

Electronic Thesis and Dissertation Repository

---

4-12-2017 12:00 AM

## Motor Unit Firing in the Human Anconeus During High Intensity Eccentric Contractions of Elbow Extensors

Christopher W. Stolworthy, *The University of Western Ontario*

Supervisor: Dr. Charles Rice, *The University of Western Ontario*

A thesis submitted in partial fulfillment of the requirements for the Master of Science degree in Kinesiology

© Christopher W. Stolworthy 2017

Follow this and additional works at: <https://ir.lib.uwo.ca/etd>



Part of the [Motor Control Commons](#)

---

### Recommended Citation

Stolworthy, Christopher W., "Motor Unit Firing in the Human Anconeus During High Intensity Eccentric Contractions of Elbow Extensors" (2017). *Electronic Thesis and Dissertation Repository*. 4471.  
<https://ir.lib.uwo.ca/etd/4471>

This Dissertation/Thesis is brought to you for free and open access by Scholarship@Western. It has been accepted for inclusion in Electronic Thesis and Dissertation Repository by an authorized administrator of Scholarship@Western. For more information, please contact [wlsadmin@uwo.ca](mailto:wlsadmin@uwo.ca).

## ABSTRACT

**PURPOSE:** To track single motor units through both isometric and eccentric elbow extensor contractions, at near maximal contraction intensity, and compare firing rates between contraction modes at an absolute torque. **METHODS:** Bipolar fine-wire electrodes were inserted into the anconeus in order to record motor unit firing behaviour during sets of high torque isometric and eccentric contractions. Contractions were performed on an isokinetic dynamometer at a pre-determined speed of 10°/s, through 60° total range of elbow joint motion, and at 50, 75 or 100% MVC. **RESULTS:** Mean motor unit firing rates were lower during eccentric contractions across all intensities ( $p < 0.05$ ), however surface EMG of the triceps brachii did not comprehensively follow the same pattern. **CONCLUSION:** Eccentric contraction is associated with an improvement in neuromechanical coupling in the anconeus, even at high torques. Previous studies have shown a similar effect but only at low to moderate contraction intensities.

### Keywords

Motor neuron discharge, Intramuscular electromyography, Voluntary activation, Maximal effort, Dynamic movement control

## Acknowledgments

I would like to thank Ontario Graduate Scholarship and Western University for sponsoring me during my graduate studies, and to acknowledge the wonderfully organized and helpful people in the Kinesiology Graduate Office for their support throughout my time in the program.

I would also like to thank my lab mates: Colin, Eric, Dave, and Kevin. It was always exciting to help with projects, and reassuring to get your assistance with my own. Your contributions to my presentations and poster were invaluable, and I always enjoyed learning about each of your unique experimental techniques.

Thanks to my thesis examiners, Dr. Matthew Heath, Dr. Jayne Garland, and Dr. Greg Marsh, for providing your insight and constructive comments regarding my thesis manuscript.

To my supervisor, Dr. Charles Rice, thank you for taking my eccentricities in stride, and for your unwavering encouragement. You have provided me with incredible opportunities to further my understanding of how the human neuromuscular system functions. As one of your students, I was given a wonderful balance of freedom, to tinker and explore, and structure, to foster productivity and success.

Lastly, I would like to thank my family for their steadfast encouragement. My younger brother Collin, who allowed me to pilot test various wire configurations, was critical to developing my understanding of intramuscular electrode technique. My youngest brother, Curtis, and my parents, Peter, Catherine and Charlie, have invariably supported me throughout all stages of my education.

I would like to dedicate this thesis manuscript to my grandfathers, George and Peter, both of whom nurtured my sense of wonder about the natural world, and emphasized to me the importance of logic and reasoning.

# Table of Contents

ABSTRACT.....	i
Acknowledgments.....	ii
Table of Contents.....	iii
List of Tables.....	v
List of Figures.....	vi
List of Appendices.....	vii
List of Abbreviations.....	viii
Glossary of Terms.....	ix
Chapter 1.....	1
1 Literature Review.....	1
1.1 Neuromuscular Structure & Function – A Brief Overview.....	1
1.2 Electromyography.....	2
1.3 Motor Unit Properties & Function.....	3
1.4 Muscle Force-Velocity Curve.....	5
1.5 Voluntary Activation.....	7
1.6 Extensors of the Elbow.....	8
1.7 Purpose & Hypotheses.....	8
Chapter 2.....	10
2 Introduction.....	10
Chapter 3.....	13
3 Methods.....	13
3.1 Experimental Set-up.....	13
3.2 Strength.....	14
3.3 Lengthening Protocol.....	15
3.4 Electromyography.....	15
3.5 Signal Processing & Analysis.....	16
3.6 Statistical Analysis.....	17
Chapter 4.....	19
4 Results.....	19
4.1 RMS EMG.....	19

4.2	Single MU Discharge .....	21
Chapter 5	.....	24
5	Discussion .....	24
5.1	Elbow Extensor Force Characteristics.....	25
5.2	Motor Unit Behaviour.....	26
5.3	Surface EMG .....	29
5.4	Conclusion .....	30
5.5	Limitations .....	31
5.6	Future Directions .....	33
References	.....	35
Appendices	.....	43
Curriculum Vitae	.....	44

## List of Tables

Table 1.	Mean RMS EMG values and statistical analysis.....	21
----------	---	----

## List of Figures

Figure 1.	General schematic of the force-frequency relationship.....	5
Figure 2.	General schematic of the force-velocity relationship.....	6
Figure 3.	Schematic of experimental set-up.....	14
Figure 4.	Example of raw torque, EMG and single MU data.....	19
Figure 5.	Mean MUFs of 12 motor units, followed across contraction mode.....	22
Figure 6.	Mean MUFs by contraction intensity, plotted with mean torque.....	23

# List of Appendices

Appendix A. Ethics approval documentation.....43



## List of Abbreviations

<b>ATP</b>	-	adenosine triphosphate
<b>CI</b>	-	confidence interval
<b>df</b>	-	degrees of freedom
<b>EMG</b>	-	electromyography, electromyogram
<b>Hz</b>	-	Hertz
<b>iEMG</b>	-	integrated electromyogram
<b>ISI</b>	-	interspike interval
<b>ITT</b>	-	interpolated twitch
<b>MU</b>	-	motor unit
<b>MUAP</b>	-	motor unit action potential
<b>MUFR</b>	-	motor unit firing rate
<b>MVC</b>	-	maximal voluntary contraction
<b>Nm</b>	-	Newton-meters
<b>RMS</b>	-	root-mean square
<b>SD</b>	-	standard deviation
<b>TA</b>	-	Tibialis Anterior
<b>VA</b>	-	voluntary activation

## Glossary of Terms

**Action potential** – a single depolarization wave that is conducted along an excitable cell (here, nerve or muscle), which encodes information via proximity in time to other action potentials

**Concentric** – a type of dynamic muscular effort where force is produced and the muscle is allowed to shorten in length

**Eccentric** – a type of dynamic muscular effort where force is produced while the muscle is being stretched or lengthened

**Electromyography** – recorded sum of electrical activity, in Volts (V), associated with muscular contraction, recorded from either the surface of the skin through the underlying tissue, or, more directly, via subcutaneous electrodes placed near muscle fibers

**Interspike Interval** – the interval of time between two successive action potentials (milliseconds, ms), inversely related to frequency in Hz

**Isometric** – a type of static muscular effort where force is produced and the muscle virtually does not change in length

**Motor unit** – consists of a motor neuron along with all of the muscle fibers that it innervates, functional contractile element

**Motor unit firing rate** – refers to the number of action potentials conducted along a motor axon, across the neuromuscular junction, and along each muscle fiber, per second (in Hertz, Hz), reciprocal of ISI

**Torque** – a force applied tangentially to an axis of rotation creates a torque, the formula for which is the product of the force and the moment arm,  $F \cdot d$ , measured in Newton-meters (Nm)

**Voluntary activation** – the extent of one's ability to utilize, or activate, the entirety of a muscle mass

## Chapter 1

### 1 Literature Review

#### 1.1 Neuromuscular Structure & Function – A Brief Overview

The smallest functional element of the neuromuscular system, the motor unit (MU), consists of a single  $\alpha$ -motor neuron, and all of the associated muscle fibers that it innervates (Enoka, 2006). Resting membrane potential of the motor neuron, or the potential (voltage) difference between the interior and exterior of the cell, is variable but on average is approximately -70 mV (Enoka, 2006). Motor neuron dendrites are projections which receive excitatory (and inhibitory) input from sensory and motor tract neurons, as well as interneurons, via synapses. Net excitatory synaptic input to the motor neuron soma will depolarize the cell body and push the soma towards its threshold potential (approximately -40 to -55 mV) (Enoka, 2006). Particularly when the axon hillock, which is the junction between the motor neuron soma and its axonal projection, reaches threshold potential, a binary change in state is initiated at the axon and an action potential begins to propagate towards the axon terminal.

The action potential is a wave of depolarization, a transient and localized reversal of cell membrane polarity caused primarily by sodium ( $\text{Na}^+$ ) and potassium ( $\text{K}^+$ ) ion fluxes, that the neuron uses to encode information of intent (Enoka, 2006). The action potential consists of an initial depolarization which is followed quickly by a repolarization and then typically a hyperpolarization of the cell membrane. These polarity phases are the result of voltage-dependent shifts in activity of membrane-embedded ion channels that permit a rapid initial inward flow of  $\text{Na}^+$  to depolarize the membrane, followed by a slower outward flow of  $\text{K}^+$  to repolarize and hyperpolarize the axon (Enoka, 2006). The repolarization phase up to the point of the threshold potential is termed the absolute refractory period, because sodium channels are inhibited at this time and no amount of excitatory stimulus can force the cell to depolarize again. The hyperpolarization phase is termed the relative refractory period, during which time the neuron may fire again with enough excitation despite the exceptionally negative membrane potential (Enoka, 2002).

The long and relatively large diameter axons of the motor nerves in the corticospinal pathway are typically myelinated to improve conduction velocity of individual action potentials and to preserve signal fidelity during transmission to the extremities via saltatory conduction (Enoka, 2002). Action potentials that reach the axon terminal cause a depolarization event that results in the release of the neurotransmitter acetylcholine (ACh) into the synaptic cleft of the neuromuscular junction, or the interface of the neuromuscular system (Enoka, 2006). Liberated ACh binds to ACh receptors on the post-synaptic membrane and then is eventually degraded via the enzyme acetylcholinesterase, however it is the binding of ACh to its receptor on the post-synaptic muscle fiber membrane that initiates another depolarization event via voltage-gated ion channels (Enoka, 2006). From the neuromuscular junction, action potentials propagate along the muscle fiber and penetrate deep into the myocyte via the transverse tubular system, an arrangement of membrane invaginations that direct current from the surface of the myocyte closer to the interior of the cell. These depolarization waves stimulate the release of calcium ions ( $\text{Ca}^{2+}$ ), from the sarcoplasmic reticulum, into the muscle fiber interior, where the  $\text{Ca}^{2+}$  binds to troponin to allow cross-bridge interactions between actin and myosin to occur (Enoka, 2006). It is the formation and functioning of these actomyosin cross-bridge complexes that generate muscle tension and, with enough input from the motor neuron, shorten the muscle belly and affect joint position.

## 1.2 Electromyography

To examine the electrical activity associated with muscular contraction, various types of electrodes can be used to record electromyograms (Kamen & Gabriel, 2010). An electromyogram is essentially a recording of net voltage fluctuation in a muscle. Recording techniques can assess gross muscle activity in the form of an interference pattern using an electrode applied to the surface of the skin (surface EMG, sEMG), or measurements can be made of action potentials from one to twenty or so muscle fibers at a time using several classes of intramuscular EMG electrodes.

Precise electromyographical measures of MU behaviour during dynamic contraction are highly susceptible to signal distortion produced by relative electrode and tissue movement. Surface electromyography during dynamic contraction can also be

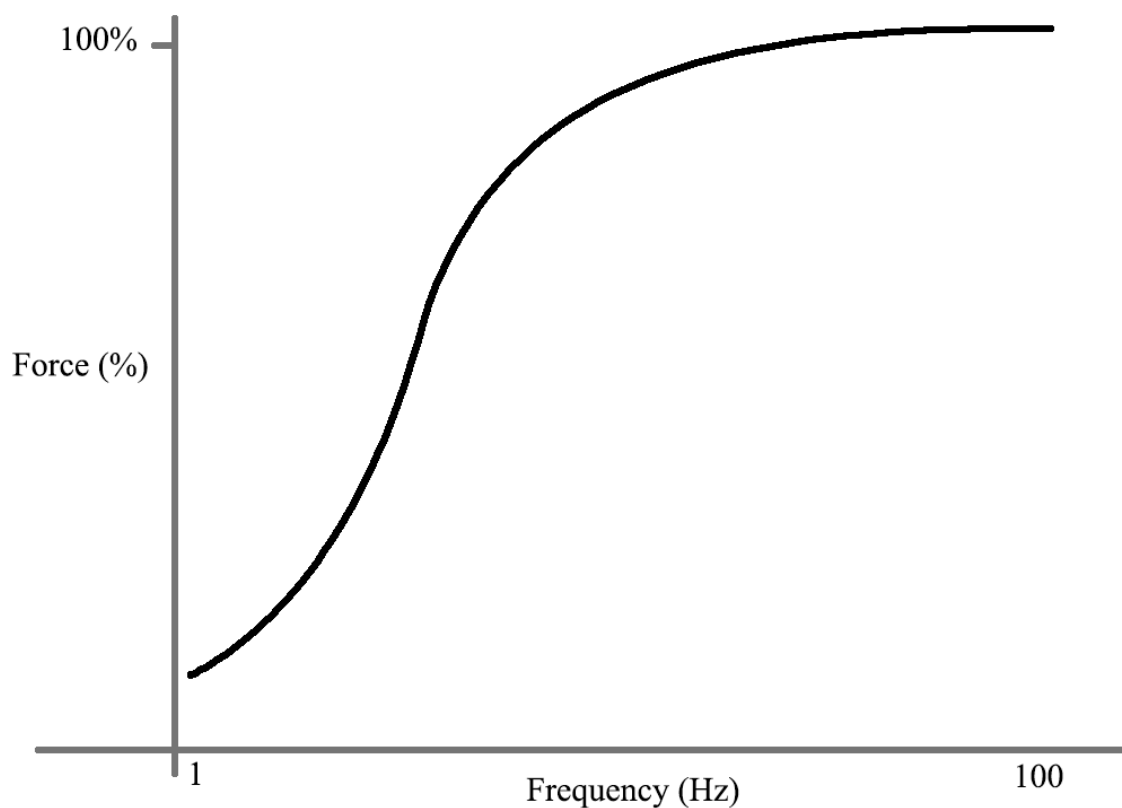
challenging to interpret, primarily due to signal non-stationarity, relative changes in electrode position over the muscle, as well as changes in intermediate tissue conductivity during movement (Farina, 2006). The fine wire intramuscular EMG technique used in this thesis relies on deposition of at least 2 thin (~100  $\mu\text{m}$  diameter), flexible, stainless steel wire filaments into the muscle tissue (Kamen & Gabriel, 2010). The ends of the wires are bent into hooks that are intended to stabilize the exposed wire tips with respect to adjacent muscle fibers. Once in position, the electrode tips record trains of action potentials as analog electrical signals that are subsequently amplified, filtered and stored digitally. Action potential waveform shapes are determined predominantly by the proximity and spatial orientation of the two electrode poles in relation to the direction of current conduction along muscle fibers (Kamen & Gabriel, 2010). Computational analysis of waveforms subsequently aims to identify action potentials that originated from a single MU via superimposition of waveforms in order to compare shape.

### 1.3 Motor Unit Properties & Function

In animal studies, motor units are classically differentiated based on properties such as contraction duration (fast vs slow twitch), fatigue resistance (fatigable vs fatigue resistant), and force production (Enoka, 2002). Motor unit contraction duration refers to the time duration of a single stimulated twitch, and probably relates to the speed of contractile machinery combined with the viscoelastic material properties of the tissue (Enoka, 2002). Resistance to fatigue is reflected by the tension profile of a motor unit over time, with repeated stimulation (Enoka, 2002, 2006). In animals, fast twitch fibers also produce greater tetanic forces than slow twitch fibers. Human motor units can also be classified by contractile duration and fatigue resistance however the correlations between twitch force and contractile duration are not as robust in humans as they are in animals (Enoka, 2002). In practice, human motor units typically do not sift out into discrete categories, but exhibit somewhat homogenous properties along a spectrum, strongly influenced by the specific innervation patterns of the motor axon, as well as training and deconditioning to a degree (Enoka, 2002). Motor unit muscle fibers may also be spatially organized according to their metabolic needs, with slower oxidative fibers typically

clustered near to the blood supply near the bone and faster twitch glycolytic fibers grouped nearer to the surface of the skin (Enoka, 2002).

The two critical parameters of motor unit (MU) behaviour, rate coding and recruitment, have been examined extensively through isometric (fixed muscle length) contractions (Enoka & Fuglevand, 2001). In order to produce muscular force, motor units are first recruited to fire according to the size principle (Henneman, 1957) which suggests that recruitment order is determined by neuron soma size, with smaller somas being recruited before larger ones. Motor units are thought to begin firing at a frequency in the range of 5 - 10 Hz and, as the force demands of the task increase, firing rate is increased to enhance the degree of twitch summation in the motor unit (Figure 1), and its contribution to total muscle tension (Enoka, 2006). Stimulated muscle experiments demonstrate that the tension response to increasing frequency of stimulation rises and then tension plateaus as the tetanus becomes fully fused (Figure 1), creating a sigmoidal force-frequency profile (Enoka, 2002). Our understanding of voluntary neuromuscular control at higher forces is more ambiguous, and likely more complicated due to asynchronous activation of motor units and the interplay between changes in recruitment and rate coding. Two proposed control schemes predominate the literature: the onion skin control schema and the afterhyperpolarization control schema. The onion skin schema suggests that units recruited early will attain higher peak firing rates than ones recruited later (De Luca & Hostage, 2010), and the afterhyperpolarization schema suggests the opposite (a positive relationship between recruitment threshold and peak discharge rate) (Enoka, 2002). Less is known about MU control strategies during dynamic muscle contractions, despite their high relevance to daily human function (Douglas et al., 2016; Duchateau & Baudry, 2014; Duchateau & Enoka, 2016). This is related to technical limitations of recording MUs in isolation during shortening and lengthening actions.

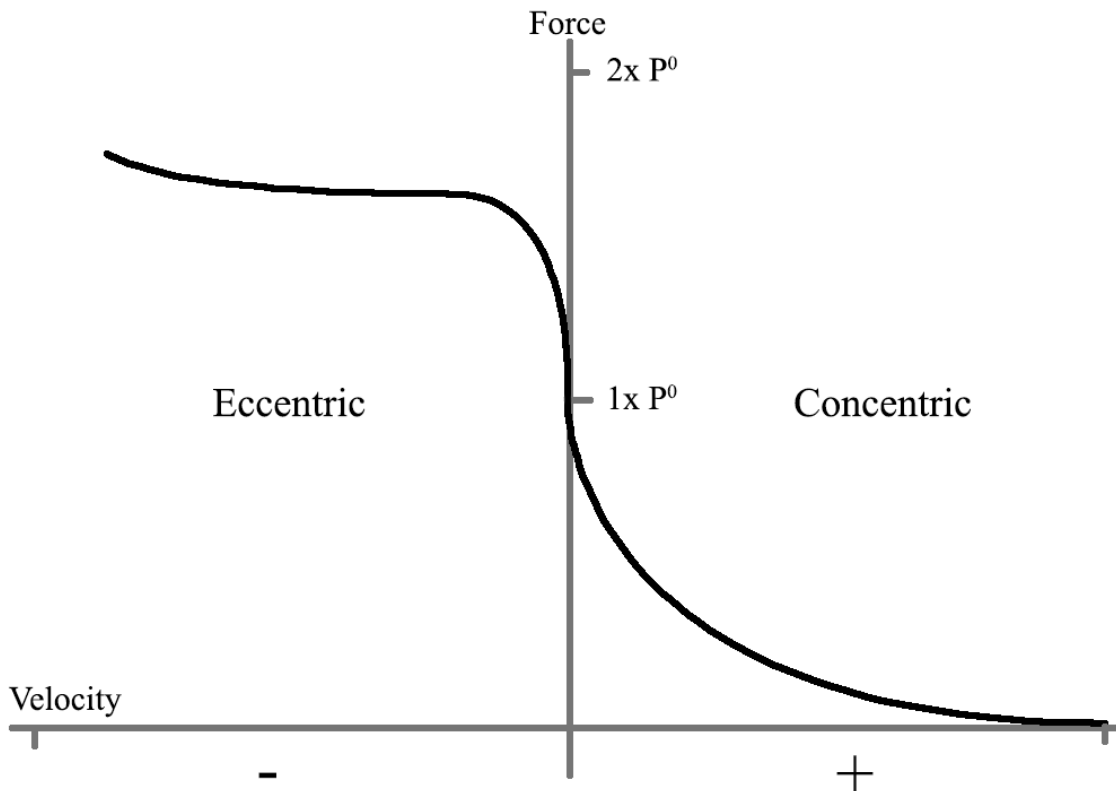


**Figure 1.** The general shape of the relationship between muscle force output and stimulation frequency.

## 1.4 Muscle Force-Velocity Curve

While producing tension, the musculotendinous unit can shorten (concentric), lengthen (eccentric), or remain a constant length (isometric) depending on the interplay between the load imposed on the joint as well as the degree of internal force produced (Figure 2). If the muscle can produce a greater opposing joint torque than the load plus the limb, the muscle will shorten, and conversely if the muscle produces a lesser opposing joint torque, it will lengthen. The foundational work of A.V. Hill using isolated muscle fibers helped to elucidate the shape of what is now termed the force-velocity curve of muscle. Hill demonstrated that as shortening velocity increased, maximum work or force decreased up to peak shortening velocity (see Figure 2) (Hill, 1938). The inverse is true for eccentric contraction, during which muscle lengthening or negative velocity contractions can produce more force than isometric or concentric actions (Figure 2) (Katz, 1939). The

same concentric force-velocity relationship has been confirmed many times in human studies, however eccentric force-velocity relations are more variable (Aagaard et al., 2000; Amiridis et al., 1996; Babault et al., 2001; Pinniger et al., 2000; Spurway et al., 2000; Valentin et al., 2012; Westing et al., 1988) as some studies *in vivo* have demonstrated that peak eccentric forces are no greater than peak isometric forces.



**Figure 2.** The generalized relationship between maximal force and contraction velocity, predicted based on single fiber experiments.  $P^0$  means peak isometric tension. Whole muscle eccentric forces do not always obtain the same degree of enhancement above peak isometric force.



## 1.5 Voluntary Activation

Voluntary activation can be defined as the ability of an individual to utilize the entirety of a muscle mass for torque production about a joint. There are several ways of measuring and estimating voluntary activation, however most of the methods involve applying a stimulated contraction during a voluntary effort and examining the resulting torque profile. A stimulus that produces a large increment in torque above a voluntary maximal effort suggests that the command issued by the brain is not sufficient to drive the full potential of the muscle (Merton, 1953). Superimposed stimulus torque is typically compared either to peak voluntary torque preceding the stimulus or to a potentiated resting twitch that is elicited after a maximal effort, producing a ratio that is meant to reflect the degree of completeness of the contraction (Merton, 1953). Typically, in healthy populations, voluntary activation measures (by percentage) are quite high (>95%) during isometric efforts in some, but not all, muscle groups (Behm et al., 2002). During dynamic muscular contraction however, there is evidence to suggest that voluntary activation may not always be complete (Aagaard et al., 2000; Altenburg et al., 2009; Amiridis et al., 1996; Babault et al., 2001; Spurway et al., 2000; Westing et al., 1990), especially during maximal eccentric contractions. This is supported by studies that often report reduced EMG during maximal eccentric contractions when compared to maximal concentric and sometimes isometric contractions (Altenburg et al., 2009; Del Valle & Thomas, 2005; Madeleine et al., 2001; Pinniger et al., 2000). It should be noted that surface EMG measures are more reflective of changes in recruitment rather than rate coding (Christie et al., 2009). Lower voluntary activation and neuromuscular activity during eccentric contraction suggest that eccentric efforts may therefore be submaximal, in relation to the peak capacity of the muscle (Figure 2). Resistance trained individuals can, however, produce eccentric efforts that are well in excess of their maximal isometric force with little to no stimulated superimposition of torque (Aagaard et al., 2000; Amiridis et al., 1996; Spurway et al., 2000).

## 1.6 Extensors of the Elbow

The elbow joint is primarily extended by the three heads of the triceps brachii (medial, lateral and long), and secondarily by the anconeus. The triceps brachii is composed of ~35% type I fibers and has a relatively fast contraction time, whereas the anconeus has a slower contraction time and a higher proportion of type I fibers (~65%) by comparison (Le Bozec & Maton, 1987). The medial head of the triceps brachii is active most frequently during elbow extension, followed by the lateral head (Travill, 1962). The long head tends to be the least active during low intensity elbow extension, perhaps because it crosses the glenohumeral joint as well as the elbow (Travill, 1962). Anconeus activity is most coherent with the medial head of the triceps brachii during elbow extensions (Travill, 1962), however its contribution to extension torque is no greater than 15% (Zhang & Nuber, 2000). Anconeus fascicles experience less absolute length change during shortening, than other muscles, however the length change is similar to other muscles, relative to its size. In addition it is only estimated to be composed of between 25 - 60 MUs (Stevens et al., 2014). It is thought that the combination of a less complex electrophysiological signal, due to small numbers of MUs, along with reduced fascicle shortening helps to produce an exceptional signal-to-noise ratio while recording trains of action potentials. Recently it has been demonstrated that action potentials can be recorded clearly during ballistic concentric contractions approaching maximal shortening velocity ( $V_{max}$ ) in the anconeus (Cowling et al., 2016; Harwood et al., 2011, 2012, 2014), and investigations of double discharges, altered recruitment thresholds and dynamic fatigue have so far been completed in this muscle. Results from these studies indicate that the anconeus is functionally similar to other limb muscles and therefore provides a useful neuromuscular model to study MU properties during dynamic contraction paradigms.

## 1.7 Purpose & Hypotheses

The purpose of this thesis is to take advantage of unique properties of the human anconeus muscle to examine the firing behaviour of single MUs during high intensity eccentric contractions, and to compare the frequency of firing to isometric contraction at the same absolute torque. Secondly, surface EMG signals from the triceps brachii will

be analyzed to determine whether a similar pattern of neuromuscular activity is found in the predominant extensor muscles of the elbow. Using the anconeus muscle as a proxy to gain insight into neuromuscular control of the elbow extensor group, it is hypothesized that MU discharge rate will be reduced during eccentric contraction, in relation to isometric discharge rate. Secondly, surface EMG amplitude will be less during the eccentric phase of contraction compared to the isometric phase. The force-velocity relationship suggests that eccentric contractions are submaximal when matched to an isometric torque, therefore to maintain a fixed mechanical output (torque), MU firing frequency and sEMG amplitude will be less during muscle lengthening.

## Chapter 2

### 2 Introduction

The capacity of a muscle to develop tension is largely dependent on the mode of contraction. Muscle force capacity is reduced when it is required to shorten (Beltman et al., 2004; Tesch et al., 1990; Thorstensson et al., 1976). Further, peak concentric force is negatively related to shortening velocity (Hageman et al., 1988; Thorstensson et al., 1976; Westing et al., 1990), and the reduced peak tension during shortening is accompanied by an increased metabolic cost of muscular contraction (Bigland-Ritchie & Woods, 1976; Ortega et al., 2015) and increased electromyogram (EMG) activity, particularly at high velocities (Aagaard et al., 2000; Tesch et al., 1990). This concentric (positive) force-velocity relationship has been well-described, however the functional implications and neural correlates of the negative (lengthening) portion of the force-velocity curve are less well understood. Studies of animal muscle, and muscle fibre function *in vitro* have demonstrated 50 - 80% greater peak tension during stimulated lengthening contractions (Figure 2) (Edman, 1988; Katz, 1939). In humans, however, the production of maximal eccentric torque via the intact motor system relies not only on the capacity of the muscle, but on the ability of the central nervous system to fully excite the relevant motor neurons as well. Studies of maximal voluntary contractions have shown minimal differences between eccentric and isometric torque values in the intact system which is contrary to the single-fiber force-velocity curve (Babault et al., 2001; Pinniger et al., 2000; Westing et al., 1988); however twitch superimposition during muscle lengthening suggests that voluntary activation can be incomplete (Altenburg et al., 2009; Babault et al., 2001). Some postulate that inhibition of maximal voluntary drive to muscles such as the quadriceps femoris during strong eccentric contraction may protect against injury (Amiridis et al., 1996; Del Valle & Thomas, 2005; Westing et al., 1990, 1991). Further, this deficit in eccentric voluntary activation can be abolished through resistance training (Aagaard et al., 2000; Amiridis et al., 1996; Spurway et al., 2000). It has also been suggested that contraction mode-dependent differences in the voluntary activation of a muscle during maximal eccentric, concentric and isometric contraction may be joint angle-dependent (Valentin et al., 2012). The metabolic demand of the muscle, or ATP

cost, is also lower during eccentric contraction when compared to isometric contraction (Ortega et al., 2015). This lower energy consumption is likely related to the passive viscoelasticity of muscle tissue, which reduces the need for actively generated cross-bridge tension (Herzog, 2014). The lesser energy requirements and greater torque-producing capacity of eccentric muscle contraction are thus reflected in the electromyogram, which becomes smaller during lengthening in comparison to velocity-matched concentric actions (Amiridis et al., 1996; Westing et al., 1991) and isometric contractions (Del Valle & Thomas, 2005) at a similar absolute torque.

Studies of individual motor unit behaviour have consistently demonstrated reduced MU firing rates (MUFRRs) during eccentric contraction when compared to concentric contraction (Altenburg et al., 2009; Del Valle & Thomas, 2005; Kallio et al., 2013; Kossev & Christova, 1998; Pasquet et al., 2006; Sogaard et al., 1996; Tax et al., 1989). The greatest differences in discharge rate are usually observed at shorter muscle lengths, specifically when the muscle is required to shorten in a mechanically disadvantaged range (Pasquet et al., 2006). Comparing discharge frequency of MUs during eccentric and isometric contraction reveals a very modest decrease in discharge behaviour during muscle lengthening in most studies (Howell et al., 1995; Kossev & Christova, 1998; Linnamo et al., 2003; Sogaard et al., 1996; Tax et al., 1989), while a few select experiments report equivocal results, particularly at low force levels (Kallio et al., 2013; Pasquet et al., 2006). Technical limitations of fine-wire single MU electromyography often restrict dynamic measures of single MU discharge to weaker contraction intensities and small ranges of joint excursion that may be less likely to induce muscle fascicle stretch. A study by Del Valle and Thomas (2005) compared motor unit firing behaviour during maximal eccentric contractions with maximal shortening and isometric contractions. Discharge frequencies of motor units that were sampled during muscle lengthening were significantly lower than motor units sampled during shortening or isometric contractions, however the tungsten microelectrode technique precluded the experimenters from tracking the same motor units throughout all contraction modes consistently.

Despite the technical challenges associated with recording single MUs during dynamic contractions, the anconeus (an accessory elbow extensor muscle) has proven to be a useful model during high velocity concentric contractions over a large range of elbow joint angles (Cowling et al., 2016; Harwood et al., 2011, 2012, 2014). The purpose of this experiment was to record single MU activity from the anconeus during strong (>50% MVC) eccentric contractions of the elbow extensors over a large range of motion. It was hypothesized that MU discharge rates would decrease during eccentric movement for the production of a given absolute torque, in comparison to isometric contractions. Reduced MU firing rates during eccentric contraction would reflect the improvement in neuromechanical coupling that is observed during muscle lengthening. The anconeus provides a unique opportunity to track single MUs during strong contractions over a large range of motion. This muscle will help to describe the degree of change in individual MU rates between task modes.

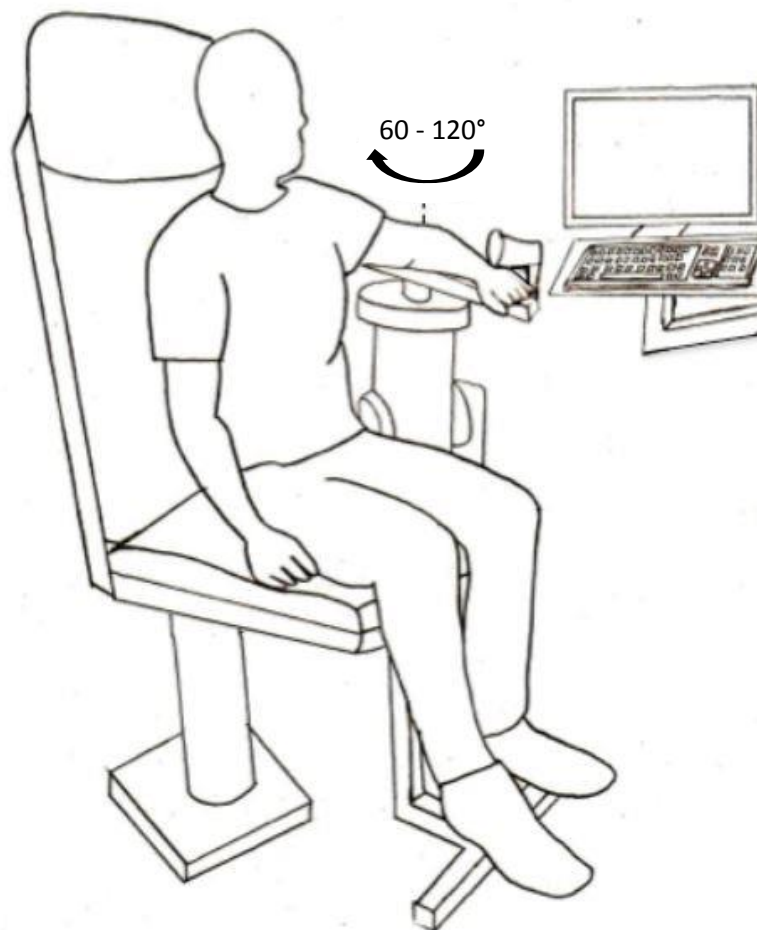
## Chapter 3

### 3 Methods

#### 3.1 Experimental Set-up

Eight recreationally active male participants, mean age of 23 years, were tested for elbow extensor strength and anconeus MU properties during 1 - 3 experimental sessions, each separated by at least 72 hours. The procedures were approved by the local institutional Research Ethics Board for human subjects. Participants provided written and verbal informed consent prior to beginning the protocol.

Participants were seated upright on a Humac-Norm dynamometer (CSMi Medical Solutions, Stoughton, MA; research toolkit software), with hip and knee joints positioned at approximately 90 degrees. A waist belt with shoulder straps restrained the participant's axial skeleton to mitigate unwanted movement during elbow extensor contractions (Figure 3). All electromyography and dynamometry was performed on the left arm; however hand dominance was not recorded. The shoulder was abducted to roughly 85° and slightly flexed in the transverse plane. Once the participant's elbow had been flexed to approximately 90°, the medial epicondyle of the elbow joint was aligned with the axis of rotation of the dynamometer arm. The participant's forearm rested comfortably on a foam pad attached to the dynamometer arm, and the hand was fixed securely to a hand brace using tensor bandages (Figure 3). During elbow extensor contractions, the forearm was also secured to the dynamometer arm tightly by a Velcro strap, in order to eliminate translation of the elbow joint away from its intended axis of rotation. The dynamometer was set to allow a range of motion (ROM) of 60°, spanning from 60 to 120° of elbow extension (180° being full extension), for each participant (Figure 3). Two muscle stimulation pads were constructed using aluminum foil and conductive electrode gel enclosed in a fold of paper towel. The anode and cathode were applied to the proximal and distal ends of the belly of the triceps brachii muscle, respectively. The pads were secured tightly with flexible wrap material to maintain the position of each pole during dynamometry.



**Figure 3.** A rough schematic of the experimental set-up, with a participant seated and arm resting on the dynamometer, modified from Cowling et al. (2016).

### 3.2 Strength

Participants performed a series of 2 - 3 isometric elbow extensor maximal voluntary contraction (MVC) attempts at an elbow joint angle of  $120^\circ$  in order to determine a maximal torque output. Although  $120^\circ$  is perhaps suboptimal for production of maximal elbow extension torque, measures were made at this joint angle to be able to compare single MU activity at a constant absolute torque. Instructions were given to activate only the elbow extensors, and to try to minimize the use of other musculature. The higher of two MVC attempts that were within 5% of each other was taken as the maximum value. A modified interpolated twitch technique (ITT) was performed in order to measure voluntary activation (VA). Double pulse (doublet) stimulations at 100 Hz, with a  $200 \mu\text{s}$



pulse width, were delivered to the triceps brachii using a constant-voltage stimulator (DS7AH; Digitimer, Ltd., Welwyn Garden City, Hertfordshire, UK). Amperage was increased in a stepwise manner until the paired pulses generated a plateau in torque without activation of the antagonists as determined by a decrease in torque. Pulses were delivered before, at the peak of, and directly following an MVC attempt, and superimposed pulses were compared to potentiated pulses to produce an estimate of voluntary activation using the following formula (Cowling et al., 2016; Merton, 1953):

$$\text{Voluntary Activation (VA\%)} = \left(1 - \frac{\text{superimposed doublet}}{\text{potentiated doublet}}\right) * 100$$

### 3.3 Lengthening Protocol

After a maximal torque value was obtained, target cursors were calculated and displayed on-screen at 50, 75, and 100% of MVC obtained at the extended joint position. Using visual torque feedback displayed live on a monitor (Figure 3), participants were asked to produce an initial isometric contraction of ~2 seconds duration, at 120° elbow extension, that matched one of the target torque values, and subsequently to maintain a constant joint torque output while movement of the dynamometer arm at 10°/s induced a lengthening of the elbow extensors. After the elbow joint reached its final position of 60° flexion, participants maintained a second isometric contraction for ~2 seconds. The order of contraction levels was pseudo-randomly chosen depending on the quality of the motor unit recordings. Participants were given a minimum of 3 minutes of rest in between lengthening contractions to prevent muscular fatigue. Contractions were repeated within each session until either recordings of satisfactory quality were obtained, or the participant began to show signs of fatigue, such as a reduction in the 100% MVC torque or reduced torque steadiness.

### 3.4 Electromyography

To obtain single MU recordings from the anconeus, intramuscular EMG signals were collected during all contractions using a pair of custom-made, bipolar, fine-wire electrodes. Each electrode consisted of a pair of ~100 µm diameter, Formvar-insulated stainless steel wires which were threaded through the cannula of a 25G x 5/8 inch

hypodermic needle (Becton Dickinson, Franklin Lakes, NJ). Wire ends were folded over the tip of the needle to form small hooks, and the electrodes were autoclaved prior to insertion. Hooked wire ends were clipped to a length of several (~2) millimetres and prepared in order to be as selective as possible for the recording of single MUs. The skin over the anconeus was cleansed thoroughly with 70% ethanol, and the hypodermic needle was inserted into the muscle belly. Carefully withdrawing the needle left the hooked wire ends embedded in the muscle tissue. Ground electrodes for the intramuscular EMG channels were placed on the styloid processes of the wrist, and ground leads were restrained at the wrist using tensor bandage. Several moderate-intensity, concentric, isotonic elbow extensions were performed in order to check signal fidelity and to help settle the wire hooks into the muscle.

For a subset of participants, surface electrodes were applied to record gross neuromuscular activity of the triceps brachii during isometric and lengthening contractions. The skin between the stimulation pads was cleansed with 70% ethanol and cloth surface electrodes (Kendall H59P, Covidien, Mansfield USA) were arranged in a bipolar manner according to the direction of muscle fibers mid-way over the muscle bellies of the lateral and long head of the triceps brachii, and electrode leads were taped to the arm to minimize movement artifact during lengthening contractions.

### 3.5 Signal Processing & Analysis

EMG signals were amplified by 1000x and high-pass filtered at 10 Hz (NL824, Digitimer Ltd., Welwyn Garden City, Hertfordshire, UK) to attenuate low frequency noise such as movement artefact. EMG Signals also passed through a 10 KHz low-pass filter before being sampled using an A/D board (Power1401, CED, Cambridge UK) at 12.5 KHz and 2500 Hz respectively, for intramuscular and surface signals. Torque was sampled at 500 Hz. Both torque and EMG signals were collected using Spike2 (v 7.16, CED, Cambridge, UK) software, and stored offline for analysis.

Waveform analysis was performed in Spike2 to verify that a given train of action potentials originated from a single MU (MU action potential, MUAP). Individual waveforms that met an amplitude threshold were sorted into templates based on

waveform shape, and superimposed to ensure similarity (see Figure 4). Non-physiological interspike intervals (ISIs) and doublets (outside of a range of 25 - 150 ms) were excluded from calculation of MU firing rates. Once a train of potentials was confidently established, raw ISI values were computed on a spike-by-spike basis for the entire train. Associated instantaneous torque and position data were also computed for each spike and these measures for each contraction were stored in separate tables in Excel. The reciprocal of each raw ISI was taken as the instantaneous frequency. Raw limb position data were manipulated within each contraction using a constant adjustment factor to express position in terms of the 60 - 120° range. For the calculation of mean MU frequency during contraction, samples were selected using position data as a means for identifying contraction mode (isometric vs eccentric), and the average value of the ISI reciprocal, as well as the average torque, was computed and stored. The benefit of MU tracking in this experiment was the opportunity to calculate mean frequency using a relatively large sample of ISIs (Figure 4). It has been suggested that under some conditions, sample sizes of 20 - 50 ISIs are required to approximate, within  $\pm 10\%$ , the true population mean in 95% of samples taken (Clamann, 1969). As a consequence, effort was made to calculate MU firing rate means using samples of 25 ISIs at minimum.

Gross triceps brachii activation was evaluated by calculating triceps mean root-mean square (RMS) amplitude, normalized to RMS amplitude at MVC (collected at 120°). Mean RMS amplitude was sampled over a 0.25 s time epoch during isometric contraction at 120°, as well as during eccentric movement at a joint angle corresponding to a short muscle length to mitigate the effect of signal non-stationarity on sEMG measures.

### 3.6 Statistical Analysis

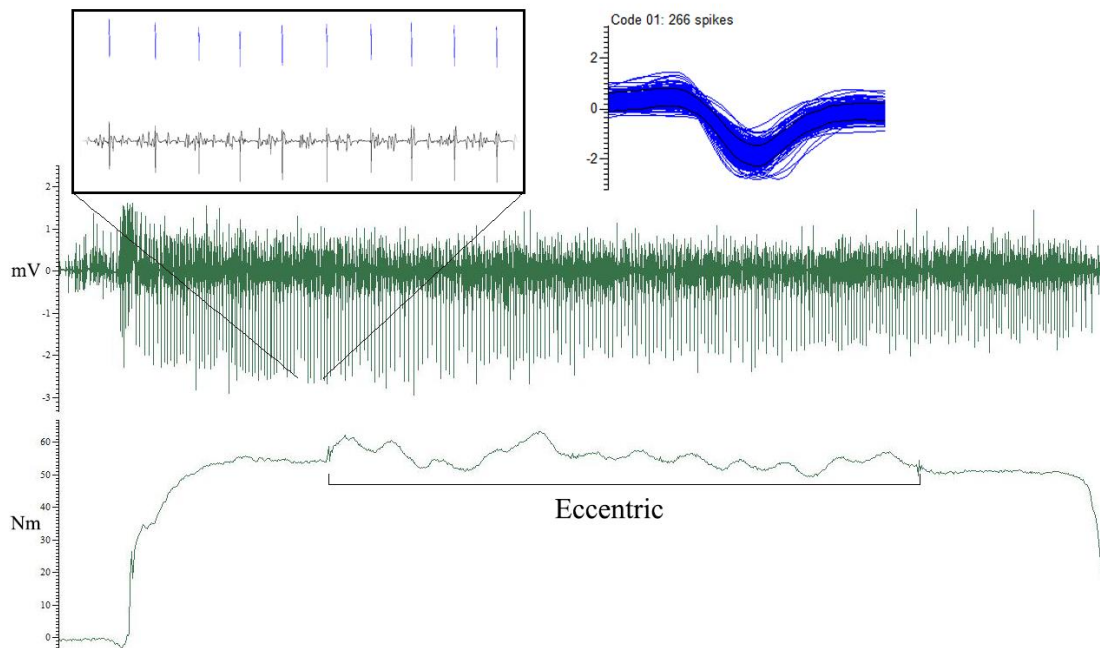
Paired t-tests were performed using SPSS Statistics 24.0 (IBM, Armonk, NY) to assess differences in mean motor unit discharge rates between isometric and eccentric contraction phases. Firing behaviour of some motor units was observed at multiple intensity levels, so paired t-tests were performed for each individual contraction intensity (50, 75 and 100% MVC) in order to avoid assigning a heavier weighting to the behaviour of a single unit in the statistical analysis. A separate paired t-test analysis was performed to compare mean torque values during isometric and eccentric contraction modes. Paired

t-tests were also conducted to assess changes in mean RMS amplitude values, from a subset of participants (some of whom single MU data was not successfully collected from), in order to examine patterns of neuromuscular activity of the triceps brachii during the muscle lengthening protocol. The long and lateral heads of the triceps group were assessed independently, at each contraction intensity level. A significance level of  $\alpha < 0.05$  was set for MUFR, torque and RMS amplitude analyses, and values are reported as mean  $\pm$  standard deviation (SD).

## Chapter 4

### 4 Results

Viable surface or intramuscular EMG data was collected from a total of 8 participants, and adequate MU spike trains were obtained from 5 out of 8. Intramuscular electrode instability and selectivity made data collection from single motor units exceptionally difficult. Mean MVC torque of the elbow extensor group was  $62.4 \text{ Nm} \pm 12.7$  and mean voluntary activation for all 8 subjects was  $96.6\% \pm 2.56$ . Force tracking proved to be challenging for most participants during these slow, relatively strong contractions and force variability often resulted in discharge variability (Figure 4). Eccentric forces tended to be larger on average than the corresponding isometric force at contraction onset.



**Figure 4.** Raw data showing a torque tracing (bottom) from a maximal contraction, with associated raw intramuscular EMG (middle), as well as isolated spike train (top). Spikes superimposed to show similarity in MUAP shape.

#### 4.1 RMS EMG

RMS amplitude (normalized to RMS amplitude at MVC) was recorded from the two superficial heads of the triceps brachii to assess whether triceps and anconeus EMG

signals were following similar patterns during the lengthening contraction protocol. Surface EMG data were collected from four individuals, at all three contractile intensities, who provided adequate force tracking during the experiment. Satisfactory single MU recordings were found in only one of these four individuals.

In the lateral and long heads of the triceps brachii respectively, mean normalized isometric RMS values were  $0.55 \pm 0.03$  and  $0.51 \pm 0.14$  during contractions targeting 50% MVC,  $0.76 \pm 0.07$  and  $0.72 \pm 0.12$  during contractions targeting 75% MVC, and  $0.93 \pm 0.12$  and  $0.92 \pm 0.16$  during contractions targeting 100% MVC. Normalized mean RMS EMG values in the long head of the triceps brachii did not significantly differ between the isometric and eccentric phases of each movement at any contraction intensity ( $p = 0.108$ ,  $p = 0.111$ ,  $p = 0.121$  at 50, 75, and 100% MVC, respectively), however the mean eccentric RMS amplitude value was always non-significantly lower than the mean isometric value, across all intensities. Normalized mean RMS EMG values in the lateral head of the triceps brachii were indeed significantly lower during the eccentric phase of contraction at 50 and 75% target intensities ( $p = 0.004$  at 50%, and  $p = 0.031$  at 75%), however not at the 100% target ( $p = 0.133$ ). Mean RMS EMG values from both isometric and eccentric contraction phases, at all intensities, are summarized in Table 1.

**Table 1.** Mean RMS amplitude from the lateral and long heads of the triceps brachii, during isometric and eccentric phases of contraction, at three different intensities.

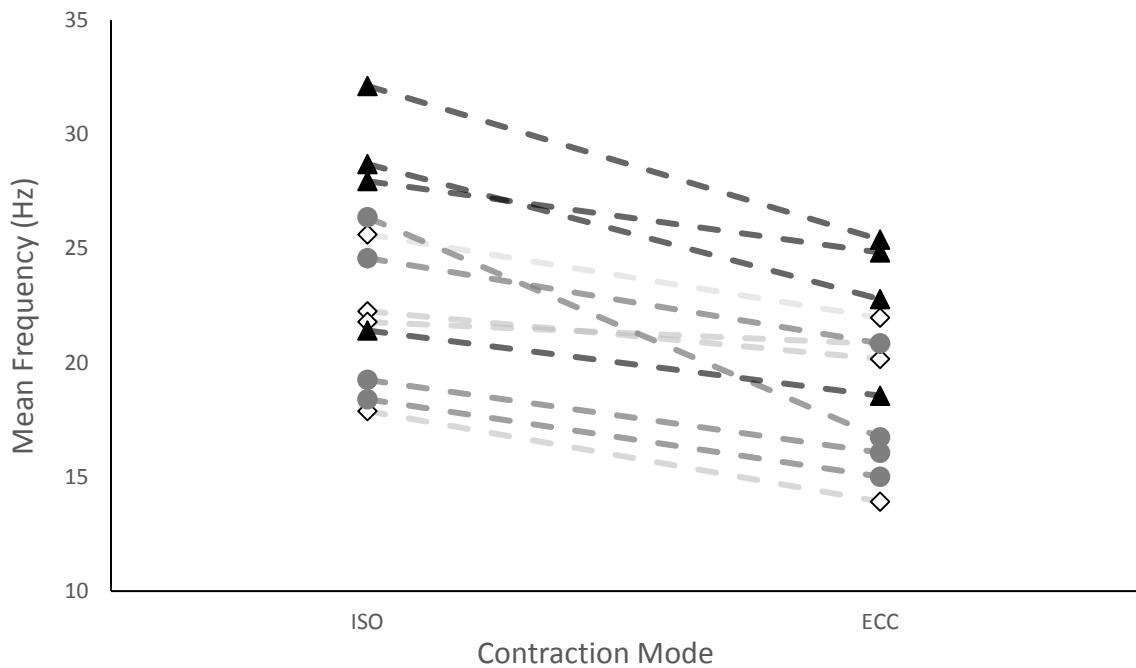
	50%		75%		100%	
	ISO	ECC	ISO	ECC	ISO	ECC
Lat sEMG (%)	0.55	0.45*	0.76	0.63*	0.93	0.82
Long sEMG (%)	0.51	0.45	0.72	0.60	0.92	0.76
Rel. Torque (Nm)	0.51	0.52	0.76	0.76	1.02	1.01
Joint Position (°)	120.3	109.7	120.8	110.2	121.1	109.9

\* denotes significant change ( $p < 0.05$ ) between paired ISO and ECC values, at each intensity. Lat represents the lateral head of the triceps brachii and Long represents the long head. ISO is the isometric phase of movement and ECC is the eccentric phase.

## 4.2 Single MU Discharge

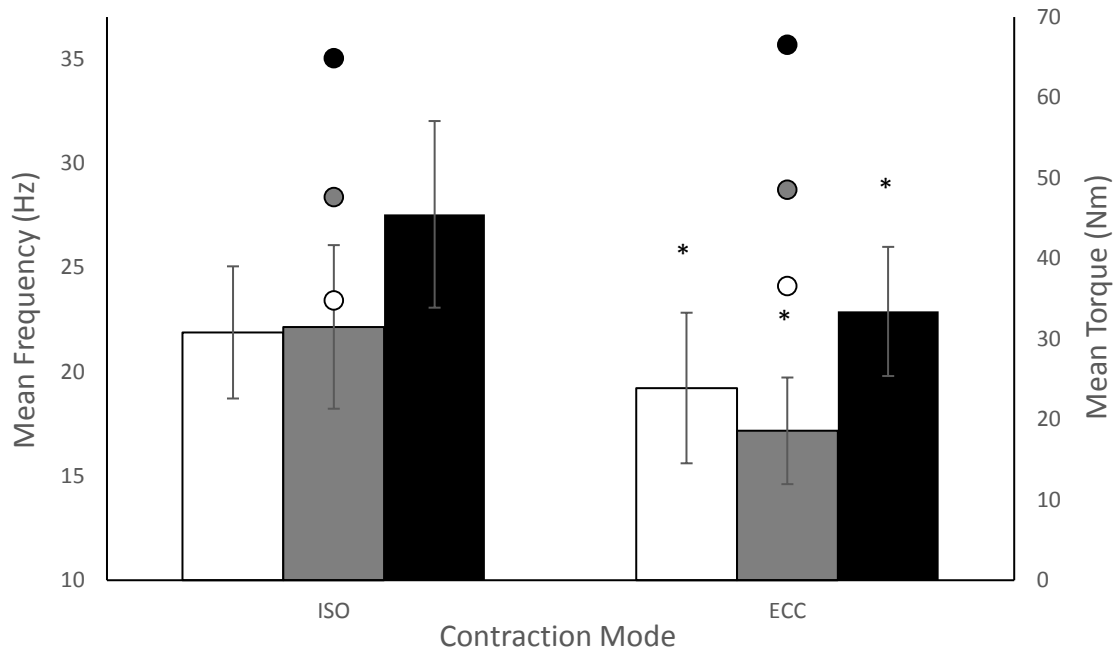
Twelve spike train recordings from 7 unique MUs were obtained from 5 out of the 8 participants (Figure 5). Some MUs were identified only at one contraction intensity, whereas others were identified at multiple relative torque targets. Spike train lengths ranged from a minimum of 110 ISIs to 265 ISIs within a given contraction, and though some spike trains did not extend throughout the full duration of the contraction, all trains were visible during the initial isometric contraction as well as the first ~40 degrees of ROM, at minimum. The mean number of ISIs sampled from a given train was 34, and the minimum was 20. The number of ISIs that were sampled from a single MU recording was always the same under both isometric and eccentric conditions. Mean isometric MU discharge rates measured at 120° were  $22.0 \pm 3.2$ ,  $22.1 \pm 3.9$  and  $27.5 \pm 4.5$  Hz at 50, 75 and 100% MVC, respectively (Figure 6). Mean discharge rates were significantly reduced during the eccentric phase of movement at 50% ( $p = 0.017$ ,  $df = 3$ ), 75% ( $p = 0.049$ ,  $df = 3$ ) and 100% ( $p = 0.018$ ,  $df = 3$ ) contraction intensity (Figure 5). Mean differences

between isometric and eccentric firing rates were 2.8 (95% CI = 0.95 - 4.68 Hz), 5.0 (95% CI = 0.04 - 9.93 Hz), and 4.7 (95% CI = 1.54 - 7.77 Hz) Hz at 50, 75 and 100% MVC, respectively. Additionally, there were no significant differences between isometric and eccentric torque values at 50, 75 or 100% contraction intensity ( $p = 0.09$ ,  $p = 0.23$ ,  $p = 0.062$ ), however the mean eccentric torque was on average 3.2% higher than the isometric torque sampled (Figure 6), indicating an improvement in neuromechanical coupling.



**Figure 5.** Mean MUFR sampled from each MU recording, during each contraction phase (ISO, isometric; ECC, eccentric). Open diamonds represent 50%, solid circles represent 75% and black triangles represent 100% MVC. Mean MUFR at each intensity level was significantly reduced during ECC from ISO.





**Figure 6.** Mean MUFR (bars) by contraction intensity, plotted with mean associated torque (dots) data, between two contraction modes. White represents 50%, gray represents 75% and black represents 100% MVC. \* denotes significant difference ( $p < 0.05$ ) from isometric MUFR value. SD bars are displayed for MUFR.

## Chapter 5

### 5 Discussion

The intent of this work was to verify the current understanding of eccentric motor control at high contraction intensities, using the anconeus to complement past work exploring motor unit discharge properties under concentric conditions (Cowling et al., 2016; Harwood et al., 2011, 2012, 2014). It was demonstrated that single MU firing behaviour could be tracked across large ranges of motion during high force eccentric contraction in the anconeus. Prior to this experiment, high force (>50% MVC) eccentric motor unit behaviour had only been observed through random population sampling via tungsten microelectrode, which generally precluded the continuous recording of the same MU under different contraction conditions (Del Valle & Thomas, 2005). The main finding in this thesis was that discharge rates during muscle lengthening were significantly reduced compared to isometric discharge rates preceding lengthening. Although this had been suggested by previous literature (Altenburg et al., 2009; Del Valle & Thomas, 2005; Howell et al., 1995; Kallio et al., 2013; Kossev & Christova, 1998; Linnamo et al., 2003; Pasquet et al., 2006; Tax et al., 1989) those studies were not done at high contraction intensities. Secondly, mean RMS EMG amplitude was shown to be significantly reduced in the lateral head of the triceps brachii during the eccentric phase of the muscle lengthening protocol, at 50 and 75% of maximal effort, however not at 100%. Mean RMS EMG amplitude did not significantly differ between isometric and eccentric phases in the long head of the triceps brachii.

In addition to exploring these features during high force contractions, another strength of this study was the relatively large number of potentials used for the calculation of MUFRR during different contraction phases, especially when compared with past studies. It has been proposed that the recommended minimum sample of 4 ISIs for the calculation of discharge rate may be inadequate (Clamann, 1969), thus a minimum sample size of 20 ISIs used in this study allows for a more accurate approximation of the true population mean.

## 5.1 Elbow Extensor Force Characteristics

The anconeus has proven to be a useful model for improving our understanding of neuromuscular physiology under dynamic contraction conditions (Cowling et al., 2016; Harwood et al., 2011, 2012, 2014). This small, predominantly slow (~63%) twitch muscle mainly assists the medial, lateral and long heads of the triceps brachii in extending and stabilizing the elbow joint (Le Bozec & Maton, 1987; Travill, 1962). It is estimated that the anconeus contributes perhaps as much as 15% of total isometric elbow extensor torque (Zhang & Nuber, 2000). Importantly, Harwood et al. (2011) demonstrated that mean MU firing rates in the anconeus increased in a bilinear manner up to maximal extension velocity, with mean discharge rates ranging from ~19 Hz at a modest velocity to 39 Hz at maximum velocity. With the anconeus contributing modest joint torques throughout a full range of elbow extension, attaining relatively high discharge rates during high force and velocity contractions (Harwood et al., 2011), and displaying many key characteristics of neuromodulatory control of force such as task-dependent recruitment thresholds (Harwood & Rice, 2012) and double discharges (Harwood & Rice, 2014), the muscle is a useful proxy for dynamic neuromuscular studies of the elbow extensor group.

The mean elbow extension MVC torque observed in this study was  $62.4 \pm 12.7$  Nm, which is quite comparable to other reports of elbow extensor torque capacity (Cowling et al., 2016; Fukunaga et al., 2001; Harwood et al., 2011; Terzis et al., 2003). Mean VA was  $96.6 \pm 2.5\%$ . Other reports of voluntary activation using the interpolated twitch technique in the triceps brachii produced values ranging from ~93% to ~99% (Bilodeau, 2006; Cowling et al., 2016). Despite selecting a non-optimal joint angle (120° elbow extension) for the production of maximum extension torque in the current experiment, mean elbow extensor VA was comparable to prior reports. Force tracking often required some familiarization within the first few contractions, especially at the transition from isometric force production to eccentric movement. The example contraction in Figure 4 demonstrates the inherent variability in force tracking during intense contractions. Initiation of muscle stretch often caused a peak in joint torque in those unaccustomed to the lengthening protocol, likely due to the improved intrinsic force capacity of muscle

fibers that undergo stretch (Edman et al., 1978; Herzog, 2014; Katz, 1939; Morgan et al., 2000). In cases where force tracking was not adequate, net elbow extension torque was often slightly higher (~3%) than the target torque which speaks to the submaximality of eccentric contraction (Aagaard et al., 2000; Amiridis et al., 1996; Herzog, 2014)

## 5.2 Motor Unit Behaviour

The major finding of the current experiment was a reduction in mean motor unit discharge rate accompanying the transition from isometric to eccentric high-torque muscular effort. Isometric motor unit firing rate ranges of the anconeus reported here (17.8 – 32.1 Hz) display a similar range to isometric rates from prior study of the anconeus (7.6 – 36.0 Hz) (Harwood et al., 2011) when accounting for the range of relative forces examined in each experiment.

Foundational work on the muscle force-velocity relation (Hill, 1938; Katz, 1939) suggest that the capacity of muscle to generate force while shortening is less than its peak isometric tension, and conversely, its capacity is greater during lengthening (Figure 2). The common rationalization for this eccentric phenomenon involves passive, viscoelastic, “spring-like” elements in muscle tissue, such as the large sarcomeric protein, titin, which produces non-cross-bridge tension during sarcomere or muscle lengthening (Herzog, 2014). Greater peak muscle tension under eccentric conditions compared to isometric conditions (Aagaard et al., 2000; Amiridis et al., 1996; Katz, 1939; Spurway et al., 2000) means that maximal isometric activation of a motor unit perhaps becomes submaximal if the muscle is forcibly lengthened, assuming absolute mechanical output (elbow extension torque) remains the same. This idea is supported by studies that report decreased voluntary activation (Altenburg et al., 2009; Babault et al., 2001), lesser amplitude sEMG signals (Altenburg et al., 2009; Del Valle & Thomas, 2005; Madeleine et al., 2001), as well as usually lower discharge rates during eccentric contraction (Altenburg et al., 2009; Del Valle & Thomas, 2005; Kossev & Christova, 1998; Tax et al., 1989).

During lengthening contractions, MUFRRs have most often been examined at low forces (typically 5 - 50% MVC), and over relatively small ranges of motion (~10 - 20°) (Altenburg et al., 2009; Howell et al., 1995; Kallio et al., 2013; Kossev & Christova,

1998; Pasquet et al., 2006; Tax et al., 1989), because dynamic intramuscular EMG measures tend to be very susceptible to signal non-stationarity and interference at high activation levels. Unfortunately, some studies of dynamic motor control do not report mean isometric values or make direct comparisons between isometric and eccentric rates (Howell et al., 1995; Kossev & Christova, 1998; Tax et al., 1989), as the focus is usually a comparison between eccentric and concentric tasks. Although not explicitly calculated in their paper, the difference in mean MU discharge rates reported during isometric and eccentric contractions in one study appeared to be 0.9 Hz, at an eccentric velocity of 10°/s, in the biceps brachii (Sogaard et al., 1996). Another study found a significant reduction in eccentric discharge rates compared to isometric at 40% MVC, however not at 10 or 20% MVC (Kallio et al., 2013). Upon examination of their tabulated data, the decrease between condition means was 1.5 Hz, however the load used for the experiment was inertial and velocity was controlled by the participant. Yet another study found a slight, but statistically significant, increase in discharge rate during eccentric contraction, where MU firing was found to be between 6 - 15% higher on average compared to control isometric discharge rates in the tibialis anterior (TA) (Pasquet et al., 2006). This study, however, employed a different strategy for controlling mechanical output of the TA by instructing participants to gradually increase joint torque over the duration of the eccentric contraction, to account for a joint angle-dependent change in peak isometric torque at the ankle. Such a protocol makes direct comparison of the study by Pasquet et al. (2006) to other literature difficult. In the quadriceps, single MU discharge rates during isometric contractions that were performed at an intensity that was adjusted to approximate the level of activation during eccentric contraction were significantly lower than non-adjusted isometric contractions (Altenburg et al., 2009). Furthermore, no statistical differences were identified between the intensity-adjusted proxy isometric contraction and its associated eccentric contraction (matched for activation, not torque) (Altenburg et al., 2009). Although the experimental design in Altenburg et al. (2009) did not directly assess MU firing rate differences between isometric and torque-matched eccentric contractions, the results of the study suggest that the differences between contraction modes are due exclusively to differences in relative torque capacity between isometric and eccentric contractions. One important aspect of the study was that MU

discharge behaviour was recorded at a mean intensity of  $\sim 21 \pm 17.6\%$  (mean  $\pm$  SD) MVC, however Altenburg et al. (2009) report a range of up to 76% MVC maximally. The absolute decrease in frequency was calculated from data reported, and the difference between mean isometric and eccentric discharge rate values was  $\sim 1.4$  Hz which is comparable to decreases observed in other experiments at relatively low contraction intensities (Altenburg et al., 2009). Lastly, investigation of maximal firing rates in motor unit pools of the triceps brachii revealed no statistically significant differences between relative intensity-matched concentric and isometric contractions, but a significant reduction in eccentric firing rate from the concentric condition was reported (Del Valle & Thomas, 2005). Using tabular values reported by Del Valle and Thomas (2005), differences between mean isometric and eccentric discharge rate values at 25, 50, 75 and 100% MVC were  $\sim 1.8, 5.2, 2.1$  and  $7.5$  Hz respectively. These differences may be exaggerated, however, as the protocol used to compare concentric, eccentric and isometric motor unit properties involved normalizing dynamic muscle efforts (both concentric and eccentric) to each subject's concentric maximal effort, whereas their isometric values were normalized to a maximal isometric effort (see Figure 2 for visualization). Comparison of isometric and eccentric firing rates, therefore, becomes difficult due to force-velocity relationship differences.

In the current study of anconeus, mean reductions of 2.8, 5.0 and 4.7 Hz, at 50, 75 and 100% MVC were observed from isometric to eccentric muscle action (Figure 6), and these mean differences are greater than most differences reported previously (Altenburg et al., 2009; Kallio et al., 2013; Sogaard et al., 1996), although similar or slightly less than the differences found in the only other study conducted involving maximal joint torques (Del Valle & Thomas, 2005). It is possible that high contraction intensity and large range of motion could be related to differential reductions in MUFR, across various studies, during eccentric contraction, as it has been shown that magnitude of stretch is an important factor in inducing residual force enhancement in lengthening contractions (Herzog, 2014). Considering the somewhat sigmoidal shape of a typical isometric, stimulated force-frequency curve (Figure 1) (Thomas et al., 1991) a relative reduction in tension demand in a single MU (eg. during lengthening) would require variable reductions in MUFR depending on what portion of the curve is being examined. In the

steep initial region (low frequency, low force), MUFR variability results in comparatively large force fluctuations, whereas larger changes in MUFR are perhaps required to grade a similar amount of tension near the point of firing rate saturation (Figure 1). In the present experiment, the possibility that the initial isometric behaviour of each MU may have been influenced in some way by the intention for subsequent muscle length change, as observed in the sEMG signal of the quadriceps (Grabiner & Owings, 2002), cannot be ruled out.

### 5.3 Surface EMG

Surface EMG in the triceps brachii was recorded in order to corroborate neuromuscular findings of the anconeus with the overall activation of the primary elbow extensors during these lengthening contractions. In the current experiment, sEMG amplitude was compared between the initial isometric phase, and subsequent lengthening phase, of a single high force elbow extensor contraction. Mean RMS amplitude was significantly lower, in the lateral head of the triceps brachii only, during the eccentric contraction phase at 50 and 75% MVC, however not at 100% (Table 1). It should be noted that, in the long head, mean RMS amplitude was typically less during the eccentric contraction phase, however small sample sizes at each contraction intensity perhaps reduced statistical power, as well as at maximal force in the lateral head. Nevertheless, the reductions that were observed in the sEMG signal after the initiation of lengthening are consistent with some of the literature (Altenburg et al., 2009; Del Valle & Thomas, 2005; Madeleine et al., 2001; Pinniger et al., 2000). Inconsistencies in the findings of this study may be the result of joint angle-dependent comparisons, force normalization methods, or the presence of a preceding isometric contraction phase prior to movement.

It has been demonstrated in the quadriceps muscle group that the EMG signal during an isometric preload period prior to concentric or eccentric movement onset differed depending on the direction of the intended movement (Grabiner & Owings, 2002). In the aforementioned study, eccentric movement intention was associated with a reduction in rectified and integrated EMG (iEMG) during the isometric preload phase, compared to the iEMG preceding concentric movement. This phenomenon may offer an explanation for a lack of significance in the analysis of RMS sEMG in the triceps brachii, at least at

the greatest intensities. It is possible that, by linking the isometric and eccentric contraction phases, the intention of a subsequent lengthening movement may have influenced the myoelectric signal during the isometric preload so as to minimize changes in RMS amplitude during the transition to dynamic muscle contraction. The most relevant prior report of sEMG signals during isometric and eccentric contractions is by Del Valle et al. (2005) who reported a 27% reduction in overall triceps brachii activation during eccentric contraction, compared to a maximal isometric (and concentric) effort. The magnitude of reduction in the present study ranges from 12 - 18%, by comparison, depending on which head of the triceps brachii is examined, and at which intensity. In the current thesis, eccentric and isometric torques were matched on an absolute basis, however Del Valle et al. (2005) matched eccentric torque to concentric maximal torque in their experiment, which confounds the comparison of eccentric against isometric muscle activation. Altenburg et al. (2009) found a comparable reduction in mean RMS amplitude (18%) during maximal eccentric contraction of the knee extensors, when compared to maximal isometric contraction, however eccentric and isometric maximal torques were not significantly different. Finally, intensity-dependent statistical decreases in RMS amplitude in the lateral head, but not the long head, during muscle lengthening could be related to the greater relative contribution to elbow extension torque by the lateral head (Travill, 1962). Using intramuscular electromyography, Travill (1962) demonstrated that the anconeus and medial head of the triceps brachii were always active during elbow extension torque generation, however the long head was comparatively the least active of the elbow extensor group during modest resisted elbow extension.

Surface EMG is a poor indicator of single MU discharge behaviour, and more strongly represents MU recruitment rather than rate coding (Christie et al., 2009), however changes in mean spike amplitude and frequency (via the intramuscular spike-amplitude frequency technique) during isometric preload prior to concentric and eccentric contractions have been reported (Linnamo et al., 2003).

## 5.4 Conclusion

This thesis expands the current understanding of MU firing behaviour during dynamic contractions (Altenburg et al., 2009; Del Valle & Thomas, 2005; Kallio et al., 2013;



Sogaard et al., 1996; Tax et al., 1989) through examination of MUFRs under eccentric conditions, at torques between 50 and 100% of isometric effort. Additionally it complements previous work in the anconeus which explored MUFRs during primarily concentric actions (Cowling et al., 2016; Harwood et al., 2011, 2012, 2014) by characterizing neuromuscular behaviour in the negative portion of the force-velocity relation of muscle. It was demonstrated, using the anconeus as a proxy for the elbow extensor group, that motor unit discharge rates are reduced during eccentric elbow extensor contractions in comparison with isometric contractions matched for absolute torque, even at near-maximal mechanical output. The reduction in MUFr, despite a slight (~3%) non-significant increase in extension torque, suggests submaximal activation during eccentric contraction in relation to the maximal isometric condition, and would likely partially explain a reduction in the magnitude of the sEMG signal during lengthening. The mean MUFr differences in this study seemed slightly larger than those reported in other studies of low torque eccentric contractions (Altenburg et al., 2009; Kallio et al., 2013; Sogaard et al., 1996), although marginally smaller than the differences reported in the only other study of near-maximal eccentric MU behaviour (Del Valle & Thomas, 2005). Perhaps this is because of the distinct sigmoidal shape of the stimulated force-frequency relationship, whereby at large forces a greater reduction in firing rate may be necessary to produce the same absolute reduction in active cross-bridge tension.

## 5.5 Limitations

Although the anconeus has been established as a useful model for the study of neuromuscular function during dynamic, high velocity concentric contractions of the elbow extensors (Cowling et al., 2016; Harwood et al., 2011, 2012, 2014), limitations in study design and the electrophysiology of this thesis exist.

An argument has been made that potential joint-angle dependence of firing rate should be controlled when comparing eccentric and isometric behaviour (Altenburg et al., 2009), however additional isometric contractions at matched joint angles were not performed in this thesis. Joint angle influences the length of associated muscles, and absolute force capacity tends to vary with muscle length, according to the prototypical length-tension curve (Rassier et al., 1999), therefore it is not only important to consider the change in

relative intensity according to contraction mode (isometric vs eccentric), but additionally according to joint angle-specific force capacity. An isometric control contraction of equal length and intensity to each isometric-eccentric combination might have been used to control for time-dependent variability in MUF<sub>R</sub>, as contractions tended to last approximately 10 seconds based on experimental design, although the use of large spike samples (minimum of 20 ISIs) (Clamann, 1969) for the calculation of MUF<sub>R</sub>s helps to mitigate time-domain variability in spike frequency.

Long rest times (minimum of 3 minutes of rest between contractions) were utilized in order to avoid the influence of neuromuscular fatigue on MUF<sub>R</sub>s (Cowling et al., 2016), however fatigue was not assessed after each experimental trial so although unlikely it is possible that MUF<sub>R</sub>s could have been affected by fatiguing processes.

As previously mentioned, it is not implausible that the intention for movement subsequent to the isometric preload phase could influence MU behaviour in some way, based on evidence from surface EMG analysis (Grabiner & Owings, 2002), however surface EMG does not accurately reflect firing activity of single MUs (Christie et al., 2009), and intermediate tissue acts as a low-pass filter which can attenuate firing behaviour detected at the surface (Farina & Rainoldi, 1999). For these reasons, it would be interesting or perhaps more accurate to compare single MU firing behaviour during eccentric contractions in relation to isolated isometric contractions at exactly comparable joint angles, as well as during eccentric contractions preceded by an isometric phase.

Although there is evidence that the anconeus is active throughout a great range of elbow extension, that it varies in rate coding across a full range of contraction torques and velocities, and experiences neuromodulation via changes in recruitment threshold, double discharge behaviour, and fatigue-related MUF<sub>R</sub> changes (Cowling et al., 2016; Harwood et al., 2011, 2012, 2014) in a similar way to other conventional muscle models, it has a relatively small contribution ( $\leq 15\%$ ) to total elbow extension torque (Zhang & Nuber, 2000). Furthermore, it has a relatively slow fiber composition (Le Bozec & Maton, 1987), and may possess secondary functions in addition to elbow extension (Bergin et al., 2013) such as humero-ulnar stabilization. Additionally, anatomical properties of the anconeus such as the small MU number estimates (~25 - 60 MUs) (Stevens et al., 2014) and lesser

absolute fascicle length changes (Stevens, Smith et al., 2014) that are thought to contribute to the muscle's high intramuscular EMG signal fidelity may also be argued to limit its usefulness as a proxy for neuromuscular function of the elbow extensors.

The greatest limitation of this thesis was likely the small number of motor unit recordings examined ( $n = 12$ ), in comparison to previous studies of the anconeus (Cowling et al., 2016; Harwood et al., 2011; Harwood & Rice, 2014) as well as single MU studies conducted in other muscles (Altenburg et al., 2009; Del Valle & Thomas, 2005). Despite testing a large number of participants, electrode placement variability and instability within the muscle tissue were likely contributors to the low number of successful recording sessions. An issue that tends to affect all invasive studies of single MU behaviour is signal non-stationarity due to movement of the intramuscular electrode's recording volume through the muscle. It is assumed that the use of hooked wire ends stabilizes the electrode recording volume in relation to nearby active muscle fibers, and thus stabilizes the temporal characteristics of the action potentials originating from those muscle fibers, however when a train of spikes ends unexpectedly, it is impossible to be certain whether the unit was de-recruited or whether it simply moved out of the active recording volume.

## 5.6 Future Directions

The behaviour of MUs in the anconeus has been characterized isometrically, across the entire range of concentric velocities, throughout fatigue, and now at low eccentric velocities. Studies in the future should seek to improve recording success through technique optimization, as well as to improve existing data sets by increasing sample sizes. Exploration at high contraction velocities would be useful to assess whether the speed of stretch influences MU discharge characteristics at high torques. Additionally, tracking of MU behaviour in the anconeus throughout a full, dynamic range in both directions of motion permits detailed studies of MU behaviour under conditions where the actual movement performed may or may not align with movement intention during the planning phase. Further, elucidation of EMG changes in relation to isometric preload torque prior to dynamic movement intention at the single MU level would also be useful. This model might also help to pin-point higher level (spinal and cortical) points of

neuromodulatory control during eccentric contractions. Lastly, fatiguing eccentric contractions could be used to evaluate firing rate changes during work of relatively high neuromechanical efficiency, in comparison to concentric and isometric fatigue protocols.

## References

- Aagaard, P., Simonsen, E., Andersen, J., Magnusson, S., Halkjaer-Kristensen, J., & Dyhre-Poulsen, P. (2000). Neural inhibition during maximal eccentric and concentric quadriceps contraction: effects of resistance training. *Journal of Applied Physiology*, *89*(6), 2249–2257. <http://doi.org/10.1097/00005768-199805001-01178>
- Altenburg, T. M., de Ruyter, C. J., Verdijk, P. W. L., van Mechelen, W., & de Haan, A. (2009). Vastus lateralis surface and single motor unit electromyography during shortening, lengthening and isometric contractions corrected for mode-dependent differences in force-generating capacity. *Acta Physiologica*, *196*(3), 315–28. <http://doi.org/10.1111/j.1748-1716.2008.01941.x>
- Amiridis, I., Martin, A., Morlon, B., Martin, L., Cometti, G., Pousson, M., & Van Hoecke, J. (1996). Co-activation and tension-regulating phenomena during isokinetic knee extension in sedentary and highly skilled humans. *European Journal of Applied Physiology*, *73*(1–2), 149–156. <http://doi.org/10.1007/BF00262824>
- Babault, N., Pousson, M., Ballay, Y., & Van Hoecke, J. (2001). Activation of human quadriceps femoris during isometric, concentric, and eccentric contractions. *Journal of Applied Physiology*, *91*(6), 2628–2634.
- Behm, D. G., Whittle, J., Button, D., & Power, K. (2002). Intermuscle differences in activation. *Muscle & Nerve*, *25*(February), 236–243. <http://doi.org/10.1002/mus.10008>
- Beltman, J. G. M., Sargeant, A. J., van Mechelen, W., & de Haan, A. (2004). Voluntary activation level and muscle fiber recruitment of human quadriceps during lengthening contractions. *Journal of Applied Physiology*, *97*(2), 619–626. <http://doi.org/10.1152/jappphysiol.01202.2003>
- Bergin, M. J. G., Vicenzino, B., & Hodges, P. W. (2013). Functional differences between anatomical regions of the anconeus muscle in humans. *Journal of Electromyography and Kinesiology*, *23*(6), 1391–1397. <http://doi.org/10.1016/j.jelekin.2013.08.008>
- Bigland-Ritchie, B., & Woods, J. J. (1976). Integrated electromyogram and oxygen

- uptake during positive and negative work. *Journal of Physiology*, 260(2), 267–77.  
<http://doi.org/10.1113/jphysiol.1976.sp011515>
- Bilodeau, M. (2006). Central fatigue in continuous and intermittent contractions of triceps brachii. *Muscle & Nerve*, 34(2), 205–213. <http://doi.org/10.1002/mus.20572>
- Christie, A., Inglis, J. G., Kamen, G., & Gabriel, D. A. (2009). Relationships between surface EMG variables and motor unit firing rates. *European Journal of Applied Physiology*, 107(2), 177–185. <http://doi.org/10.1007/s00421-009-1113-7>
- Clamann, H. P. (1969). Statistical analysis of motor unit firing patterns in a human skeletal muscle. *Biophysical Journal*, 9(10), 1233–1251.  
[http://doi.org/10.1016/S0006-3495\(69\)86448-9](http://doi.org/10.1016/S0006-3495(69)86448-9)
- Cowling, B. L., Harwood, B., Copithorne, D. B., & Rice, C. L. (2016). Rate modulation of human anconeus motor units during high-intensity dynamic elbow extensions. *Journal of Applied Physiology*. <http://doi.org/10.1152/jappphysiol.00131.2016>
- De Luca, C. J., & Hostage, E. C. (2010). Relationship between firing rate and recruitment threshold of motoneurons in voluntary isometric contractions. *Journal of Neurophysiology*, 104(2), 1034–1046. <http://doi.org/10.1152/jn.01018.2009>
- Del Valle, A., & Thomas, C. K. (2005). Firing rates of motor units during strong dynamic contractions. *Muscle & Nerve*, 32(3), 316–325. <http://doi.org/10.1002/mus.20371>
- Douglas, J., Pearson, S., Ross, A., & McGuigan, M. (2016). Eccentric Exercise: Physiological Characteristics and Acute Responses. *Sports Medicine*, 1–13.  
<http://doi.org/10.1007/s40279-016-0624-8>
- Duchateau, J., & Baudry, S. (2014). Insights into the neural control of eccentric contractions. *Journal of Applied Physiology*, 116(11), 1418–1425.  
<http://doi.org/10.1152/jappphysiol.00002.2013>
- Duchateau, J., & Enoka, R. M. (2016). Neural control of lengthening contractions. *Journal of Experimental Biology*, 219(2), 197–204.  
<http://doi.org/10.1242/jeb.123158>

- Edman, K. (1988). Double-Hyperbolic Force-Velocity Relation in Frog Muscle Fibres. *Journal of Physiology*, 404, 301–321. <http://doi.org/10.1113/jphysiol.1988.sp017291>
- Edman, K., Elzinga, G., & Noble, M. (1978). Enhancement of mechanical performance by stretch during tetanic contractions of vertebrate skeletal muscle fibres. *Journal of Physiology*, 281, 139–155. <http://doi.org/10.1113/jphysiol.1978.sp012413>
- Enoka, R. M. (2002). *Neuromechanics of Human Movement* (3rd ed.). Champaign: Human Kinetics.
- Enoka, R. M. (2006). Motor Unit. *Encyclopedia of Biomedical Engineering*, (April). <http://doi.org/10.1002/9780471740360.ebs0798>
- Enoka, R. M., & Fuglevand, A. J. (2001). Motor unit physiology: some unresolved issues. *Muscle & Nerve*, 24(1), 4–17. [http://doi.org/10.1002/1097-4598\(200101\)24:1<4::AID-MUS13>3.0.CO;2-F](http://doi.org/10.1002/1097-4598(200101)24:1<4::AID-MUS13>3.0.CO;2-F)
- Farina, D. (2006). Interpretation of the surface electromyogram in dynamic contractions. *Exercise and Sport Sciences Reviews*, 34(3), 121–127. <http://doi.org/10.1249/00003677-200607000-00006>
- Farina, D., & Rainoldi, A. (1999). Compensation of the effect of sub-cutaneous tissue layers on surface EMG: A simulation study. *Medical Engineering and Physics*, 21(6–7), 487–497. [http://doi.org/10.1016/S1350-4533\(99\)00075-2](http://doi.org/10.1016/S1350-4533(99)00075-2)
- Fukunaga, T., Miyatani, M., Tachi, M., Kouzaki, M., Kawakami, Y., & Kanehisa, H. (2001). Muscle volume is a major determinant of joint torque in humans. *Acta Physiologica Scandinavica*, 172(4), 249–255. <http://doi.org/10.1046/j.1365-201X.2001.00867.x>
- Grabner, M., & Owings, T. (2002). EMG differences between concentric and eccentric maximum voluntary contractions are evident prior to movement onset. *Experimental Brain Research*, 145(4), 505–511. <http://doi.org/10.1007/s00221-002-1129-2>
- Hageman, P. A., Gillaspie, D. M., & Hill, L. D. (1988). Effects of Speed and Limb Dominance on Eccentric and Concentric Isokinetic Testing of the Knee. *Journal of Orthopaedic and Sports Physical Therapy*, 10(2), 59–65. <http://doi.org/1874> [pii]

- Harwood, B., Davidson, A. W., & Rice, C. L. (2011). Motor unit discharge rates of the anconeus muscle during high-velocity elbow extensions. *Experimental Brain Research*, *208*(1), 103–113. <http://doi.org/10.1007/s00221-010-2463-4>
- Harwood, B., & Rice, C. L. (2012). Changes in motor unit recruitment thresholds of the human anconeus muscle during torque development preceding shortening elbow extensions. *Journal of Neurophysiology*, *107*(10), 2876–84. <http://doi.org/10.1152/jn.00902.2011>
- Harwood, B., & Rice, C. L. (2014). Short interspike intervals and double discharges of anconeus motor unit action potentials for the production of dynamic elbow extensions. *Journal of Neurophysiology*, *111*, 2039–2046. <http://doi.org/10.1152/jn.00412.2013>
- Henneman, E. (1957). Relation between size of neurons and their susceptibility to discharge. *Science*, *126*(3287), 1345–1347.
- Herzog, W. (2014). Mechanisms of enhanced force production in lengthening (eccentric) muscle contractions. *Journal of Applied Physiology*, *116*(11), 1407–17. <http://doi.org/10.1152/jappphysiol.00069.2013>
- Hill, A. V. (1938). The heat of shortening and the dynamic constants of muscle. *Proceedings of the Royal Society B*, *126*(843). <http://doi.org/10.1098/rspb.1938.0050>
- Howell, J. N., Fuglevand, A. J., Walsh, M. L., & Bigland-Ritchie, B. (1995). Motor unit activity during isometric and concentric-eccentric contractions of the human first dorsal interosseus muscle. *Journal of Neurophysiology*, *74*(2), 901–904.
- Kallio, J., Sjøgaard, K., Avela, J., Komi, P. V., Selänne, H., & Linnamo, V. (2013). Motor Unit Firing Behaviour of Soleus Muscle in Isometric and Dynamic Contractions. *PLoS ONE*, *8*(2), e53425. <http://doi.org/10.1371/journal.pone.0053425>
- Kamen, G., & Gabriel, D. A. (2010). *Essentials of Electromyography*. Windsor, ON: Human Kinetics.
- Katz, B. (1939). The relation between force and speed in muscular contraction. *Journal of Physiology*, *96*(1), 45–64. <http://doi.org/10.1113/jphysiol.1939.sp003756>



- Koshev, A., & Christova, P. (1998). Discharge pattern of human motor units during dynamic concentric and eccentric contractions. *Electroencephalography and Clinical Neurophysiology*, *109*(3), 245–255. [http://doi.org/10.1016/S0924-980X\(98\)00012-5](http://doi.org/10.1016/S0924-980X(98)00012-5)
- Le Bozec, S., & Maton, B. (1987). Differences between motor unit firing rate, twitch characteristics and fibre type composition in an agonistic muscle group in man. *European Journal of Applied Physiology*, *56*(3), 350–355. <http://doi.org/10.1007/BF00690904>
- Linnamo, V., Moritani, T., Nicol, C., & Komi, P. V. (2003). Motor unit activation patterns during isometric, concentric and eccentric actions at different force levels. *Journal of Electromyography and Kinesiology*, *13*(1), 93–101. [http://doi.org/10.1016/S1050-6411\(02\)00063-9](http://doi.org/10.1016/S1050-6411(02)00063-9)
- Madeleine, P., Bajaj, P., Sogaard, K., & Arendt-Nielsen, L. (2001). Mechanomyography and electromyography force relationships during concentric, isometric and eccentric contractions. *Journal of Electromyography and Kinesiology*, *11*(2), 113–121. [http://doi.org/10.1016/S1050-6411\(00\)00044-4](http://doi.org/10.1016/S1050-6411(00)00044-4)
- Merton, P. (1953). Voluntary Strength and Fatigue. *Journal of Physiology*, *123*(3), 553–564.
- Morgan, D. L., Whitehead, N. P., Wise, A. K., Gregory, J. E., & Proske, U. (2000). Tension changes in the cat soleus muscle following slow stretch or shortening of the contracting muscle. *The Journal of Physiology*, *522*(3), 503–513. <http://doi.org/10.1111/j.1469-7793.2000.t01-2-00503.x>
- Ortega, J. O., Lindstedt, S. L., Nelson, F. E., Jubrias, S. A., Kushmerick, M. J., & Conley, K. E. (2015). Muscle force, work and cost: a novel technique to revisit the Fenn effect. *The Journal of Experimental Biology*, *218*(Pt 13), 2075–2082. <http://doi.org/10.1242/jeb.114512>
- Pasquet, B., Carpentier, A., & Duchateau, J. (2006). Specific modulation of motor unit discharge for a similar change in fascicle length during shortening and lengthening contractions in humans. *Journal of Physiology*, *577*(2), 753–765.

<http://doi.org/10.1113/jphysiol.2006.117986>

- Pinniger, G., Steele, J., Thorstensson, A., & Cresswell, A. (2000). Tension regulation during lengthening and shortening actions of the human soleus muscle. *European Journal of Applied Physiology*, *81*(5), 375–383.  
<http://doi.org/10.1007/s004210050057>
- Rassier, D. E., MacIntosh, B. R., & Herzog, W. (1999). Length dependence of active force production in skeletal muscle. *Journal of Applied Physiology*, *86*(5), 1445–1457. <http://doi.org/10.1152/ajpregu.00109.2011>
- Sogaard, K., Christensen, H., Jensen, B. R., Finsen, L., & Sjogaard, G. (1996). Motor control and kinetics during lowlevel concentric and eccentric contractions in man. *Electroencephalography and Clinical Neurophysiology*, *101*, 453–460.
- Spurway, N., Watson, H., McMillan, K., & Connolly, G. (2000). The effect of strength training on the apparent inhibition of eccentric force production in voluntarily activated human quadriceps. *European Journal of Applied Physiology*, *82*(5–6), 374–80. <http://doi.org/10.1007/s004210000221>
- Stevens, D. E., Harwood, B., Power, G. A., Doherty, T. J., & Rice, C. L. (2014). Anconeus motor unit number estimates using decomposition-based quantitative electromyography. *Muscle & Nerve*, *50*(1), 52–59. <http://doi.org/10.1002/mus.24092>
- Stevens, D. E., Smith, C. B., Harwood, B., & Rice, C. L. (2014). In vivo measurement of fascicle length and pennation of the human anconeus muscle at several elbow joint angles. *Journal of Anatomy*, *225*(5), 502–509. <http://doi.org/10.1111/joa.12233>
- Tax, A. A., Denier van der Gon, J. J., Gielen, C. C., & van den Tempel, C. M. (1989). Differences in the activation of m. biceps brachii in the control of slow isotonic movements and isometric contractions. *Experimental Brain Research*, *76*(1), 55–63. <http://doi.org/10.1007/BF00253623>
- Terzis, G., Georgiadis, G., Vassiliadou, E., & Manta, P. (2003). Relationship between shot put performance and triceps brachii fiber type composition and power production. *European Journal of Applied Physiology*, *90*(1–2), 10–15.

<http://doi.org/10.1007/s00421-003-0847-x>

- Tesch, P. A., Dudley, G. A., Duvoisin, M. R., Hather, B. M., & Harris, R. T. (1990). Force and EMG signal patterns during repeated bouts of concentric or eccentric muscle actions. *Acta Physiologica Scandinavica*, *138*(3), 263–271.  
<http://doi.org/10.1111/j.1748-1716.1990.tb08846.x>
- Thomas, C. K., Bigland-Richie, B., & Johansson, R. S. (1991). Force-frequency relationships of human thenar motor units. *Journal of Neurophysiology*, *65*(6), 1509–16.
- Thorstensson, A., Grimby, G., & Karlsson, J. (1976). Force-velocity relations and fiber composition in human knee extensor muscles. *Journal of Applied Physiology*, *40*(1), 12–6.
- Travill, A. A. (1962). Electromyographic study of the extensor apparatus of the forearm. *The Anatomical Record*, *144*(4), 373–376. <http://doi.org/10.1002/ar.1091440408>
- Valentin, D., Valentin, R., Arnaud, G., Gael, G., Lucile, C., & Marc, J. (2012). Specific joint angle dependency of voluntary activation during eccentric knee extensions. *Muscle & Nerve*, 1–27.
- Westing, S., Cresswell, A., & Thorstensson, A. (1991). Muscle activation during maximal voluntary eccentric and concentric knee extension. *European Journal of Applied Physiology*, *62*(2), 104–108. <http://doi.org/10.1007/BF00626764>
- Westing, S., Seger, J., Karlson, E., & Ekblom, B. (1988). Eccentric and concentric torque-velocity characteristics of the quadriceps femoris in man. *European Journal of Applied Physiology*, *58*(1–2), 100–104. <http://doi.org/10.1007/BF00636611>
- Westing, S., Seger, J., & Thorstensson, A. (1990). Effects of electrical stimulation on eccentric and concentric torque-velocity relationships during knee extension in man. *Acta Physiologica Scandinavica*, *140*(140), 17–22. <http://doi.org/10.1111/j.1748-1716.1990.tb08971.x>
- Zhang, L. Q., & Nuber, G. W. (2000). Moment distribution among human elbow extensor muscles during isometric and submaximal extension. *Journal of Biomechanics*,

33(2), 145–154. [http://doi.org/10.1016/S0021-9290\(99\)00157-8](http://doi.org/10.1016/S0021-9290(99)00157-8)

# Appendices



Research Ethics

## Western University Health Science Research Ethics Board HSREB Annual Continuing Ethics Approval Notice

Date: May 13, 2016

Principal Investigator: Dr. Charles Rice

Department & Institution: Schulich School of Medicine and Dentistry/Anatomy & Cell Biology, Western University

Review Type: Full Board

HSREB File Number: 100732

Study Title: Neuromuscular control of human movement

Sponsor: Natural Sciences and Engineering Research Council

HSREB Renewal Due Date & HSREB Expiry Date:

Renewal Due -2017/05/31

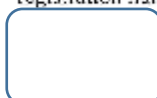
Expiry Date -2017/06/07

The Western University Health Science Research Ethics Board (HSREB) has reviewed the Continuing Ethics Review (CER) Form and is re-issuing approval for the above noted study.

The Western University HSREB operates in compliance with the Tri-Council Policy Statement Ethical Conduct for Research Involving Humans (TCPS2), the International Conference on Harmonization of Technical Requirements for Registration of Pharmaceuticals for Human Use Guideline for Good Clinical Practice (ICH E6 R1), the Ontario Freedom of Information and Protection of Privacy Act (FIPPA, 1990), the Ontario Personal Health Information Protection Act (PHIPA, 2004), Part 4 of the Natural Health Product Regulations, Health Canada Medical Device Regulations and Part C, Division 5, of the Food and Drug Regulations of Health Canada.

Members of the HSREB who are named as Investigators in research studies do not participate in discussions related to, nor vote on such studies when they are presented to the REB.

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



on behalf of Dr. Joseph Gilbert, HSREB Chair

Chief Officer to Contact for Further Information:  Diha Desai  Katelyn Lewis  Nicole Koriki  Grace Kelly  Yvonne Tran

## Curriculum Vitae

### Name

Christopher William Stolworthy

### Degrees

MSc. Integrative Physiology, School of Kinesiology, Faculty of Health Sciences,  
University of Western Ontario, 2015 - present

BSc. Honors Specialization in Kinesiology, Faculty of Health Sciences, University of  
Western Ontario, 2015

### Honours & Awards

Ontario Graduate Scholarship, Summer 2016 - Winter 2017

Dean's Honour List, 2013 - 2015

### Teaching Assistantships

GTA in Systemic Approach to Functional Anatomy KIN2222A, Winter 2016

GTA in Biomechanical Analysis of Human Locomotion KIN3353A, Fall 2015

### Presentations & Publications

**Stolworthy, C.W.**, and Rice, C.L. 2016 Motor unit firing rates during near-maximal eccentric contractions in the human anconeus Appl. Physiol. Nutr. & Metab. 41: 9 (Suppl. 4): S390.

Copithorne, D.B., **Stolworthy, C.W.**, McNeil, C.J., and Rice, C.L. 2016 Corticospinal excitability during sustained elbow flexion contractions with and without blood flow restriction Appl. Physiol. Nutr. & Metab. 41: 9 (Suppl. 4): S349.