed it constitutes the foundation for a central principle of force and presumably movement production (45), that of orderly recruitment (46, 74). Thus it has been shown that the range of intrinsic motoneuron recruitment thresholds varies 10-fold within a motoneuron pool (41). According to orderly recruitment, the greater input resistance at the cell body of low-threshold MUs materializes in lower relative forces than higher-threshold MUs (46, 74). As the synaptic input to the motoneuron pool is increased, recruitment of higher-threshold MUs occurs. Higher-threshold MUs have a number of physiological characteristics, including high rates of force development (10), short contraction times (10), and potentially higher MU firing rates compared with low-threshold MUs (58), which may provide a distinct advantage for the generation of fast isometric contractions (24, 60, 61, 72) and dynamic movements (40).

Studies by Hammond et al. (38), Vallbo (71) and Angel (3) showed that fast human movements are unique in that the initial agonist burst is relatively inflexible and insensitive to afferent input. Recent studies of cortical and spinal activity in preparation for movement (65) show similar, but not identical, responses (19). A vast amount of neuromodulation occurs at the level of the motoneuron to alter excitability, predominantly as a consequence of serotonergic influences on persistent sodium currents (45). Despite large reductions in MU recruitment threshold in response to increased monoaminergic input (34, 53) and the potent neuromodulatory effects of monoaminergic input on the intrinsic excitability of the motoneuron (45), the likelihood that these inputs are responsible for generating motor commands of specific actions is very low (44). Less well-defined cortical projections provide an alternative or supplementary means by which motoneuron excitability may vary (19), potentially creating a scenario in which variable activation of motoneurons may occur. For example, the strength of motoneuronal inputs from the rubrospinal tract, which receive cortical input from premotor areas and are specific to cervical motoneurons, is much greater in higher-threshold (fast-fatigable) MUs compared with lower-threshold (slow) MUs (11, 42). In the present study, of the seven MUs demonstrating significant recruitment threshold-resultant peak elbow extension velocity relationships, three (Figure 10B; MUs 2, 6, 15) possessed the highest average relative MU recruitment thresholds recorded (Table 4). Two additional MUs, one exhibiting a significant recruitment threshold-resultant peak velocity relationship (Figure 10B, MU 7) and another showing a trend (Figure 10B, MU 10), were recruited at a highest relative torque that differed 3%MVC from the three highest MU recruitment thresholds recorded (Table 4).

Although no systematic investigation of a relationship between motoneuron size and resultant velocity-dependent properties was explored in the present study, these observations coupled with the advantageous physiological characteristics of higher-threshold MUs properties advocate a role of MU recruitment threshold range compression for the production of the fastest human movements. However, a limitation of these data is the technique used to quantify MU activation in vivo. As a result of MU recruitment thresholds being expressed relative to mechanical responses (i.e., %MVC), the excitability of a MU initially recruited at low thresholds or prior to any recordable mechanical response may continue to increase without any noticeable change in MU recruitment threshold (75). To further confound this limitation, rapidly shortening muscle fascicles are capable of less force generation according to the force-velocity relationship (47, 51). Thus, despite MU recruitment thresholds being recorded during the force production phase of the non-isokinetic dynamic contraction in the present study, it is possible that MU recruitment thresholds during rapid contractions do not unequivocally reflect the magnitude of modulation of MU excitability in response to the demand for faster force generation and resultant peak velocity. Thus a potential bias exists wherein MU recruitment thresholds may underestimate the change in MU excitability that occurs in order to produce high resultant rates of force development and contraction velocities, further confounded by the current method of quantifying MU recruitment thresholds, whereby higher-threshold MUs possess a much greater range over which declines in MU recruitment threshold may be expressed compared with lower-threshold MUs. Nevertheless, significant reductions in recruitment threshold were observed in a large proportion of the sampled MUs with increasing relative resultant peak velocity (Figure 10B). One MU (Table 4; Figure 10B, MU 11) that possessed a maximum recruitment threshold of 5%MVC demonstrated that although the greatest reductions in recruitment threshold appear to be characteristic of higher-threshold MUs, reductions in lower-threshold MU recruitment thresholds were still able to be captured in the present study. Moreover, the relative frequency plots clearly demonstrate a reduction in the number of MUs with higher recruitment thresholds (>20%MVC) at relative resultant peak velocities exceeding 75%V_{max25}, which is approximately equal and opposite to the difference observed for the <10%MVC MU recruitment threshold range at 75%V_{max25} (Figure 10A). The progressive decline in the strength of this relationship with slower resultant peak elbow extension velocities (25–75%V_{max25}) and the apparent lack of relationship at 25%V_{max25} (Figure 10A), that occurred with 5% of the constitutive data from the 5%MVC MU recruitment threshold range, provides further support that these data were relatively insensitive to the potential limitations of the in vivo MU recruitment threshold quantification method.

In summary, anconeus MUs show a reduction in recruitment thresholds with increasing elbow extension velocity. However, within the motoneuron pool, considerable variability exists among MUs with respect to the resultant velocity-dependent response of MU recruitment thresholds. This variability suggests that MUs possessing advantageous physiological characteristics may demonstrate a heightened sensitivity to the abundance of neuromodulatory influences converging on the motoneuron pool during fast human movements potentially compressing the range of MU recruitment thresholds. Despite advancements, the potential exists that these differential responses to increasing resultant velocity may be confounded by limitations of the technique used to quantify MU activation in vivo in humans. It would be imprudent to disregard these limitations altogether; however, these data appear less sensitive to confounding influences by design and likely represent a role for neuromodulation in the velocity-dependent modulation of MU recruitment thresholds.

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Chapter 4 : Reduced motor unit discharge rates of maximal velocity dynamic contractions in response to a submaximal dynamic fatigue protocol

4 Introduction

The expression of neuromuscular fatigue is highly dependent on a number of variables including, but not limited to, the nature of the task (9), the muscle under investigation (1, 35), the age (1, 17) and sex (41) of the participants, and the method used to quantify fatigue (26). Consideration of these variables is essential in any investigation of neuromuscular fatigue-related changes to motor unit (MU) behavior especially during voluntary tasks (58). Unlike isometric tasks, additional important variables related to movement through a range of motion may affect the assessment of fatigue (26), and for these reasons limited information is available concerning MU properties during dynamic contractions. In an attempt to minimize some of these movement-related influences, several studies have used constant velocity (isokinetic) contraction tasks to investigate MU properties (2-4, 52). However, less power output is generally observed for isokinetic compared with more natural human movements (42, 53), especially when these movements are performed rapidly (13). In this study, the term dynamic contractions will be used to indicate contractions in which a relatively constant load is moved voluntarily at angular velocities that can freely vary throughout the joint range of motion, and from which power can be calculated.

During any type of dynamic contraction the ability to successfully record and analyze single MUs potentially is affected adversely by changes in the electrode–muscle interface during active contractile shortening of fibers and whole muscle architectural changes (28, 49). These factors are further compounded by repetitive contractions which can lead to neuromuscular fatigue in which alterations in both muscle forces and velocities add extra challenges in the ability to record from single MUs (23, 30).

Consequently, investigations of MU control properties during fatiguing protocols, especially those dynamic in nature, are very limited in humans. Only two studies (38, 50), both in the triceps brachii, investigated MU control strategies in response to a submaximal dynamic fatiguing protocol. These recordings were accomplished during very slow (50°/s) and lightly loaded (20% of maximal voluntary isometric contraction (MVC)) elbow extensions. After fifty contractions, MU discharge rates recorded during the submaximal efforts changed variably (some units' rates were unchanged, some increased, and some decreased) resembling results of isometric studies in which no change (18, 29, 38, 43, 56, 59) or decreased (14, 27, 33, 34, 36, 57) MU discharge rates were observed in response to submaximal isometric fatiguing protocols. Studies of sustained or repeated maximal isometric contractions, however, consistently reported a decline in MU discharge rates with neuromuscular fatigue (8, 10, 48, 54, 56).

Furthermore, in a few studies that investigated MU discharge behavior during isometric fatiguing protocols comprised of both submaximal and periodic maximal (MVC) contractions, pre- to post-fatigue MU discharge rates were unchanged for the submaximal target contractions, but MU discharge rates recorded at MVC post-fatigue were reduced ~30% (7, 59) (consistent with results above). Critically, however, it is unknown how MU discharge rates may change for maximal dynamic contractions in response to a submaximal dynamic fatiguing protocol, and their relationship to fatigue-related reductions in shortening velocity and muscle power (15, 16). It has been reported that higher MU discharge rates than those observed at isometric MVC (20, 21, 39, 61) are required to summate twitch tensions of MUs with faster contractile properties (21), which subsequently generate the high rates of force development (21, 61) required for the production of maximal dynamic contraction velocities (39). These characteristics of dynamic contractions imply fatigue-related reductions in MU discharge rate may be greater relatively for dynamic contractions compared with those reported for isometric contractions, but this has not been evaluated.

The effect of submaximal fatiguing contractions on MU recruitment thresholds is less well defined than for discharge rates. One isometric study of intermittent submaximal fatiguing contractions at 30-50%MVC observed an ~10% decrease in recruitment thresholds of the lateral head of the triceps brachii (18). Lower average MU recruitment thresholds may arise as a consequence of two mechanisms; 1) MU recruitment threshold reductions across the entire motoneuron pool or, 2) reductions in recruitment thresholds of a subsection of the MU population (i.e. higher threshold MUs). The latter mechanism may manifest as a compression in the MU recruitment threshold range providing that larger reductions in recruitment threshold are observed in high threshold MUs. Compression of the MU recruitment threshold range has been reported in response to submaximal intermittent isometric fatiguing contractions (14), and separately shown to contribute substantially to the production of non-fatiguing dynamic contractions (40). High threshold MUs possess fast twitch contractile properties (51, 55) that are related to the maximal shortening velocities in a human extensor muscle model (60). Thus, fatigue-related changes in recruitment of high threshold MUs may represent a mechanism by which high rates of torque development, and therefore maximal contraction velocities and muscle power, are maintained in an effort to minimize fatigue (10, 11, 14).

The purpose of the present study, therefore, was to evaluate anconeus MU properties in relation to the generation of submaximal and maximal dynamic elbow extensions in response to a submaximal dynamic fatiguing protocol. In order to minimize some of the technical limitations of recording successfully MUs during dynamic contractions, the anconeus muscle, which has shown to be a very useful model for exploration of MU properties for this task (39, 40), was investigated It was hypothesized, based on earlier studies of MUs recorded at MVC following high–intensity isometric fatiguing protocols (18, 29, 38, 43, 56, 59), that MU discharge rates responsible for the production of maximal dynamic contractions will decrease as task failure is approached, but as shown previously (38, 55) will be unchanged for the submaximal or target dynamic contractions. Also, it was hypothesized that

MU recruitment thresholds will decrease with increased time to task failure (TTF) in accordance with earlier studies of submaximal isometric fatigue (34, 59). However, MU recruitment thresholds of maximal dynamic contractions will be reduced to compensate for fatigue-related changes in twitch contractile properties and to sustain maximal contraction velocities and muscle power.

4.1 Methods

Seven young men (23.5±1.3y, 183.0±6.3cm, 80.4±11.9kg) free from orthopaedic, neuromuscular, and cardiorespiratory limitations participated in the study. Subjects provided informed written and verbal 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 torque, position, and velocity measures were recorded using a Biodex System 3 multi-joint dynamometer (Biodex Medical Systems, Shirley, NY, USA), while single MU action potentials from the anconeus and global intramuscular electromyography (EMG) of the anconeus, and lateral and long heads of the triceps brachii were recorded. One to three visits (~1.5hr/visit) were required to ensure an adequate quantity and quality of single MU recordings.

4.1.1 Setup and baseline measures

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

Following MVCs, three pairs (1 per muscle investigated) of custom made insulated stainless steel fine wire electrodes (100μm, California Fine Wire Company, Grover Beach, CA) were each passed through separate 27.5 gauge hypodermic needles (Becton Dickinson and Company, Franklin Lanes, NJ) and the needles inserted into the muscle bellies of the anconeus, and lateral long heads of the triceps brachii to record intramuscular EMG signals in a bipolar configuration. The insulation of the fine wires for this type of EMG recording was removed prior to insertion into the muscle by applying a flame to the tips of the wires so that ~5mm in length of stainless steel was exposed allowing a more global recording to be obtained. The global intramuscular EMG recording resembles that of surface EMG, but provides a distinct advantage in that it minimizes the low-pass filtering effect of subcutaneous tissue and the existence of movement artifact as a consequence of the skin-electrode interface (19). The intramuscular electrode pairs (inter-electrode distance of ~2cm) were inserted in alignment with the muscle fascicles of: 1) the lateral head of the triceps brachii above the mid-shaft of the posterio-lateral humerus, 2) the long head of the triceps brachii mid-shaft above the posterio-medial humerus, and

3) the anconeus ~1-2cm distal to the midpoint between the lateral epicondyle of the humerus and the olecranon process of the ulna. The corresponding ground electrode for these recordings was positioned on the clavicle just proximal to the acromioclavicular joint.

Additional fine wire electrodes, specifically designed for selectivity, were inserted into the anconeus to record single MU action potential trains from this muscle. The tips of these fine wire pairs were also exposed briefly to a flame, but were severed so that the length of exposed wire was minimal (<1mm). Two pairs of hooked tip fine wires (15-30cm length) were inserted into the belly of the anconeus ~2-4cm distal to the space between the olecranon process of the ulna and the lateral epicondyle of the humerus to increase the probability of recording a single MU throughout the fatigue protocol. The common ground electrode corresponding to these two fine wire electrode pairs was placed over the styloid process of the radius and secured with surgical tape.

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

4.1.2 Fatigue protocol

A schematic depiction of the fatigue protocol is presented in Figure 11a. Following 30-s rest, subjects began the fatigue protocol, which consisted of sets, each one comprised of ten *submaximal dynamic* contractions (40%MVC, 60%V_{max40}) followed by two *maximal dynamic* contractions (40% MVC, V_{max40}). Horizontal cursors were displayed on the monitor indicating V_{max40}, the 60%V_{max40} target peak velocity, a maximum error margin, and a minimum error margin. The maxima and minima error margins were calculated as greater, or lesser than 5% of the target peak velocity, respectively (10% error range). At the completion of each set, subjects began a subsequent set with the only rest provided during the return to starting position. The fatigue protocol sets were continued to task failure, which was defined as the point at which two consecutive elbow extensions failed to reach the minimum error margin. Irrespective of their position within a set, the final two contractions of the whole fatigue protocol were performed at maximal dynamic effort. Immediately following task failure, the arm was returned to 90° elbow flexion and subjects performed an isometric MVC sustained for ~3 seconds with no percutaneous electrical stimulation delivered.

High-pass filtered (10Hz) intramuscular EMG of the anconeus , and global intramuscular EMG of the anconeus, and lateral and long heads of the triceps brachii were pre-amplified (100-1000x, Neurolog, Welwyn City, England) and digitized with an analog-to-digital converter (Cambridge Electronics Design, Cambridge, UK) at a rate of 10kHz. Torque, position, and velocity data were sampled at 100Hz and all data were stored offline for analysis. Offline, intramuscular and global intramuscular EMG signals were high pass filtered at 100Hz to remove any remaining movement artifact.

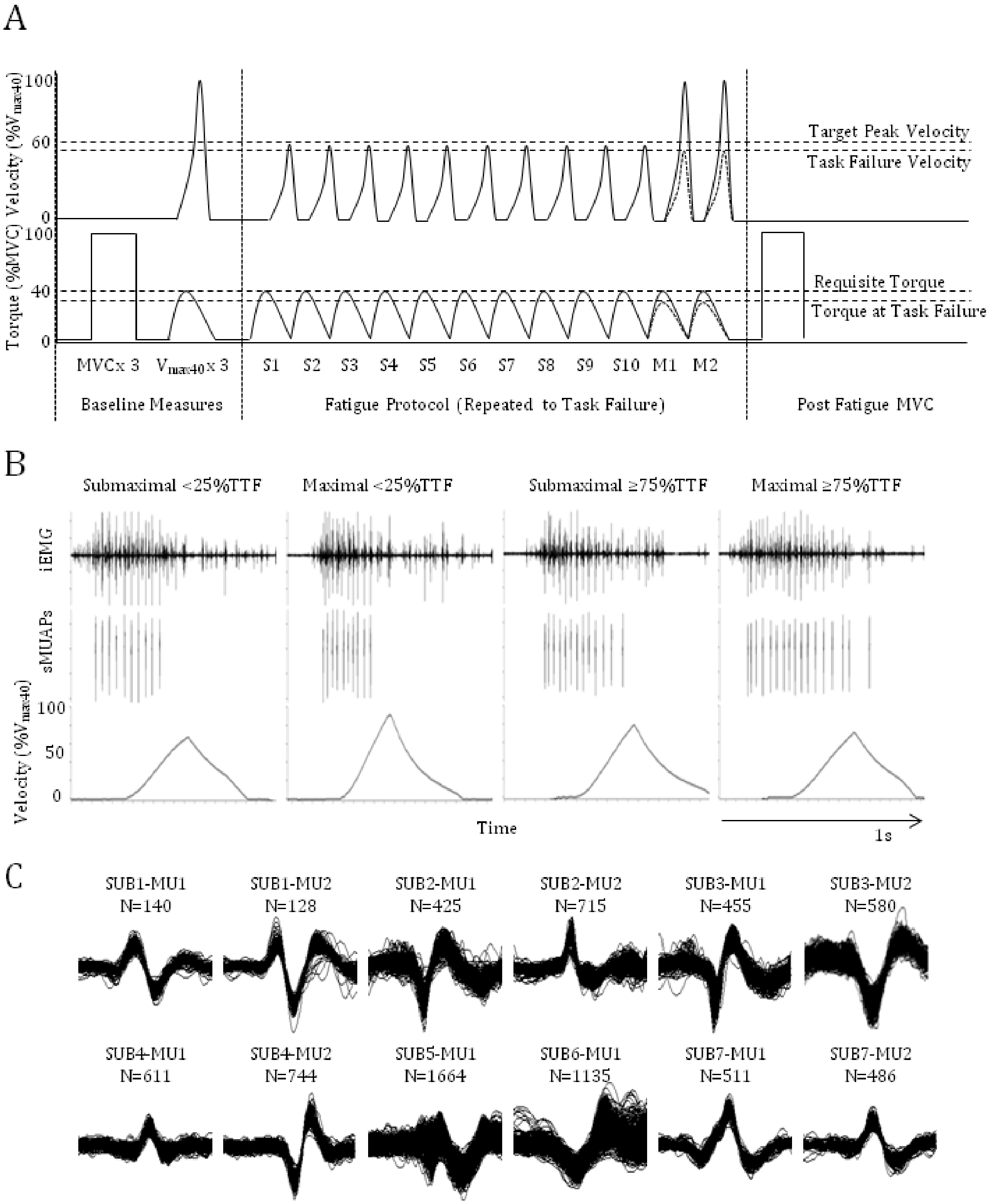

Figure 11. Schematic diagram of protocol and representative data. (A) Velocity and torque profiles of baseline measures, fatigue protocol, and post fatigue contractions. Vertical dotted lines separate each phase of the protocol. The upper horizontal dotted lines in both traces indicate the target torque and velocity, and the lower

dotted lines represent the approximate torque and velocity at task failure. (B) Representative intramuscular electromyography (top panel), single motor unit action potentials (middle panel), and relative velocity (bottom panel) for *submaximal* and *maximal* dynamic contractions at <25% of time to task failure (left panel) and ≥75% of time to task failure (right panel). (C) Overlays of the twelve single motor units tracked in the present study. The subject from which each motor unit was recorded is indicated above each overlay along with the number of individual motor unit action potentials contributing to each overlay. V_{max40}, maximal peak velocity with a 40% maximal voluntary torque load; MVC, maximal voluntary isometric contraction; S, submaximal contraction; M, maximal contraction; TTF, time to task failure; iEMG, intramuscular electromyography; sMUAPs, single motor unit action potentials; SUB, subject; MU, motor unit; N, number.

4.1.3 Data analyses

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

Average root mean square of the anconeus, and lateral and long heads of the triceps brachii global intramuscular EMG (EMG_{ANC}, EMG_{LT}, and EMG_{LH}, respectively) was determined for each *dynamic* elbow extension in which a MU discharge rate was obtained. Average root mean square was calculated for a period of time beginning with the initial rise in EMG amplitude from baseline to peak elbow extension velocity because the cessation of the initial agonist burst in the triphasic EMG pattern, which is characteristic of fast movements, is related to peak contraction velocity (5). Each EMG_{ANC}, EMG_{LT}, and EMG_{LH} was first expressed relative to the highest EMG_{ANC}, EMG_{LT}, and EMG_{LH}, respectively, recorded during baseline V_{max40} elbow extensions. Percent changes from the relative baseline values of EMG_{ANC}, EMG_{LT}, and EMG_{LH} were then calculated for each subsequent contraction.

Single MU analysis was performed with a template matching algorithm (Spike 2 version 7.0, CED, Cambridge, UK) that identified single MU action potentials using waveform shape by overlaying sequential action potentials with respect to temporal and spatial characteristics. The ultimate determinant of whether a MU action potential belonged within a MU train was made by visual inspection by an experienced investigator. Single MU action potentials were identified for baseline contractions, post-fatigue isometric MVCs, and for the dynamic elbow extensions comprising the fatigue protocol. The criteria for inclusion in the statistical analysis required that MUs: 1) fired at least five consecutive action potentials, 2) fired continuously following MU recruitment threshold (no inter-spike intervals greater than 150ms), and for dynamic contractions, were: 3) active during both the initiation phase (torque development) and movement phase of each dynamic elbow extension, and 4) present during at least two thirds of the fatigue protocol. Motor unit discharge times (s) were determined for each MU action potential and MU discharge rates were calculated as the number of MU action potentials fired per second for each contraction. Short inter-spike intervals (<10ms) usually recorded at recruitment were removed from the analysis. Absolute MU discharge rates of were determined for the torque development (ballistic isometric) phase (MU recruitment threshold to attainment of MVC torque) of baseline and post-fatigue MVCs, and for baseline V_{max40} contractions. Motor unit discharge rates of the dynamic contractions comprising the fatigue protocol were expressed relative to the maximal MU discharge rate recorded during the baseline V_{max40} elbow extensions

(%V_{max40}). The relative torque at which a MU fired its first action potential was considered the MU recruitment threshold and was expressed relative to the highest MU recruitment threshold recorded for a respective MU (%Maximum).

A priori sample size calculation was performed using MU discharge rate and MU recruitment threshold values recorded during pilot investigations to determine the minimum number of subjects required to show significant differences between pre- and post-fatigue group averages (31). It was determined that seven subjects and twelve MUs were a sufficient sample size for these variables (d=1.23-1.87, $1 - \beta$=0.80-0.95). Descriptive statistics were calculated for all dependent variables. A paired student's t-test was used to determine whether MVC torque changed in response to the fatigue protocol.

Within each subject, two average values for each set were determined for dependent variables; one for submaximal (60%V_{max40}), and one for maximal (V_{max40}) elbow extensions. Given that the number of sets completed prior to task failure varied among subjects, average values (submaximal and maximal) were each associated with the percentage of time to task failure (TTF) at which they were recorded. For example, a subject completing three sets prior to task failure contributed one submaximal average and one maximal average at 33.3%, 66.6%, and 99.9%TTF for each dependent variable, whereas a subject completing ten sets prior to task failure contributed a total of ten submaximal and ten maximal averages for each dependent variable corresponding to every 10% interval of TTF. Average values for each dependent variable were stratified according to four TTF ranges (<25%, 25-<50%, 50-<75%, ≥75% TTF). The result of stratification was 8, 14, 17, and 22 points for both submaximal and maximal groups of each dependent variable in the <25%, 25-<50%, 50-<75%, and ≥75%TTF ranges, respectively.

Using SPSS 17.0 (IBM, Armonk, NY), Shapiro-Wilk tests of normality verified that each dependent variable exhibited a normal distribution following standardization to TTF ($p>0.05$, W=0.88-0.94). One factor (%TTF) ANOVAs were performed for submaximal and maximal values separately for the dependent variables percent change in EMG_{ANC}, EMG_{LT}, and EMG_{LH}; relative peak elbow extension torque, velocity, and power; and relative anconeus MU recruitment threshold and MU discharge rate. Levene's test for equality of variances determined four of these dependent variables (MU recruitment threshold, MU discharge rate, and peak elbow extension torque and power) to be homoscedastic ($p>0.05$) following standardization to TTF. Accordingly, Tukey's HSD post hoc comparisons were used to examine differences between the four TTF ranges when a main effect was observed. Games-Howell post hoc comparisons were used for the remaining four dependent variables (relative peak elbow extension velocity, and percent change in EMG_{ANC}, EMG_{LT}, and EMG_{LH}) due to the heteroscedasticity of these measures. Paired t-tests were used to compare maximal and submaximal MU discharge rates and MU recruitment thresholds at each %TTF range. Effect sizes were calculated (25) and expressed as Hedge's g effect size metrics (g). An alpha level of $p\leq0.05$ was set for all statistical procedures, and all values in the text and figures are means ± standard deviations (SDs).

4.2 Results

Motor unit properties and global intramuscular EMG of the anconeus, and lateral and long heads of the triceps brachii were tracked in seven subjects throughout baseline and post-fatigue isometric MVCs, baseline V_{max40} elbow extensions, and during sets comprised of ten submaximal fatiguing ($60\%V_{max40}$) and two maximal dynamic elbow extensions to task failure. Representative data of a MU recorded during maximal and submaximal dynamic contractions at <25%TTF and ≥75%TTF are provided in Figure 11b. Anthropometric, and baseline and fatigue characteristics are summarized in Table 5. Twelve MUs (1-2 per subject) satisfied the strict inclusion criteria (see Methods) and were included in the statistical analysis (Figure 11c).

Table 5. Subjects' anthropometric, and baseline and fatigue characteristics (absolute values)

	Subject							
	1	2	3	4	5	6	7	μ±SD
Age, y	25	26	23	23	23	23	23	23.7±1.3
Height, cm	183.0	177.0	180.0	180.0	183.0	178.5	175.0	179.5±3.0
Weight, kg	83.2	77.0	90.0	78.0	89.0	76.1	56.0	78.5±11.4
VA, %	93.5	100.0	94.6	94.9	95.5	100.0	96.8	96.5±2.61
mMVC, Nm	89.4	101.3	117.8	109.6	81.4	71.3	48.2	91.1±25.5
mV_{max40}, *°/s*	223.0	297.4	297.5	251.4	247.3	247.8	241.9	258.1±28.4
mPower, W	244.2	322.6	305.8	310.1	244.2	242.3	234.3	271.9±38.7
STF, #	3	4	5	10	5	6	7	6.2±2.1
TTF, s	76.0	115.5	117.7	258.7	136.3	162.1	187.6	163.0±54.4
V_{max40} *mMUDR, Hz*	34.3	37.5	45.1	51.5	40.5	37.5	34.3	39.6±5.8

SD, standard deviation; m, maximal; MVC, maximal voluntary isometric torque; Nm, Newton-meters; V_{max40}, maximal *dynamic* elbow extension; W, Watts; VA, voluntary activation; STF, sets to task failure; TTF, time to task failure; μ, average; MUDR, motor unit discharge rate; Hz, hertz.

The fatigue protocol did not affect the peak elbow extension torque ($p=0.96$) or power ($p=0.90$) of the submaximal dynamic contractions. A main effect of %TTF was determined for peak velocity of submaximal dynamic contractions ($p<0.05$), but post hoc comparisons did not reveal any differences between the four TTF ranges (Figure 12a). In comparison, main effects for peak torque ($p<0.05$), velocity ($p<0.05$), and power ($p<0.05$) of the maximal dynamic elbow extensions occurred in response to the fatigue protocol (Figure 12b). Both velocity and power were lower for the 50-<75%TTF (18% and 30%, respectively) and ≥75%TTF (44% and 55%, respectively) ranges compared with the <25%TTF range ($p<0.05$, Figure 12b). Post hoc comparisons also revealed a difference between ≥75%TTF and <25%TTF for torque ($p<0.05$) of maximal dynamic elbow extensions and the average isometric MVC torque following the fatigue protocol decreased ~35% ($p<0.05$).

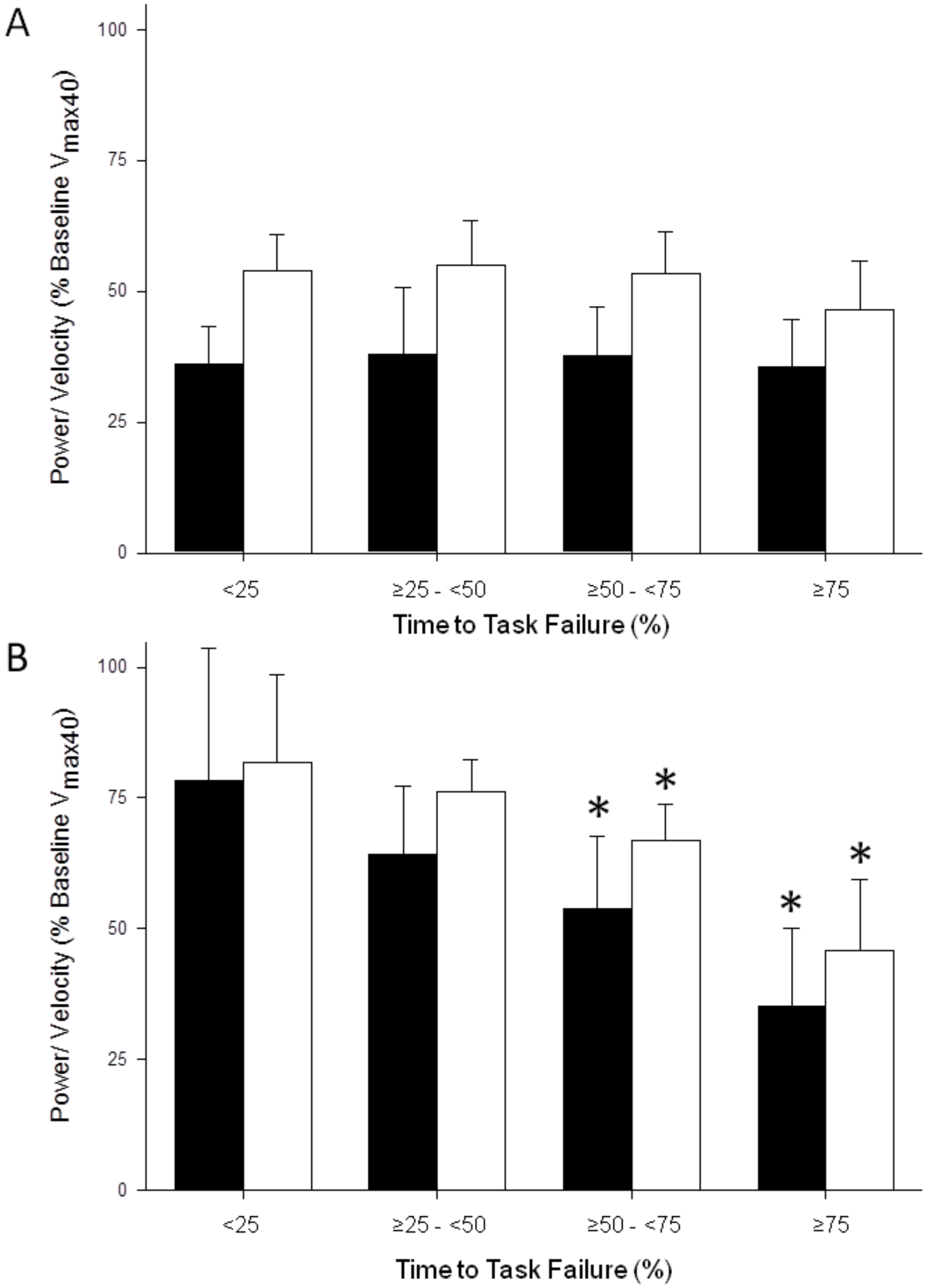

Figure 12. Relative power and velocity of (A) submaximal and (B) maximal dynamic elbow extensions as a function of time to task failure. Closed and open bars represent relative power and velocity, respectively. *$p<0.05$, significantly differs from <25%TTF. V_{max40}, maximal peak velocity with a 40% maximal voluntary torque load.

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

The maximal average MU discharge rate recorded during V_{max40} contractions (39.6±5.8Hz, Table 5) was greater compared with MU discharge rates recorded during the ballistic isometric phase of baseline MVCs (33.3±6.1Hz) ($p<0.05$, $g=1.03$) and post-fatigue MVC (26.8±5.2Hz) ($p<0.05$, $g=1.03$). Univariate ANOVAs of maximal dynamic elbow extensions showed a main effect of %TTF for MU discharge rate ($p=0.05$), but not for MU recruitment threshold ($p=0.52$, Figure 13). Post hoc comparison of MU discharge rates for maximal dynamic elbow extensions revealed an approximate 20% reduction in MU discharge rates at both 50-<75%TTF (30.7±6.1Hz) and ≥75%TTF (30.5±7.9Hz) compared with <25%TTF ($P<0.05$, Figure 13b). In comparison, there was a main effect of %TTF for MU recruitment thresholds ($p<0.05$, Figure 13a), but not for MU discharge rates ($p=0.36$, Figure 13b) for submaximal dynamic elbow extensions. Post hoc comparison revealed a 52% reduction in MU recruitment threshold at ≥75%TTF compared with <25%TTF ($p<0.05$, Figure 13a) for submaximal dynamic elbow extensions. Differences were also observed for MU discharge rates between maximal and submaximal dynamic contractions at the <25 and 25-<50%TTF ranges ($p<0.05$, $g=1.67$ and 0.98, respectively).

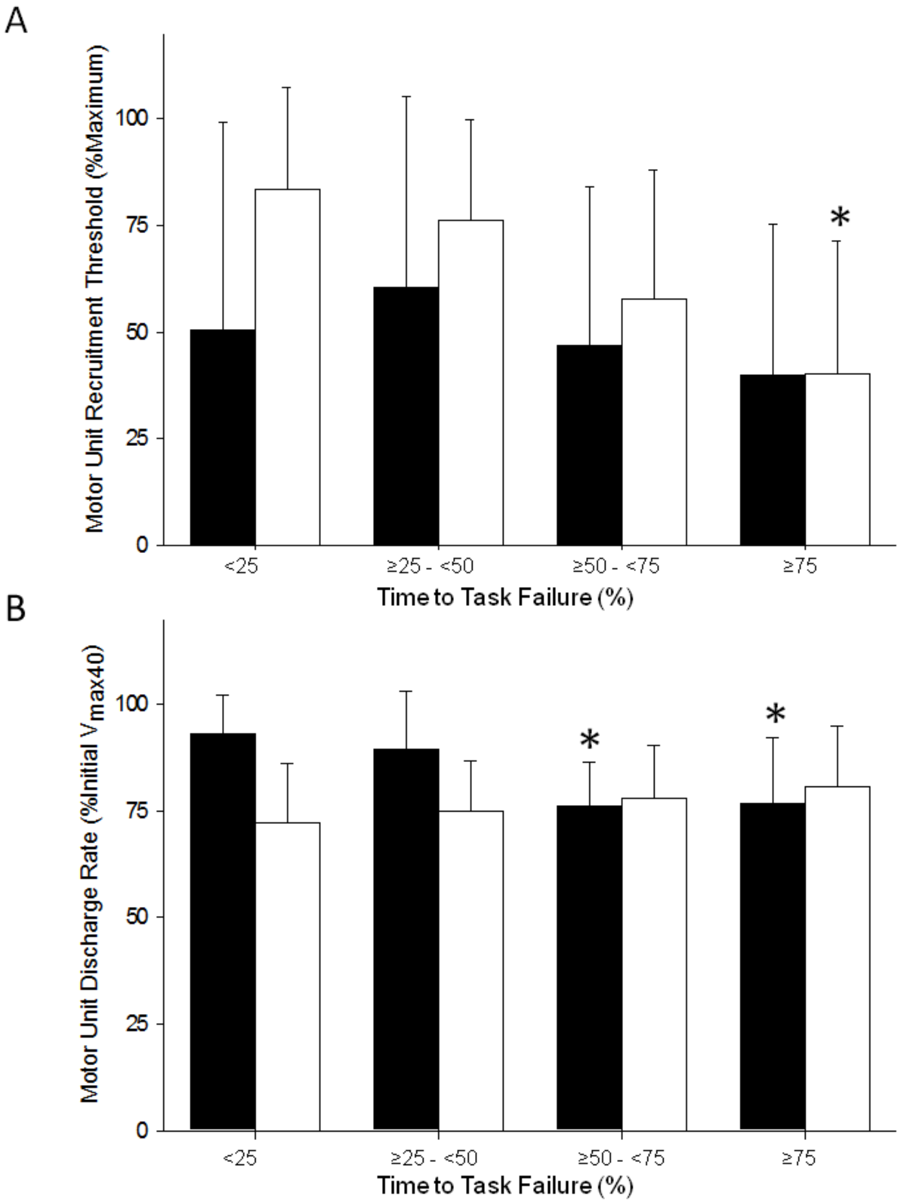

Figure 13. Relative (A) motor unit recruitment thresholds, and (B) motor unit discharge rates of the anconeus as a function of time to task failure. For both (A) and (B), closed bars represent average values for maximal dynamic contractions, whereas open bars are average values for submaximal dynamic contractions. $^{*}p<0.05$, significantly differs from <25%TTF. V_{max40}, maximal peak velocity with a 40% maximal voluntary torque load.

4.3 Discussion

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

4.3.1 Motor unit discharge rates

Average maximal dynamic MU discharge rates of the anconeus in the present study were similar to those previously reported in our laboratory (39) (Table 5). For submaximal dynamic elbow extensions, MU discharge rates were unchanged through all time points leading to task failure (Figure 13a). These results are similar to observations from prior studies of the elbow extensors (38, 50) during relatively slower, submaximal, lightly loaded, dynamic contractions. In the present study, MU discharge rates of maximal dynamic elbow extensions were reduced by ~20% for the last half of the fatigue protocol (Figure 13b). Studies of submaximal isometric fatiguing contractions at comparable loads (50%MVC) to that used in this study (40%MVC) reported somewhat similar declines in MVC MU discharge rates (~30%) at task failure (7, 59). Thus, despite differences in the fatiguing task (isometric versus dynamic), a fundamentally similar response of maximal MU discharge rates provided support for the concept that common underlying factors affect the response of anconeus MU output to maximal fatiguing isometric and dynamic contractions.

In the present study, velocity and power were reduced (~45% and ~55%, respectively) in the final 25% of the fatigue protocol (Figure 12b). However, MU discharge rates did not decline further after the 50-<75%TTF range (Figure 13b). The reductions in velocity (~20%) and power (~30%) at the 50-<75%TTF range were very similar to those observed for MU discharge rates in the same range (~20%, Figure 13b), for the ballistic isometric phase of the post-fatigue MVC (~20%, Table 5), and for sustained isometric MVCs of the elbow and knee extensors (~30%) in earlier studies of neuromuscular fatigue (7, 59). Therefore, it appears the relative decline in MU discharge rates is comparable across contraction types. This indicates the relative response of anconeus MUs to submaximal fatigue is not modified by task-specific MU discharge rate differences commonly reported between contraction types (24), which were also observed in the present study.

The average discharge rate of anconeus MUs in the present study for baseline V_{max40} elbow extensions was 39.6±5.8Hz. At 50-<75%TTF, anconeus MU discharge rates for maximal dynamic elbow extensions declined to 30.7±6.1Hz ($p<0.05$), which did not differ from the pre-fatigue (33.3±6.1Hz) or post-fatigue (26.8±5.2Hz) ballistic isometric MU discharge rates ($p=0.30$ and $p=0.14$, respectively). However, MU discharge rates pre- and post-fatigue for both maximal dynamic and ballistic isometric contractions were higher ($p<0.05$) than those recorded without fatigue in one earlier study in the anconeus at sustained maximal isometric torques (23.8±7.7Hz) (39). These comparisons indicate, at least in the anconeus, that although maximal MU discharge rates declined following submaximal fatigue they remained sufficiently high to generate and sustain an isometric MVC torque. Furthermore, these observations indicate the importance of maintenance of relatively high MU discharge rates for the production of fast dynamic contractions and that regulatory mechanisms are modified differently depending on the task.

The lack of additional declines in anconeus MU discharge rates beyond 50%TTF is potentially the result of the fatigue-resistant nature of this muscle model as indicated by its twitch contractile properties and fiber composition (45). However, a number of additional factors may explain the disproportionate changes between velocity and power, and MU discharge rates of the anconeus as fatigue continued. Fatigue-related reductions in activating calcium concentrations and cross bridge kinetics of skeletal muscle (for review see 32, 44) are potent modulators of muscle fiber power and velocity. These peripheral factors likely affect both maximal isometric torque and loaded shortening velocity in the elbow extensor model as demonstrated by reductions in both these parameters despite near maximal voluntary activation (92.3±8.8%) as assessed by 50Hz tetanus delivered at MVC torque (15).

Thus depending on the task, a minimal threshold of MU discharge rate reductions is preserved despite continuing declines in contractile function. An additional consideration is that the anconeus is a relatively small contributor to the resultant elbow extension torque (<15%) (63). Despite being active throughout the entire joint range of motion (39, 63) and at all elbow extension torques (12, 45, 47) and velocities (39, 46) , the possibility exists that fatigue-related neuromuscular changes occur at different amplitudes and rates in the three heads of the triceps brachii compared with the anconeus. This muscle-dependent response to the fatigue protocol is likely due to differences in muscle fiber type composition and twitch contractile properties (45), joint angle-dependent mechanical advantages (19, 62), or torque- and velocity- related differences in contribution to the resultant mechanical output (46, 47, 62, 63). Global intramuscular EMG of the elbow extensors in the present study, and one earlier study of sustained isometric fatiguing contractions (19), supports muscle-specific differential responses to neuromuscular fatigue. However, the interpretation of these data is limited due to fatigue-related changes to MU action potential waveform characteristics which can alter the EMG amplitude independent of mechanical output (22, 23). With these considerations , MU discharge rates of the anconeus for maximal dynamic and ballistic isometric elbow extensions both declined ~20% in response to the fatigue protocol demonstrating that isometric and dynamic contractions share common features with respect to MU discharge behavior for maximal contractions. However, differences in the absolute MU discharge rates with fatigue-related torque or velocity loss indicate a task-specific disparity in the relationship between anconeus MU discharge rates and task failure as a consequence of submaximal dynamic fatiguing contractions.

4.3.2 Motor unit recruitment thresholds

Fatigue-related declines in MU recruitment thresholds were observed for submaximal rather than maximal dynamic contractions. That motor unit recruitment thresholds of maximal dynamic contractions did not change as a function of %TTF (Figure 13b) is contrary to our original hypothesis, but is reasonable in view of the results because in order to produce maximal dynamic elbow extensions, it seems the anconeus may have been operating above the upper limit of its MU recruitment range (39, 46, 47). Recruitment thresholds of MUs for submaximal dynamic contractions were reduced 52% at ≥75%TTF, which corresponded with higher EMG amplitudes (45-64%) in the three elbow extensors studied. Fatigue-associated increases in EMG amplitude are commonly reported in response to repeated or sustained submaximal contractions and are often attributed to increases in MU recruitment, but not without limitations (23). Although MU recruitment thresholds have been shown to decrease in response to repeated contractions in the absence of neuromuscular fatigue (37), a more probable explanation for the decline in MU recruitment threshold in relation to increasing %TTF is that recruitment of higher threshold MUs occurred at progressively lower relative torques in response to the fatigue protocol resulting in a compression of the MU recruitment threshold range. Harwood and Rice (40) have shown a compression of anconeus MU recruitment thresholds is related to an increase in peak elbow extension velocity in non-fatiguing contractions. Similar recruitment threshold reductions, largely in higher threshold MUs, during submaximal fatiguing intermittent isometric contractions in the first dorsal interosseus also have been demonstrated (14). This effect provides an advantage for the production of greater rates of torque development (21, 40, 61), peak velocities(40), and peak power (40) because higher threshold MUs, which have higher peak twitch tensions and shorter time to peak tensions (51, 55), require higher excitation rates for maximal summation of twitch tensions (6). For example, a shift to lower MU recruitment thresholds following a 12 week dynamic training program corresponded to an 82% increase in rate of tension development (61). Thus, during the submaximal fatiguing contractions in the present study, it is likely compression of the MU recruitment threshold range contributed to the maintenance of requisite torque of the dynamic contractions specifically after ~75%TTF (Figure 13a).

Together, these findings show important changes in anconeus MU properties of maximal and submaximal dynamic contractions in relation to TTF during fatigue. Decreases in average MU recruitment threshold for submaximal dynamic contractions, and in average MU discharge rate for maximal dynamic contractions, occurred in relation to %TTF. Fatigue-related declines in anconeus MU recruitment thresholds for submaximal dynamic elbow extensions in the absence of any change in anconeus MU discharge rates offers evidence in support of MU recruitment threshold range compression for the maintenance of contraction velocity and muscle power in response to the fatigue protocol. Similar relative MU discharge responses of maximal contractions to submaximal dynamic fatigue in the present study, and to submaximal isometric fatigue in previous studies (7, 59) indicate a common underlying neural mechanism regulates both contraction types with neuromuscular fatigue. This concept is further supported by similar MU discharge rate reductions to submaximal dynamic fatigue regardless of the contraction type (maximal dynamic versus ballistic isometric) used to quantify changes at task failure. However, the disparity between absolute MU discharge rates of different contraction types [maximal dynamic, ballistic isometric, and sustained MVC (39)] pre- and post-fatigue stresses the role of high discharge rates of anconeus MUs for the production of fast dynamic contractions.

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Chapter 5 : Motor unit properties of three elbow extensor muscles in man during isometric force production

5 Introduction

Isometric force production is accomplished primarily through modulation of two motor unit (MU) properties, recruitment threshold and discharge rate. The orderly recruitment of MUs relative to the size of the motoneuron cell body (42) is well established (21) and has been shown to be preserved following remodeling of the motoneuron pool (30, 35), and despite relatively few equivocal observations (58, 59, 67), in all contraction types (22, 66, 73). However, the discharge behavior of MUs is more sensitive to functional influences (20, 32, 75), and various tasks including fatigue for one example (20-22, 68). Generally upon recruitment, MUs increase in a linear fashion relative to increasing force. Some suggest recruited MUs and their discharge patterns create an 'onion skin' pattern wherein MUs which are recruited at low thresholds fire at higher rates relative to subsequently recruited higher threshold MUs (11, 12, 14, 29). However, many studies have reported higher MU discharge rates of high threshold recruited MUs compared to low threshold recruited MUs during ramp isometric contractions (54-56). These relationships are even more complex when force by multiple muscles possessing varying architectural properties, force vectors, and length-dependent mechanical properties are used collectively (7, 28, 69, 70). The human elbow extensors is an excellent example.

The elbow extensors, which are composed of the long, lateral, and medial heads of the triceps brachii, and the anconeus have different fascicle lengths and pennation angles (3, 39, 57), force distribution profiles (3, 57) and length-dependent mechanical advantages (76). Further, 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 muscle of the elbow extensors, the anconeus (60-67% type I) (45, 49). Despite the considerable differences between these muscles, all four elbow extensors are innervated by same nerve root supply (C7-C8) (31, 43). An early concentric needle electromyography (EMG) study of the elbow extensors described varying ('slight', 'moderate', and 'marked') levels of muscle activation during extension at the shoulder at 0° (neutral), wherein the medial head and anconeus were active throughout the entire contraction and the lateral and long heads primarily exhibited 'slight' secondary activity (74). However, concentric needle EMG waveform characteristics are highly dependent on the depth (24) and location (23, 25, 26) of needle insertion, which was not accounted for by the subjective nature of EMG quantification exercised in this study.

Subsequent investigations of intramuscular global EMG (3, 4, 57) at low (~30%MVC) to moderate (~60%MVC) isometric elbow extension forces showed all four elbow extensor muscles active at varying levels of muscle activation (30-100% of maximal EMG), but did not systematically study EMG-force relationships. Few studies (2, 50) have determined EMG-force relationships of the elbow extensors. Le Bozec et al. (50) suggested the anconeus reached a plateau in muscle activation at <30%MVC, however, one other study (2) showed EMG amplitude of the anconeus increasing up to 80%MVC. In the long head and anconeus, lesser increases in EMG relative to increasing force were observed compared with the medial and lateral heads of the triceps brachii, which both behaved similarly (50). Whereas the medial and lateral heads of the triceps brachii and the anconeus were active from the onset of force production, the activation of the long head occurred predominantly at higher force levels (50). Several factors affect the global EMG-force relationships (EMG cross talk contamination (34), fascicle strain rates (61, 64), and motor unit control strategies (19)), especially during contractions that may induce neuromuscular fatigue (16-18). Thus, a more precise and accurate way of describing muscle activation in relation to force is to record single MU properties during ramp isometric contractions because these recordings address and minimize many of the limitations of the global EMG signal.

Although many studies have reported MU properties of the elbow extensors during isometric contractions (8, 15, 33, 37, 44, 46, 47, 49, 72), only one has investigated an elbow extensor other than the lateral head of the triceps (49), and no study has systematically evaluated MU properties of multiple elbow extensor muscles concurrently during force production up to high force levels (>60%MVC). Thus, the purpose of the present study 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 up to 75% of MVC. It was hypothesized based on previous studies (3, 48-50, 57) that the order of recruitment of these three elbow extensors would be as follows: the anconeus, the lateral head of triceps brachii, and finally the long head of triceps brachii. However, based on the force distribution data (3, 57), it was believed motor unit recruitment of the anconeus would continue above 30%MVC despite limited information indicating that anconeus muscle activation would reach a plateau at <30%MVC (50). Lastly, it was hypothesized that MU discharge rates of the anconeus would increase at a lesser rate compared with the lateral and long heads of the triceps brachii as indicated from results of previous studies (3, 50, 57).

5.1 Methods

Four young men (26.3±1.9y, 184.3±6.2cm, 86.6±8.0kg) free from orthopaedic, neuromuscular, and cardiorespiratory limitations participated in the study. Subjects provided informed written and verbal 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 a standard examination plinth on which subjects laid supine. The non-dominant (left) arm rested in a padded elbow support attached to the horizontal platform of the dynamometer. The arm was slightly abducted (<10°) and positioned at 0° and 90° flexion of the shoulder and elbow, respectively. The medial surface of the wrist rested against a stiffly padded U-shaped 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 U-shaped support and the arm to the horizontal support. Force feedback at a gain relative to each individual's MVC was displayed on a monitor suspended from the ceiling at a distance of 1m from the face (Appendix B).

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

Single twitches of the elbow extensors were evoked using a stimulator (DS7AH; Digitimer, Ltd., Welwyn Garden City, Hertfordshire, UK) at a pulse width of 100μs through two custom gel-coated aluminum foil stimulation electrodes (5 x 6cm to 5 x 12cm in size) placed transversely over the muscle belly of the triceps brachii. The anode was positioned ~10cm proximal to the olecranon process of the ulna and the cathode ~10cm distal to the axilla. Current intensity (80-160mA) was increased until no additional twitch force was generated, and then increased by 15% to ensure supramaximal stimulation.

5.1.1 Experimental protocol

The experimental protocol is depicted in Appendix B. Initially, three single twitches were elicited at supramaximal stimulation intensities at 1s intervals to determine the resting twitch tension amplitude prior to determining maximal isometric force. Next, three brief (~5s) isometric elbow extension MVCs were performed with supramaximal twitch stimuli delivered immediately preceding (resting twitch), during the plateau in MVC torque (interpolated twitch), and immediately following a return to baseline torque levels (post-MVC twitch). Two minutes rest was allotted between each MVC. Percentage voluntary activation (VA) was calculated using the twitch interpolation technique [VA (%)= (1-(interpolated twitch/control twitch)) x 100%], where the control twitch is the post-MVC twitch (63).

Following MVCs, three horizontal cursors at 25, 50, and 75% of MVC were placed on the screen with the top and bottom of the monitor adjusted to 100%MVC and 5%MVC, respectively, and the x-axis frame was constant at 5s. Subjects were asked to increase elbow extension force at a rate of 5%MVC/s paced by the experimenter's verbal enumeration and a metronome. Upon achievement of the target force, subjects held the force steady for 5s before returning to baseline at a rate of 5%MVC/s. Three ramp isometric contractions at each target force were performed in a randomized fashion with 2 minutes rest between low (25%MVC) and moderate (50%MVC) contractions, and 5 minutes rest following each 75%MVC ramp isometric contraction. Following completion of the targeted ramp isometric contractions, a MVC was performed to determine whether the protocol induced neuromuscular fatigue.

5.1.2 Data analyses

Offline data analyses were performed using custom software package (Spike 2 version 7.0, CED, Cambridge, UK). Percent VA was calculated for each subject from the baseline MVCs preceding ramp isometric contractions and maximal torque was determined for a 1s period during the plateau of the pre- and post-protocol MVC. Group averages were determined for VA, pre MVC, and post MVC.

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 an experienced investigator. Inclusion criteria for statistical analysis required that MUs fired for at least 3s consecutively following recruitment. No inter-spike intervals less than 10ms or greater than 150ms were included in the analysis.

Motor unit discharge times (s) and instantaneous MU discharge rates were determined for each MU action potential. Average MU discharge rate of individual MUs were calculated each second of the ramp isometric contractions up to target force. The relative force at which each MU fired 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.

5.1.3 Statistical analysis

Using SPSS 16.0 (SPSS Inc., Chicago, Illinois), a two factor (muscle, force) analysis of variance (ANOVA) and a one factor ANOVA (muscle) were performed for the dependent variables MU discharge rate and MU recruitment threshold, respectively. Levene's test of equality of error variance was performed and determined there were unequal variances across groups ($p<0.05$), therefore upon determination of a interaction or main effect, Games-Howell pairwise comparison test was used to test differences between groups, and Hedge's g effect sizes were determined for each significant difference. Alpha level was set at $p \leq 0.05$. Regression analyses were also performed for each muscle using average discharge rates from individual MUs at each 1s interval and a coefficient of determination (R^2) was calculated to demonstrate the amount of shared variance between elbow extension force and MU discharge rates in each muscle. For MU recruitment thresholds, stacked percent histograms were generated at bin widths of 10%MVC for the three elbow extensors. All values are mean ± standard deviation.

5.2 Results

Average MU recruitment thresholds and average MU discharge rates at 1s intervals were recorded for 56 MUs from the lateral (N=24) and long (N=11) heads of the triceps brachii, and the anconeus (N=21). The majority of MUs were recorded at force below 50%MVC, however, 6 MUs were tracked at force above 50%MVC (Figure 14a). Average MU discharge rates over the first 1s interval for all muscles was 11.4±3.8Hz (3.8-18.9Hz) and shared no variance ($R^2<0.01$) with MU recruitment threshold. The two factor (muscle, force) ANOVA for MU discharge rate revealed main effects of force ($p<0.05$) and muscle ($p<0.05$). Post hoc comparisons showed MU discharge rates to be 15% and 22% higher in the anconeus and lateral head of the triceps brachii, respectively, compared with the long head of the triceps brachii ($p<0.05$, $g=0.55$; $p<0.05$, $g = 0.85$, respectively). The anconeus ($R^2=0.31$) and lateral head of the triceps brachii ($R^2=0.28$) demonstrated the greatest amount of shared variance with elbow extensor force, however, MU discharge rates of the lateral head increased ~35% faster compared with the anconeus (Figure 14b). Discharge rates of MUs in the long head of the triceps brachii shared little variance ($R^2=0.08$) with elbow extension force and increased at rates that were 55% and 70% slower than those of the anconeus and lateral head of the triceps brachii, respectively (Figure 14b).

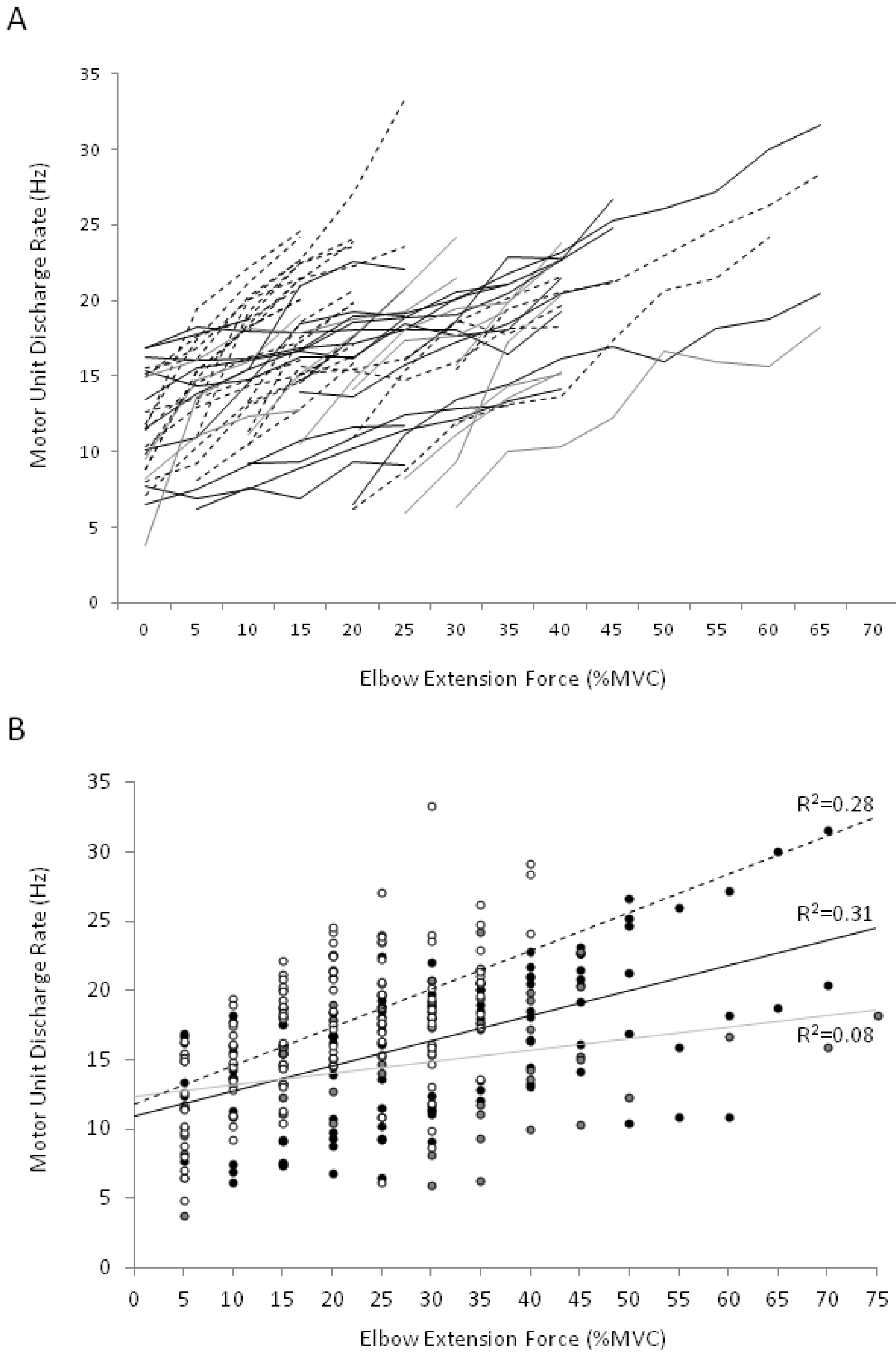

Figure 14. Discharge rates of individual MUs relative to elbow extension force (A) and (B) regressions between MU discharge rate and elbow extension force. (A)

Grey, broken, and black lines represent the long and lateral heads of triceps brachii, and anconeus, respectively. (B) Grey, open, and filled circles represent the long and lateral heads of the triceps brachii, and anconeus, respectively. The coefficients of determination associated with each group in (B) are positioned next to their respective least squares regression lines.

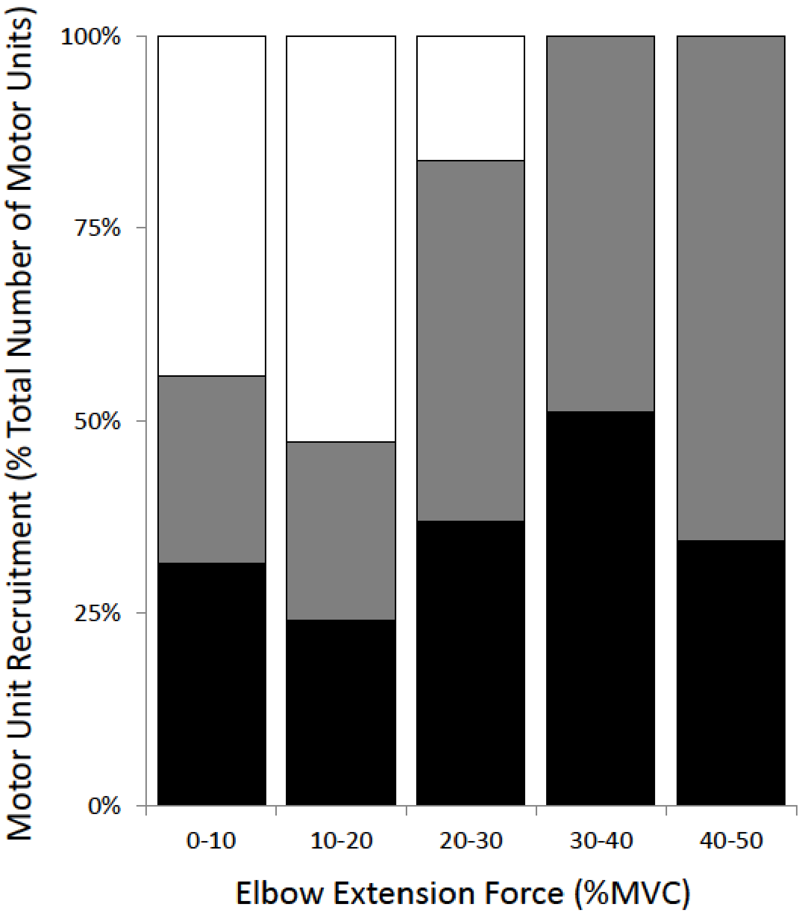

Figure 15. Stacked percent histograms of the anconeus (black), long (grey) and lateral (white) heads of the triceps brachii relative to five elbow extension force ranges. Each bar represents the percentage of MUs recruited from a respective muscle relative to the total number of MUs recruited for that range in all elbow extensor investigated.

One way ANOVA of MU recruitment thresholds revealed a main effect of muscle ($p<0.05$) for which post hoc comparisons showed recruitment thresholds of the anconeus MUs were ~50% lower compared with those of MUs in the long head of the triceps brachii ($p<0.05$, $g = 0.78$). No MU recruitment threshold differences were observed between the lateral head of the triceps brachii and either the anconeus ($p=0.23$), or long head of the triceps brachii ($p=0.14$). Motor units of the lateral head of the triceps brachii were all recorded at forces less than 30% of maximal isometric torque, but in the anconeus and long head of the triceps brachii, additional MU recruitment was observed up to 45% and 40%MVC, respectively (Figure 15).

5.3 Discussion

These findings show modulation of MU properties of three elbow extensor muscles is different in relation to increasing force. The hypothesized order of recruitment based on prior studies (3, 48-50, 57) was confirmed in that the lowest MU recruitment thresholds were observed in the anconeus and the highest in long head of the triceps brachii. Furthermore, despite having the lowest MU recruitment thresholds, the anconeus continued to recruit MUs above 30%MVC as was previously suggested (50). However, in contrast to the final hypothesis, MU discharge rates of the anconeus were greater than those of the long head of the triceps brachii and did not differ from those of the lateral head of the triceps brachii. There is considerable evidence to support lower MU discharge rates in long head of the triceps brachii in the current experimental design (10, 13, 29, 76), however a number of factors may confound this relationship.

Modulation of MU discharge rate is an important mechanism for the gradation of force, one which varies depending on the muscle investigated (62). Larger muscles adopt a recruitment-based force generation strategy and smaller muscles rely more on discharge rate to grade force (62). Furthermore, both the elbow extensors (49) and plantar flexors (1, 7) provide support for the concept that muscles with a greater type I muscle fiber composition fire MU action potentials at a lower rate compared to muscles with a greater type II fiber composition even when contraction results in a similar action. In the present study, the long head of the triceps brachii (14.9±4.5Hz) exhibited lower MU discharge rates compared with the lateral head of the triceps brachii (17.4±5.1Hz) ($p<0.05$) despite similar and relatively high type II muscle fiber compositions (27, 65). However, in accordance with the 'onion skin' pattern of motor unit control, the long head, in which the highest recruitment thresholds were observed, fired at the lowest MU discharge rates. Although these results appear to support an 'onion skin' pattern, there was effectively no shared variance between MU recruitment threshold and average MU discharge over the first 1s interval ($R^2<0.01$) similar to MUs observed in prior studies of isometric force production (54, 56). Moreover, MUs in the present study shared similar initial discharge rates (11.4±3.8Hz, 3.8-18.9Hz) to these two studies (~8Hz) (54, 56). Discharge rates were not recorded above 75%MVC in this study, however, other studies (54-56) showed maximal discharge rates of high threshold MUs exceeded those of low threshold MUs at higher forces during voluntary contraction. Thus, MU discharge behavior in the present study represents an integration of both the 'onion skin' pattern and the MU discharge behavior-force relationship observed by Monster and colleagues (54, 56).

In addition to increases in MU discharge rate, progressive MU recruitment also increases force in a roughly linear fashion in a variety of human muscles (6). Although many studies (8, 15, 33, 37, 44, 46, 47, 49, 72) have recorded discharge rates in the elbow extensor muscles, primarily the lateral head of the triceps brachii, fewer (36, 40, 44, 51, 53) have recorded MU recruitment thresholds. In the lateral head of the triceps brachii, MUs have been recorded up to ~50%MVC (36), but never above 20%MVC concurrently in multiple elbow extensor muscles. According to the size principle (42), MUs with larger cell bodies (fast type II MUs) are recruited at higher relative forces compared to those with smaller cell bodies (slow MUs). The fiber composition of the triceps brachii is ~65% type II and therefore it likely is comprised of a greater proportion of fast MUs (45, 49), whereas the anconeus is predominantly composed of type I muscle fibers (65%) and has slow twitch contractile properties (49) suggesting it is comprised primarily of slow MUs (38). In view of these characteristics of the two muscles, it is reasonable to expect that the anconeus would exhibit lower MU recruitment thresholds compared with either the long or lateral heads of the triceps brachii. Results of the present study support this hypothesis whereby the anconeus had the lowest average MU recruitment threshold (10.1±8.6%MVC) followed by the lateral head of the triceps brachii (14.2±13.6%MVC), and finally the long head of the triceps brachii (20.7±12.2%MVC). Anatomical studies have shown the fiber composition of the long and lateral heads of the triceps brachii to be nearly identical (27, 65, 71), thus it is unlikely the proportion of fast-to-slow MUs is responsible for the difference between MU recruitment thresholds of the two heads. The discrepancy may be the result of a greater mechanical advantage of the lateral head in the 0° shoulder flexion position compared to the long head of the triceps brachii (9, 76), however, investigations of moments at the shoulder and elbow suggest the bi-articular long head of the triceps brachii covaries more with the mono-articular elbow muscles than with the mono-articular shoulder muscles (34, 60).

A specific strength of the present study was the ability to record MU action potentials of three elbow extensors concurrently up to high forces, which revealed additional MU recruitment of the anconeus above the previously suggested plateau in muscle activation at 30%MVC (49). The anconeus recruited new MUs up to 45%MVC (Figure 15), which exceeded the observed recruitment range of the both the lateral and long head of the triceps brachii in this study. However, due to the selectivity of the intramuscular EMG recordings (52), it is likely MUs outside the detection area were recruited at forces higher than those observed for the long and lateral heads of the triceps brachii in the present study because surface EMG studies of the elbow extensors show EMG increasing linearly to 80% MVC (2), which may in part be due to additional MU recruitment (5). Despite its slow fiber composition and small size (43), and low average MU recruitment thresholds the anconeus continues to recruitment MUs up to moderate forces (45%MVC). These observations indicate that this small elbow extensor contributes force over a greater range than previously suggested (47, 48). As a result of its unique and advantageous qualities for the recording of single MUs (40, 41), it may be a useful model for investigation of MU properties in previously unattainable situations.

5.3.1 Conclusions

Results of the present study demonstrate differential motor unit control properties in long and lateral heads of the triceps brachii, and the anconeus for forces ranging 0-75%MVC. The discharge behavior of single MUs in the elbow extensors followed an integrated pattern combining aspects of the 'onion skin' pattern (10, 29) and the pattern described by Monster and colleagues (54, 56) wherein the long head of the triceps brachii, which possessed the highest MU recruitment thresholds, exhibited the lowest MU discharge rates; but, discharge rates of all elbow extensor MUs shared no variance with recruitment threshold. This integrated pattern may better represent MU activity of muscle synergies such as those observed between the elbow extensors, but the full range of elbow extension forces and varying shoulder and elbow joint angles must be considered to discount the possibility that the range of relative forces studied or different mechanical advantages of the elbow extensors contributed to the MU discharge rate-force relationships observed in the present study.

The hypothesized order of MU recruitment was confirmed, but recruitment thresholds of anconeus MUs were also observed above the previously suggested plateau in muscle activation for this muscle (49). Recent studies (40, 41) have demonstrated modulation of anconeus motor unit properties is associated with the maximal dynamic outputs and these findings provide further evidence from isometric contractions that MUs in the anconeus change in relation to moderate and high intensity efforts. These findings provide further support for the use of the anconeus model for recording of single MUs in more technically challenging situations.

5.4 References

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Chapter 6 : General discussion and summary

6 General discussion

In this thesis, single motor unit (MU) recordings of the anconeus revealed changes in discharge and recruitment behaviour dependent upon the peak velocity of constant load dynamic contractions (Chapters 2 and 3); behaviour which was altered in a task-dependent manner following a submaximal fatiguing dynamic protocol (Chapter 4); and this muscle (anconeus) was determined to be distinct from that of the lateral and long heads of the triceps brachii in the production of the high force ramp isometric contractions in Chapter 5. Specifically in Chapter 2, the bilinear relationship established between anconeus MU discharge rates and peak velocity tracked throughout loaded elbow extension ranging from 93°/s-494°/s, demonstrated a shift at ~55% of the maximal velocity from a primary range of the input-output relationship to a secondary range. The gain of the secondary range was twice that of the primary range. These results support the existence of multiple functional ranges of the input-output relationship, whether in relation to current-MU firing frequency relationships from reduced animal preparations(9, 24, 34, 35), or human models of motor unit behavior (22, 52), and have provided indirect evidence that neuromodulatory influences (32, 39) may alter the input-output relationships of MUs to achieve maximal contraction velocities.

Using the same MU tracking design, recruitment thresholds of anconeus MUs were recorded over a similar range of loaded elbow extension velocities (64°/s -500°/s) in Chapter 3. Although MU recruitment thresholds decreased as a function of increasing velocity for the group, variable responses to increasing velocity of single MUs were related to recruitment threshold. The frequency at which MUs decreased recruitment threshold with increasing velocity was greater in MUs recruited at higher forces. These data support the notion that a compression of the MU recruitment range contributes to the production of maximal velocity dynamic contractions and suggest that premotor areas may act on the motoneuron pool through accessory spinal tracts to modulate MU recruitment behavior of the anconeus (8, 31).

Due to the successful tracking of MU recruitment thresholds and discharge rates through a range of resultant peak contraction velocities, Chapter 4 determined whether repeated submaximal fatiguing dynamic contractions would affect MU properties of the anconeus in relation to the task performed. Results from that study confirmed prior indications that elbow extensor MU discharge rates are unchanged and MU recruitment thresholds of submaximal contractions decrease during a submaximal fatiguing dynamic protocol (26, 42). However for maximal dynamic contractions, reductions in power and velocity were associated with an approximate 20% decrease in MU discharge rates of maximal dynamic and ballistic isometric contractions. These reductions in MU discharge rate, which are similar to reductions in motoneuron excitability for a similar protocol (41), are comparable to those observed for MVCs following a submaximal isometric fatiguing protocol (2, 53). Thus, despite task-related differences in absolute MU discharge rates between isometric and dynamic contractions, it appears a common underlying mechanism regulates the response to submaximal fatigue regardless of contraction type.

In the last chapter, MUs were recorded concurrently in three elbow extensors (the long and lateral heads of the triceps brachii, and the anconeus) to elucidate how closely the existing surface-detected EMG-force relationships of the elbow extensors (3, 38) corresponded with MU recruitment threshold and force, and MU discharge rate and force relationships during isometric force production. Furthermore, this study aimed to address equivocal findings (3, 37) regarding the posited rather limited (30%MVC) MU recruitment range of the anconeus muscle. Preliminary data determined anconeus MUs to have the lowest recruitment thresholds of the three muscles, followed by MUs of the lateral and long head of the triceps brachii confirming the hypothesized order of MU recruitment. Despite possessing the lowest average MU recruitment thresholds, continued MU recruitment was observed up to 45%MVC extending the previously reported (37) upper limit of motor unit activation in the anconeus muscle. Average MU discharge rates were lower in the long head of the triceps brachii compared with the anconeus and lateral head of the triceps brachii. The relationship between MU recruitment and discharge behavior in the long head of the triceps brachii resembled to some degree the 'onion skin' pattern (12, 13). But the lack of shared variance between MU recruitment thresholds and initial discharge rates suggested a neural control pattern that combined aspects of the 'onion skin' pattern (13, 14) and the pattern observed by Monster (46) and Monster and Chan (47) to describe the interplay between recruitment and rate coding during isometric force production by elbow extensor MUs.

Together, these results suggest the anconeus is a viable model for the investigation of MU properties across a range of isometric and dynamic intensities, and in a variety of different tasks. The force and velocity ranges over which the anconeus operates (3), and is modulated (29, 30), in addition to its architectural and presumptive neurophysiological properties, render it an enticing model for the study of MU properties in technically challenging situations.

6.1 Limitations and opportunities

The limitations of the four studies of this thesis can be categorized as architectural or mechanical, electrophysiological, and technical. Architecturally, the anconeus differs substantially from the other elbow extensor muscles (1, 33, 48), which together (long, medial and lateral heads) provide about 85% of elbow extension torque (55). The volume and cross-sectional area (33, 48), average fascicle length and pennation angle (28), and elbow extension moments (28) of the anconeus differ also from the three heads of the triceps brachii. Furthermore, the anconeus fiber composition (~65% type I) is approximately equal and opposite to the other muscles of the triceps brachii. The anconeus has a twitch tension of 3.8±0.9Nm, which is ~25% of the lateral head of the triceps brachii (16.5±3.6Nm) (37). As a consequence the length-tension, and force-frequency relationships (37) of these two muscles in particular differ, and the contribution of the individual elbow extensors to the resultant torque, velocity and power is dependent upon the joint angle of isometric force production, and the range of motion of dynamic contractions (54). The mechanical outputs used to form the relationships in this thesis are dependent upon the interaction of all four elbow extensor, notwithstanding the potential interface of muscles in the forearm and shoulder for elbow extensor torque, velocity, and power production (36, 49, 54). Without a direct recording of the mechanical output from the anconeus in vivo relative to that of the other elbow extensors, it is difficult to determine the contribution the anconeus makes to these actions. Nevertheless, within the limitations of the study of MU physiology in humans, the anconeus offers a unique model of study in vivo.

Although single MU recordings significantly improve the precision with which relationships between EMG and mechanical outputs are formed due to the elimination of some confounding variables that affect the surface-detected EMG signals (19), the same aforementioned limitations pertaining to EMG-force relationships affect the interpretation of relationships between mechanical output and MU properties. Seminal studies (43-45) demonstrated how twitch tensions of individual MUs differ in human muscle and are dependent upon MU recruitment threshold and discharge rate. Based on these studies (43-45) and many others (16), it is assumed the MUs recorded in our studies adhere to these basic principles. However, it is unclear how for example twitch tensions are distributed among the MUs comprising the anconeus motoneuron pool. Without this information, the mechanical output of the anconeus in response to MU activation can only be inferred. This limitation is further complicated in Chapter 4 because neuromuscular fatigue disrupts the input-output relationships of the MU due to fatigue-associated changes in the muscle fibers ability to produce force, velocity, and power (20, 21)

The issue of fascicle length change relative to elbow joint range of motion must also be addressed as a potential limitation of the current studies performed dynamically. Anconeus MU properties were recorded in relation to a 120° range of motion in Chapters 2 and 3, and a 60° joint range of motion in Chapter 4. Fascicle lengths of the lateral and long heads of the triceps brachii, and anconeus all change ~40% (11.9cm, 10.0cm, and 1.7cm, respectively) over 120° joint range of motion when recorded passively and in static joint positions (28, 48). However, it is unclear how these muscles behave during active contraction and in what way these fascicle length changes are coordinated. As a result, in Chapters 2, 3, and 4, an assumption was made that the anconeus was shortening throughout the full joint range of motion owing to the continued MU discharge during elbow extension.

The electrophysiological limitations of this thesis are inherent to all studies of MU properties. Single MU action potentials are recorded from the sarcolemma at the muscle level, but originate as a consequence of the integration of multiple inputs on the motoneuron pool, and electrophysiological properties of each single motor unit (i.e. input conductance). Thus, the activity of a single MU reflects a number of spinal and supraspinal processes, but is limited in that it is not able to elucidate changes in any of these factors. It can only be regarded as a final common pathway (40) and as result, all hypotheses as to the origin of changes in MU properties must be regarded as speculation without additional measures. However, the advantage of single MU recordings is that, provided the position of the electrode is relatively stable, the waveform of these potentials is fairly constant and distinctive from neighboring MUs (17). The fine wire intramuscular technique employed in the current studies was designed specifically to ensure that the position of the electrode remained stable relative to the single MU action potential source, and the overlaid potentials in Figures 5 and 8 in Chapter 2 and 3 provide compelling evidence that the technique was successful. However, with the onset of neuromuscular fatigue, changes occur to the intracellular action potentials that are subsequently recorded in the extracellular space surrounding the muscle fibers (14, 15, 18). Although a somewhat conservative approach was taken for the classification of waveforms to a single MU, it is possible fatigue-associated changes to the MU waveform characteristics may have resulted in potentials being erroneously sorted both by the wave sorting algorithm and ultimately by the experienced investigator.

Technically, the anconeus model facilitated the recording, and tracking, of single MU action potentials in previously unattainable situations (i.e. maximal velocity dynamic contractions), but despite many repeated trials, sample sizes for Chapter 4 were low in comparison to prior studies (25, 42) investigating the elbow extensors . An a priori sample size calculation determined a sufficient number of MUs were recorded, but to address the issue of small sample size, we tracked the behavior of single MUs so that a within comparison could be made in addition to the group comparisons between different ranges of the time to task failure. However, the number of MUs in the anconeus is unknown and thus the proportion of the motoneuron pool that these data represent is unknown. Therefore, it is possible that the MUs recorded from the anconeus in Chapter 4 represent a cohort of similarly behaving MUs, but the considerable range of average MU recruitment thresholds (0-39%MVC) and discharge rates (28-42Hz) challenge this limitation and imply a sample representative of the anconeus motoneuron pool was recorded. Moreover, this rationale and approach is consistent with many prior studies of MU behavior under isometric and non-isometric conditions.

6.2 Future directions

Although these studies have advanced our knowledge of the MU activity associated with the production of fast dynamic contractions, many questions remain. In Chapters 2 and 3, the relationship between anconeus MU properties, recruitment threshold and discharge rate, and peak elbow extension velocity was determined. However, studies (4-7, 10, 11) show the triphasic EMG pattern is altered for movements about the elbow joint in relation to many parameters including, but not limited to , movement amplitude (range of motion), acceleration-deceleration ratio, and even preceding torque perturbations. In Chapters 2 and 3, the goal was to target a peak velocity of a 120° movement, but characteristics of these movements (i.e. acceleration-deceleration ratio) were not accounted for and thus, future studies should systematically investigate MU properties in paradigms that explore varying single joint movement parameters.

Moreover, the whole muscle mechanical outputs that emerge as a consequence of MU activity are dependent upon the active and passive properties of each muscle (50). A preliminary, indirect MU discharge rate-fascicle length relationship of the anconeus has been reported (28), but this relationship and others related to single muscle fiber property changes should be explored in the anconeus and the heads of the triceps brachii so that a more precise representation of the elbow extensor input-output relationship may be established.

In Chapter 4, MU recruitment threshold and discharge rate were recorded during maximal velocity elbow extensions in response to a submaximal fatiguing protocol. Neuromuscular fatigue is task-, muscle-, sex-, and age-dependent among other variables and represents an area in which MU properties of dynamic contractions can be examined. Specifically, the recovery of MU properties to pre-fatigue values is of great interest in the protocol employed in Chapter 4. Furthermore, because voluntary drive is reduced an equivalent amount to that of MU discharge rates of the anconeus in response the submaximal fatiguing protocol, it would be of great interest to determine the source of the reduction in voluntary drive through studies using transcranial magnetic stimulation, cervicomedullary stimulation and relevant sources of afferent stimulation during dynamic contractions.

Lastly, Chapter 5 investigated MU recruitment and discharge behavior of isometric force production in the elbow extensors. Although, muscle-dependent differences were observed between the three elbow extensors studied, the question still remains whether common modulation occurs among these muscles. One possible future direction is to conduct a cross-correlation analysis between MU action potentials of different MUs within the same muscle, and between MUs from different muscles to determine the amount of common modulation that occurs for the production of isometric elbow extension. Moreover, other MU properties (double discharge) have been shown to affect the production of force (23, 27) and should be investigated in synergistic muscle groups such as the elbow extensors.

Finally, the test-to-test reliability of these MU recordings in synergistic muscle groups must be examined to discount the possibility that these properties are organized differently for the same task each time. At least one theory of motor behavior (51) proposes movement is organized differently each time it is performed. An examination of trial-to-trial differences in MU behavior in the elbow extensors for isometric force production would advance the discussion of this issue.

6.3 Summary

The key objective of this thesis was to exploit the favorable signal characteristics of the anconeus muscle model to explore the relationships between the two primary MU properties, MU recruitment threshold and MU discharge rate, and resultant peak elbow extension velocity in an unfatigued state and in response to a dynamic submaximal fatiguing protocol. A secondary objective was to determine whether the MU properties of the anconeus, and the lateral and long heads, of the triceps brachii are modulated differently during ramp isometric force production. The main findings from these studies were a bilinear relationship between MU discharge rate and resultant contraction velocity, a general reduction in MU recruitment thresholds relative to increasing resultant velocity with a tendency for larger declines in higher threshold MUs, and a reduction in MU discharge rates recorded during maximal velocity elbow extension in response to a submaximal dynamic fatiguing protocol with no change in MU recruitment thresholds. A muscle specific pattern of MU recruitment and MU discharge rate modulation was also observed in three elbow extensors during ramp isometric force production wherein MUs of the anconeus were recruited at lower relative forces compared with those MUs of the long head of the triceps brachii, which possessed lowest MU discharge rates. Together, these findings show the utility of the anconeus muscle model for the investigation of MU properties in challenging situations and suggest an extended operating range of the anconeus for both isometric and velocity-dependent contractions.

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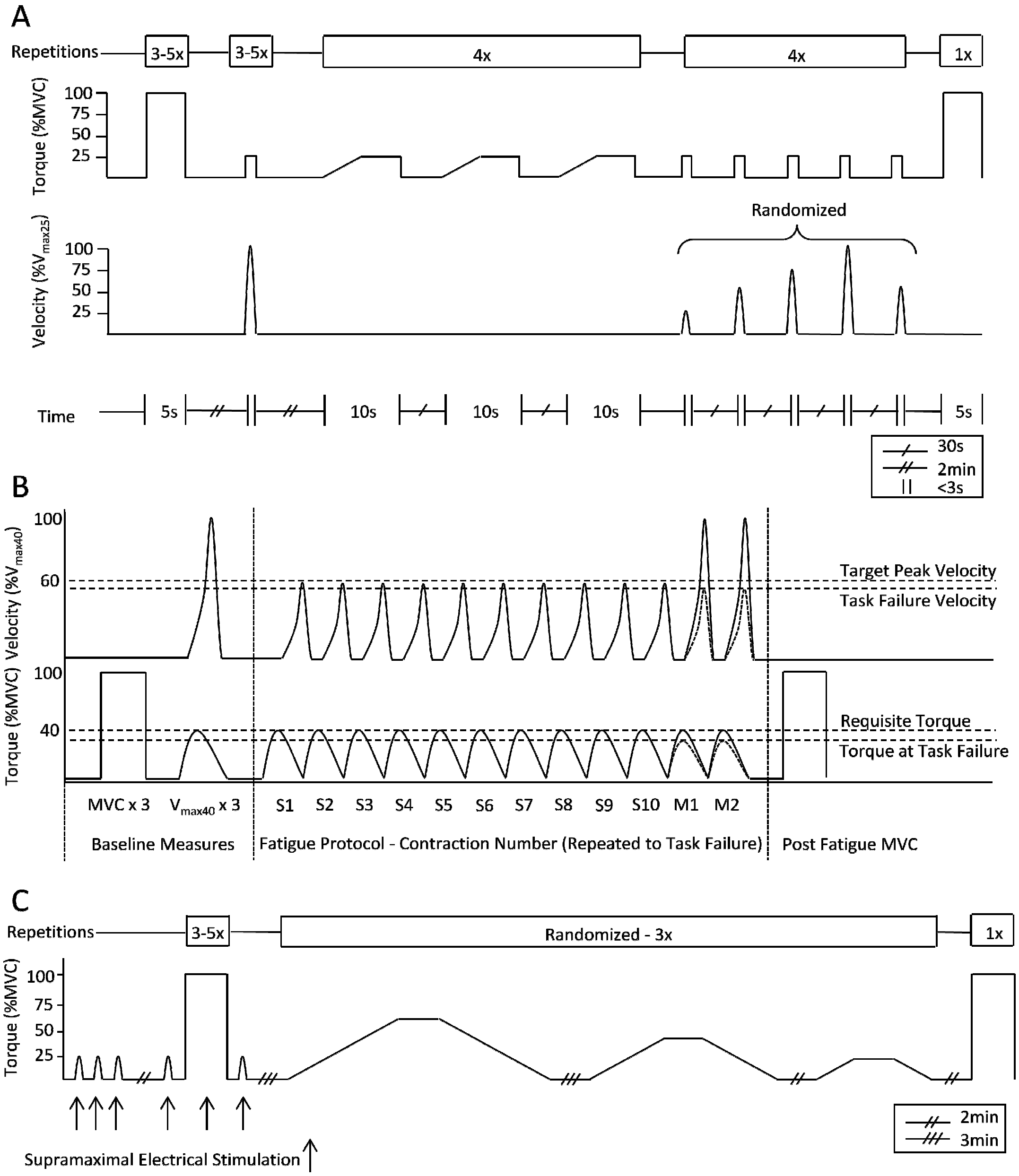
Appendix A

Schematics of experimental protocols of A) Chapters 2 and 3, B) Chapter 4, and C) Chapter 5

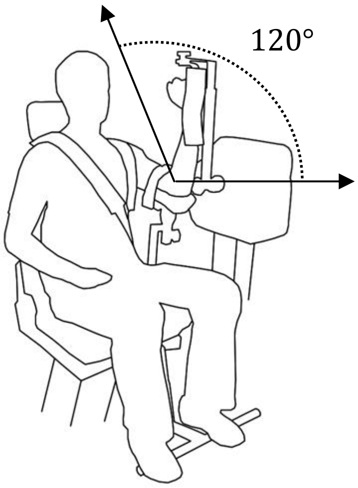


- MVC, maximal voluntary isometric contraction; V_{max25}, maximal velocity at 25%MVC; V_{max40}, maximal velocity at 40%MVC; S, submaximal contraction; M, maximal contraction

Appendix B

Experimental setups of A) Chapters 2 and 3, B) Chapter 4, and C) Chapter 5

A



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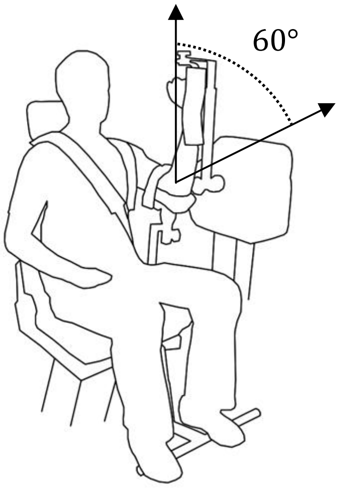

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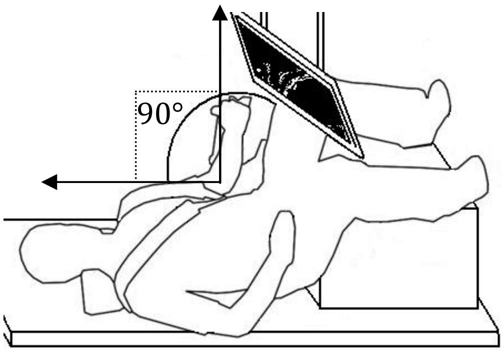
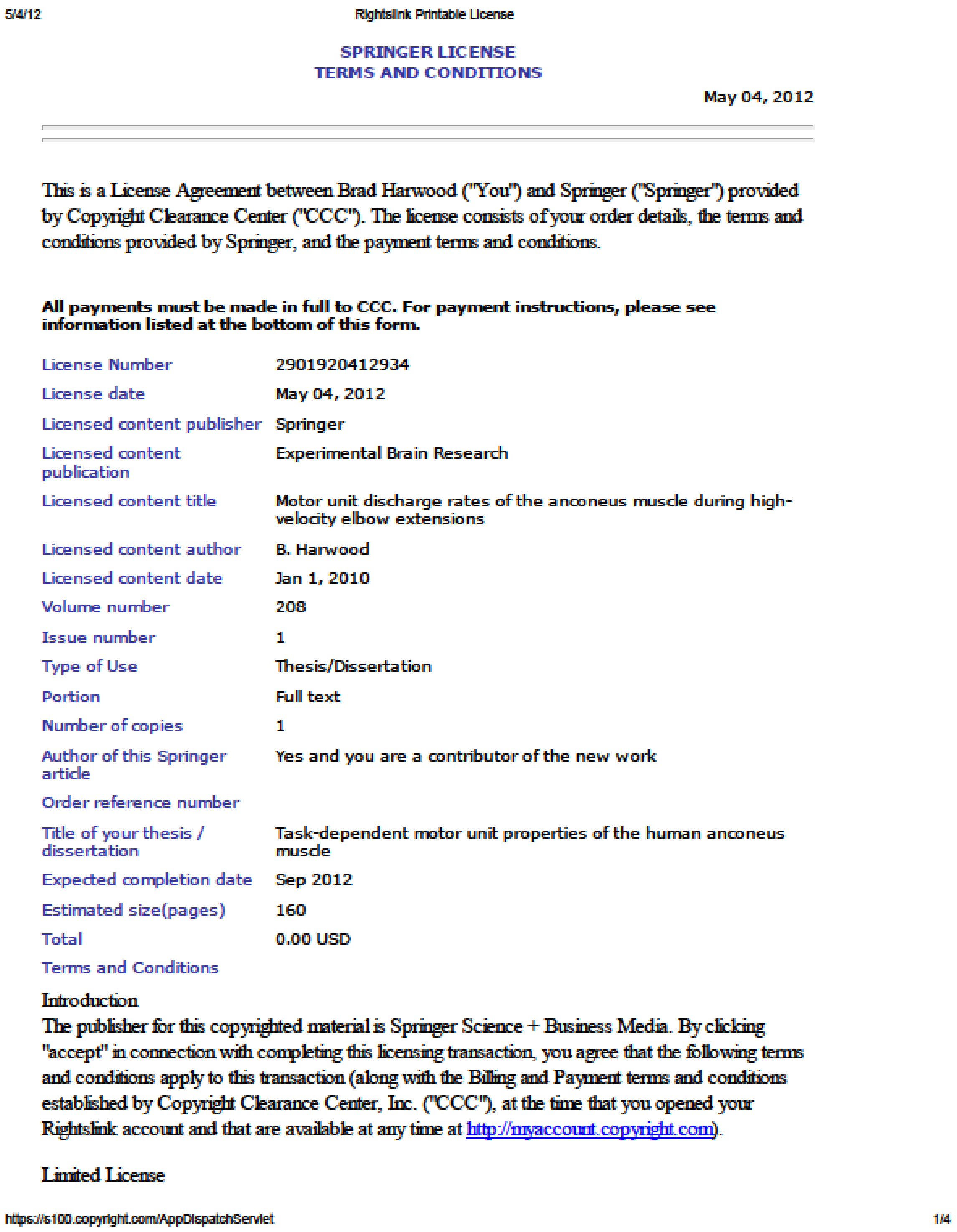


Appendix C



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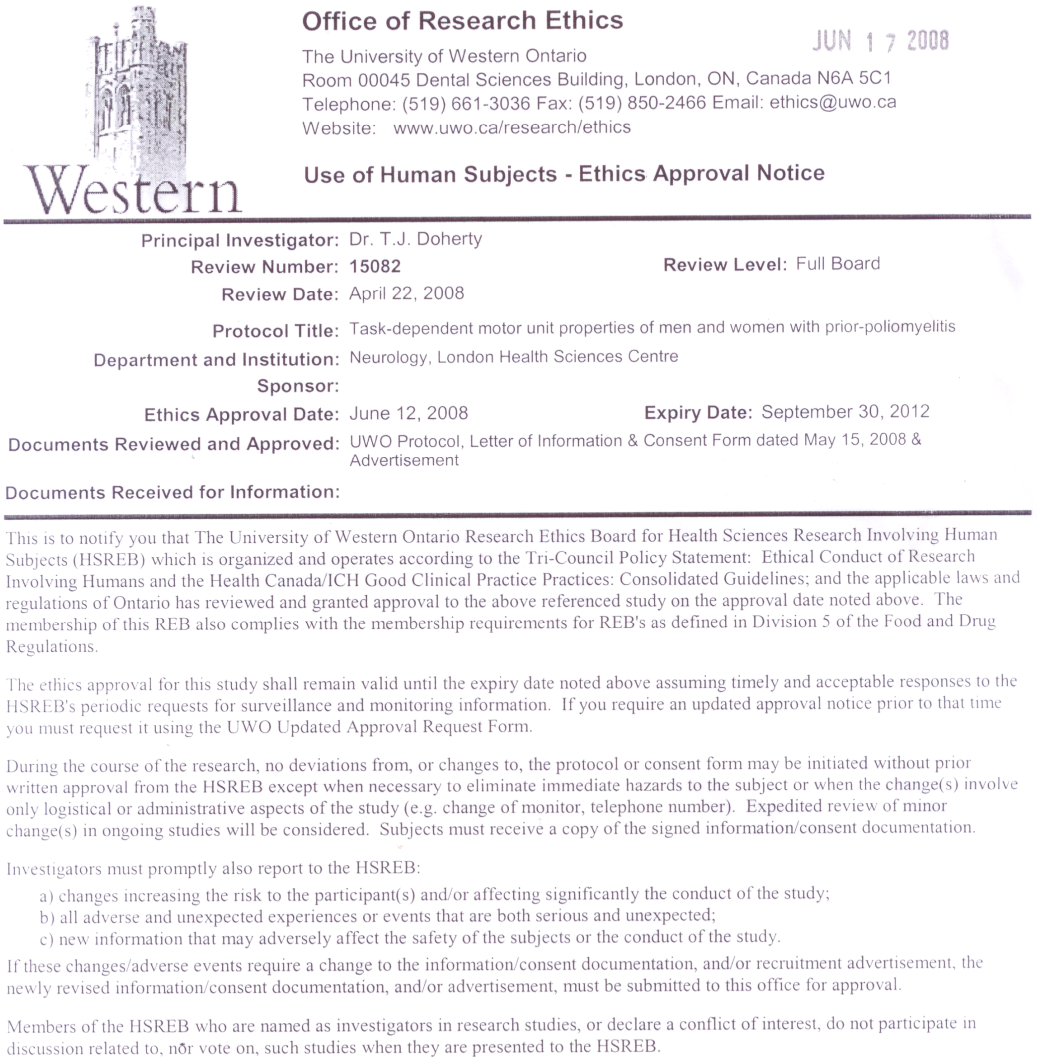

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JUN 17 2008

Western

Use of Human Subjects - Ethics Approval Notice

Principal Investigator: Dr. T.J. Doherty
Review Number: 15082 **Review Level:** Full Board
Review Date: April 22, 2008
Protocol Title: Task-dependent motor unit properties of men and women with prior-poliomyelitis
Department and Institution: Neurology, London Health Sciences Centre
Sponsor:
Ethics Approval Date: June 12, 2008 **Expiry Date:** September 30, 2012
Documents Reviewed and Approved: UWO Protocol, Letter of Information & Consent Form dated May 15, 2008 & Advertisement
Documents Received for Information:

This is to notify you that The University of Western Ontario Research Ethics Board for Health Sciences Research Involving Human Subjects (HSREB) which is organized and operates according to the Tri-Council Policy Statement: Ethical Conduct of Research Involving Humans and the Health Canada/ICH Good Clinical Practice Practices: Consolidated Guidelines; and the applicable laws and regulations of Ontario has reviewed and granted approval to the above referenced study on the approval date noted above. The membership of this REB also complies with the membership requirements for REB's as defined in Division 5 of the Food and Drug Regulations.

The ethics approval for this study shall remain valid until the expiry date noted above assuming timely and acceptable responses to the HSREB's periodic requests for surveillance and monitoring information. If you require an updated approval notice prior to that time you must request it using the UWO Updated Approval Request Form.

During the course of the research, no deviations from, or changes to, the protocol or consent form may be initiated without prior written approval from the HSREB except when necessary to eliminate immediate hazards to the subject or when the change(s) involve only logistical or administrative aspects of the study (e.g. change of monitor, telephone number). Expedited review of minor change(s) in ongoing studies will be considered. Subjects must receive a copy of the signed information/consent documentation.

Investigators must promptly also report to the HSREB:

a) changes increasing the risk to the participant(s) and/or affecting significantly the conduct of the study;
b) all adverse and unexpected experiences or events that are both serious and unexpected;
c) new information that may adversely affect the safety of the subjects or the conduct of the study.

If these changes/adverse events require a change to the information/consent documentation, and/or recruitment advertisement, the newly revised information/consent documentation, and/or advertisement, must be submitted to this office for approval.

Members of the HSREB who are named as investigators in research studies, or declare a conflict of interest, do not participate in discussion related to, nor vote on, such studies when they are presented to the HSREB.

Western

Office of Research Ethics
The University of Western Ontario
Room 4180 Support Services Building, London, ON, Canada N6A 5C1
Telephone: (519) 661-3036 Fax: (519) 850-2466 Email: ethics@uwo.ca
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MAR 0 5 2009

Use of Human Subjects - Ethics Approval Notice

Principal Investigator: Dr. T.J. Doherty
Review Number: **15082** **Revision Number:** **1**
Review Date: September 30, 2008 **Review Level:** Expedited
Protocol Title: Task-dependent motor unit properties of men and women with prior-poliomyelitis
Department and Institution: Neurology, London Health Sciences Centre
Sponsor:
Ethics Approval Date: February 27, 2009 **Expiry Date:** September 30, 2012
Documents Reviewed and Approved: Revised Study Methodology, Letter of Information and Consent (ver. Feb.2/09)
Documents Received for Information:

This is to notify you that The University of Western Ontario Research Ethics Board for Health Sciences Research Involving Human Subjects (HSREB) which is organized and operates according to the Tri-Council Policy Statement: Ethical Conduct of Research Involving Humans and the Health Canada/ICH Good Clinical Practice Practices: Consolidated Guidelines; and the applicable laws and regulations of Ontario has reviewed and granted approval to the above referenced revision(s) or amendment(s) on the approval date noted above. The membership of this REB also complies with the membership requirements for REB's as defined in Division 5 of the Food and Drug Regulations.

The ethics approval for this study shall remain valid until the expiry date noted above assuming timely and acceptable responses to the HSREB's periodic requests for surveillance and monitoring information. If you require an updated approval notice prior to that time you must request it using the UWO Updated Approval Request Form.

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Investigators must promptly also report to the HSREB:

a) changes increasing the risk to the participant(s) and/or affecting significantly the conduct of the study;
b) all adverse and unexpected experiences or events that are both serious and unexpected;
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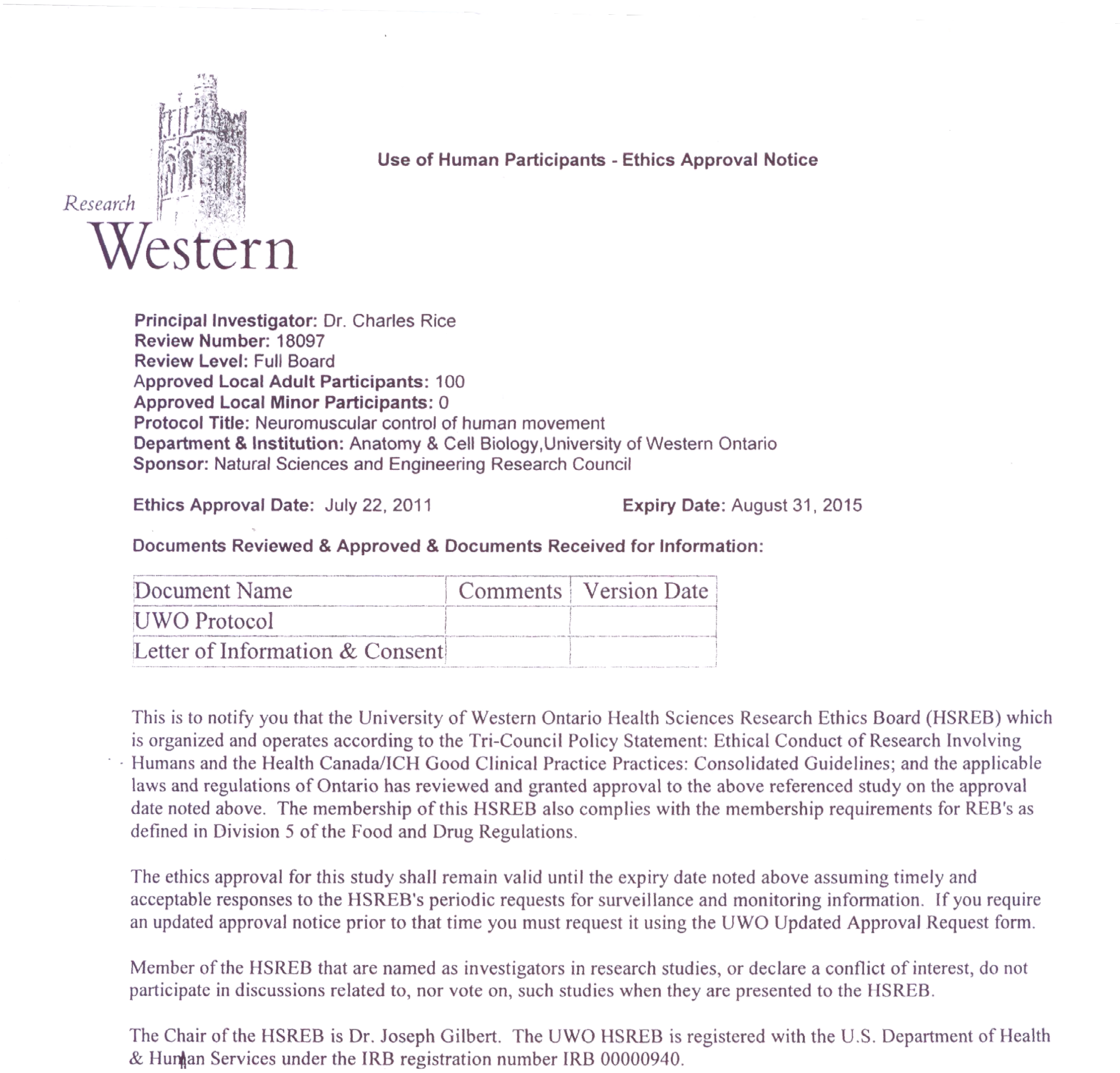

Research
Western

Use of Human Participants - Ethics Approval Notice

Principal Investigator: Dr. Charles Rice
Review Number: 18097
Review Level: Full Board
Approved Local Adult Participants: 100
Approved Local Minor Participants: 0
Protocol Title: Neuromuscular control of human movement
Department & Institution: Anatomy & Cell Biology,University of Western Ontario
Sponsor: Natural Sciences and Engineering Research Council

Ethics Approval Date: July 22, 2011 **Expiry Date:** August 31, 2015

Documents Reviewed & Approved & Documents Received for Information:

Document Name	Comments	Version Date
UWO Protocol		
Letter of Information & Consent		

This is to notify you that the University of Western Ontario Health Sciences Research Ethics Board (HSREB) which is organized and operates according to the Tri-Council Policy Statement: Ethical Conduct of Research Involving Humans and the Health Canada/ICH Good Clinical Practice Practices: Consolidated Guidelines; and the applicable laws and regulations of Ontario has reviewed and granted approval to the above referenced study on the approval date noted above. The membership of this HSREB also complies with the membership requirements for REB's as defined in Division 5 of the Food and Drug Regulations.

The ethics approval for this study shall remain valid until the expiry date noted above assuming timely and acceptable responses to the HSREB's periodic requests for surveillance and monitoring information. If you require an updated approval notice prior to that time you must request it using the UWO Updated Approval Request form.

Member of the HSREB that are named as investigators in research studies, or declare a conflict of interest, do not participate in discussions related to, nor vote on, such studies when they are presented to the HSREB.

The Chair of the HSREB is Dr. Joseph Gilbert. The UWO HSREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000940.

Curriculum vitae

Brad Harwood, BHK, MHK, PhD
Neuromuscular Physiology Laboratory • The University of Western Ontario •
London, Ontario

Education:

The University of Western Ontario: 2007-Present
Thesis: Task-dependent motor unit properties of the human anconeus muscle
PhD Kinesiology: Neuromuscular Physiology
Supervisor: Dr. Charles L. Rice

University of Windsor: 2005-2007
Thesis: Task-dependent motor unit subpopulations in older adults.
Masters of Human Kinetics: Human Performance
Supervisor: Dr. Jennifer M. Jakobi

University of Windsor: 2002-2005
Thesis: Central and peripheral contributions to rhythmic coordination.
Bachelor of Human Kinetics (Honours): Movement Science
Supervisor(s): Dr. Jennifer M. Jakobi, Dr. Nancy McNevin

Published Articles in Refereed Journals

9. **Harwood B**, Rice CL. (2012) Changes in motor unit recruitment thresholds of the human anconeus muscle during torque development preceding shortening elbow extensions. J Neurophysiol. Feb 29;107:2876-2884

8. **Harwood B**, Power GA, Allen MD, Booth WJ. (2011) Tendon vibration does not alter decreased responsiveness of motoneurones in the absence of motor cortical input during fatigue. J Physiol. Dec 1;589(Pt 23):5559-60.

7. **Harwood B**, Edwards DL, Jakobi JM. (2011) Age- and sex-related differences for electromyography gaps during daily activity and a discrete task. Gait Posture. May;34(1):6-12.

6. **Harwood B**, Davidson AW, Rice CL. (2011) Motor unit discharge rates of the anconeus muscle during high-velocity elbow extensions. Exp Brain Res. Jan;208(1):103-13.

5. **Harwood B**, Edwards DL, Jakobi JM. (2010) Age independent and position-dependent alterations in motor unit activity of the biceps brachii. Eur J Appl Physiol. Sep;110(1):27-38.

4. Dalton BH, **Harwood B**, Davidson AW, Rice CL. (2010) Recovery of motoneuron output is delayed in old men following high-intensity fatigue. J Neurophysiol. Feb;103(2):977-85.

3. Dalton BH, **Harwood B**, Davidson AW, Rice CL. (2009) Triceps surae contractile properties and firing rates in the soleus of young and old men. J Appl Physiol. Dec;107(6):1781-8.

2. Boe SG, Dalton BH, **Harwood B**, Doherty TJ, Rice CL. (2009) Inter-rater reliability of motor unit number estimates and quantitative motor unit analysis in the tibialis anterior muscle. Clin Neurophysiol. May;120(5):947-52.

1. **Harwood B**, Edwards DL, Jakobi JM. (2008) Age- and sex-related differences in muscle activation for a discrete functional task. Eur J Appl Physiol. Aug;103(6):677-86.

<u>Presented and Published Abstracts</u> (Total of 17)

17. **Harwood B**, Power GA, Allen MD, Rice CL. (2011). The relationship between elbow extension velocity and motor unit recruitment thresholds of anconeus motor units. Society for Neuroscience, Washington, DC. November 12-16, 2011: 920.15.

16. Power GA**, Harwood B**, Dalton BH, Vandervoort AA, Rice CL. (2011). Motor unit recruitment and initial discharge rate of the elbow extensors: The triceps brachii and anconeus. Society for Neuroscience, Washington, DC. November 12-16, 2011: 920.14.

15. Allen MD, **Harwood B**, Rice CL. (2011). Motor unit recruitment thresholds in relation to the rate of torque development in the anconeus.

Society for Neuroscience, Washington, DC. November 12-16, 2011: 920.13.

14. Dalton BH, **Harwood B**, Power GA, Vandervoort AA, Rice CL. (2011). Motor unit properties of the triceps surae during a sustained sub-maximal plantar flexion task. Society for Neuroscience, Washington, DC. November 12-16, 2011: 920.16.

13. **Harwood B**, Choi IH, Rice CL. (2011). Fatigue-associated reduction in motor unit discharge rates (MUDRs) of the anconeus at maximal velocity in response to a submaximal dynamic fatiguing protocol. Canadian Society of Exercise Physiology, Quebec City, PQ. *Applied Physiology, Nutrition, and Metabolism*, 36(S2): S299-S360*.*

12. **Harwood B**, Choi IN, Rice CL. (2011). Motor unit discharge rates of the anconeus during a fatiguing dynamic contraction. Exercise Neuroscience Group, Waterloo, ON. June 18-19. http://www.wix.com/oeng2011/oeng2011.

11. **Harwood B**, Rice CL. (2010). Motor unit recruitment thresholds of the anconeus during maximal velocity elbow extensions. Canadian Society of Exercise Physiology, Toronto, ON. *Applied Physiology, Nutrition, and Metabolism*, 35(S1): S1-S116.

10. **Harwood B**, Rice CL. (2010). Motor unit discharge pattern of the anconeus during maximal velocity elbow extensions. Society for Neuroscience, San Diego, CA. November 13-17: 180.51.

9. Dalton BH, **Harwood B**, Power GA, Rice CL. (2010). Motor unit properties of the triceps surae. Society for Neuroscience, San Diego, CA. November 13-17: 180.50.

8. **Harwood B**, Davidson AW, Rice CL. (2010). Effect of elbow joint angle on anconeus fascicle length and motor unit firing rates. American College of Sports Medicine Annual Meeting, Baltimore, MD. *Med Sci Sports Exerc*, 42(5): S413.

7. **Harwood B**, Dalton BH, McNeil CJ, Doherty TJ, Rice CL. (2009). Inter-limb variability of the estimated number of motor units in aged poliomyelitis survivors: a pilot study. Canadian Society of Exercise Physiology, Vancouver, BC. *Applied Physiology, Nutrition, and Metabolism*, 34(S1): 1-114.

6. **Harwood B**, Rice CL. (2009). Velocity dependent motor unit discharge rates of the anconeus during elbow extension. American College of Sports Medicine Annual Meeting, Seattle, WA. *Med Sci Sports Exerc*, 41(5).

5. **Dalton BH**, Davidson AW, Harwood B, Rice CL. (2009). High-intensity fatigue in the soleus of young and old men. American College of Sports Medicine Annual Meeting, Seattle, WA. *Med Sci Sports Exerc*, 41(5).

4. **Harwood B**, Davidson AW, Rice CL. (2008). Time course of motor unit discharge of the short and long heads of the biceps brachii following radial nerve stimulation. Canadian Society of Exercise Physiology, Banff, AB. *Med Sci Sports Exerc*, 33(S1): 1-124.

3. **Harwood B**, Edwards DL, Jakobi JM. (2008). Differential derecruitment thresholds of the long and short heads of the biceps brachii in young and old men. American College of Sports Medicine Annual Meeting, Indianapolis, IN. *Med Sci Sports Exerc*, 40(5):S446.

2. **Harwood BJ**, Edwards DL, Jakobi JM. (2007). Quantifying muscular activation and rest in a discrete functional task of older men and women. *Med Sci Sports Exerc*, 39(5): S267.

1. **Harwood BJ**, Jakobi JM. (2007). Task-dependent motor unit activity in young and old adults. Canadian Society of Exercise Physiology, London, ON. *Applied Physiology, Nutrition, and Metabolism*, 32(S1): 1-97.

Academic and Professional Experience:

Teaching Assistantship

4430 Muscle Function and Metabolism 2009-2011
School of Kinesiology, The University of Western Ontario
Duties: Assignment assessment, design and management of course website

2300 Introductory Exercise Physiology 2008
School of Kinesiology, The University of Western Ontario
Duties: Supervision of laboratories and provision of tutorials

95-490 Neurophysiology 2007
Faculty of Human Kinetics, University of Windsor
Duties: Assignment assessment, design and implementation of laboratory demonstrations, delivery of special topic lectures

95-360 Exercise Physiology 2005-2007
Faculty of Human Kinetics, University of Windsor

Duties: Assignment assessment, creation and implementation of tutorials

Research Assistantship

Research Assistantship, School of Kinesiology, The University Of Western Ontario, London, ON. 2008/2009/2010

Duties:
Ethical approval application
Participant recruitment
Data collection and analysis
Supervision of undergraduate students

Scholarships and Awards:

Kinesiology Graduate Board Research and Service Award	2010
Natural Sciences and Engineering Research Council (NSERC) Postgraduate Scholarship	2009
Ontario Graduate Scholarship	2009, 2011
The University of Western Ontario Graduate Travel Award	2008-2012
Faculty of Health Sciences and Kinesiology Graduate	2008-2012
Faculty of Health Sciences Dean’s Entrance Scholarship	2007
Dr. Frank DeMarco Award	2006-2007
Grace Lamoureux - Howitt Pinfold Memorial Award	2005