EXAMINING MOTOR UNIT DISCHARGE PROPERTIES DURING DYNAMIC MUSCLE ACTIONS IN MALES AND FEMALES

by

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B.S in Kinesiology, 2023, Texas Christian University

A Thesis

Submitted to the Faculty of

Harris College of Nursing and Health Sciences

Texas Christian University

in partial fulfillment of the requirements for the degree of

Master of Science, Exercise Physiology

May

2025

APPROVAL

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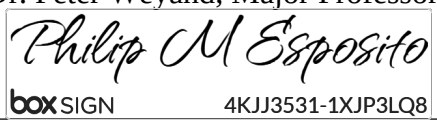

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ACKNOWLEDGEMENTS

I would first like to begin by thanking my family. To my mother Daisy, you have been my anchor that keeps me grounded, the light that guides me through every situation, and a voice of reason. It is through your support and compassion that I am able to set high ambitions, knowing your support will not cease. To my sister Samantha, your support parallels mom's, offering a unique perspective that blends the best of our family values and your unique experiences to ensure I can be the best I can be. Above that, you help me laugh and remember the important things in life outside of my academic and professional aspirations. Seeing all that you have accomplished and will accomplish pushes me to continue my journey. To my girlfriend Jessica, I cannot thank you enough for putting up with me and for your unwavering support. Lastly, to my father Eddie, I know you cannot physically see the man that I have grown up to be and the work I have and will accomplish, but I hope that from wherever you are watching, you are proud. It is through the collective support of this family that I am reminded of who I am and that I have the strength to accomplish what I set my mind to.

To my mentor, Dr. Joshua C. Carr, I cannot begin to thank you for shaping me into the academist that I have become. From taking me into your lab as a rising sophomore, you harnessed my curiosity and ambition to promote innovation. You cultivated an environment founded on camaraderie, purpose, and excellence, and I am humbled to have been chosen to contribute to this. Above this, your relentless and unconditional support alludes to your character traits that I greatly appreciate and aim to embody. To the rest of my lab mates, Caleb, Monique, Channing, Alisa, Jon, Evan, and Paige, thank you for your support and all the good moments we shared. Our lab was more than just that; we are and will continue to be a family.

Lastly, to my friends and classmates, I appreciate the times we shared over the past few years. While we have endured many things together, we did not falter and are stronger because of it. Thank you for pushing me to be the best classmate and friend that I can be.

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ABSTRACT

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Motor unit firing behavior is influenced by task demands and sex differences. This study compares motor unit population firing behavior of the biceps brachii between two dynamic muscle action intensities *(~90% and ~98% 1RM)*. Using surface EMG decomposition, we analyzed the average motor unit action potential amplitude ($MUAP_{amp}$) and firing rate (FR) relationship, identifying the Y-intercepts and slopes. A total of 1,361 motor units were identified across loading conditions. Our results indicate that Y-intercept, but not slope, increases with load. Notably, females exhibited significantly lower Y-intercepts, FR, $MUAP_{amp}$, and slopes *(steeper)* than males. These findings suggest that, during these conditions, motor unit populations adapt their discharge properties in a load-dependent manner. The observed sex-dependent differences are likely attributed to variations in muscle fiber composition and neural control strategies. These findings provide novel evidence of load-dependent motor unit firing behavior and divergent firing characteristics between sexes during maximal-intent dynamic muscle actions.

CHAPTER I: INTRODUCTION

In 1906, Sir Charles Sherrington termed the motor unit "the final common pathway" (Sherrington, 1906), opening the door to a new frontier in understanding the neural control of movement. Sherrington later defined a motor unit as a motor neuron and all the muscle fibers it innervates (Sherrington & Liddell, 1925). Building upon this foundation and in conjunction with advancements in technology, Edgar Adrian and Detlev Bronk were then the first to record the activity of individual motor units in humans as detailed in Part I of their report using intramuscular electrode placement within the triceps brachii (Adrian & Bronk, 1928). The later addition of a loudspeaker to the collection method allowed Adrian and Bronk to listen to nerve discharges and assess slight differences in discharge properties of the motor neuron during varying intensities and quality of the activity. As a follow-up to Part I, one conclusion from the Part II paper by Adrian and Bronk states that the ability of force gradation is due to the change in the discharge frequency of the neuron and the number of fibers contributing to the action. This publication was the first to link the electrical activity of motor nerve fibers and recordings from the muscle fiber (Adrian & Bronk, 1929).

The observation in force gradation put forth by Adrian and Bronk led to the work by Derek Denny-Brown and Jospeh Pennybacker introduced the concept of "orderly recruitment", which is that the same motor unit initiates any movement and more intense contractions are a result of the addition of contributing motor unit (Denny-Brown & Pennybacker, 1938). These findings influenced Elwood Henneman and others to fully investigate the properties of motor units, resulting in a series of papers describing the discharge properties of motor units (Henneman et al., 1965a, 1965b, 1965b; McPhedran et al., 1965; Wuerker et al., 1965). These papers resulted in the proposed theory known as the "size principle", which describes the orderly, stereotyped

recruitment of motor neurons. The anatomical basis for the size principle is a result of the findings from Henneman and Mendell, stating "*neural energy to discharge the neuron, the energy transmitted and released by the neuron, its excitability and inhibitability, the mean rate of firing, and the rate of protein synthesis are all well correlated with its [motor neuron] size,"* (Henneman & Mendell, 1981). The Size Principle is a governing neurophysiological principle of motor units that states that motor units are recruited from smallest to largest based on the size of the α-motor neuron and the number of muscle fibers it innervates, allowing for the ability to finely modulate force output and energy efficiency.

Following the introduction of the size principle, this sparked debate on the efficacy of this theory in humans, considering that Henneman's experiments were conducted using cats. For example, John Basmajian stated that under certain conditions, adding certain visual and audio feedback from the participants' motor units during muscle actions resulted in varied motor unit recruitment patterns (Basmajian, 1963, 1967). Bryan Ashworth furthered the results of Basmajian, stating that while the most important factor in motor unit recruitment is its intrinsic properties when humans were trained using certain audio feedback, nearby motor units would exhibit a reversal in motor unit recruitment during slow muscle contractions (Ashworth et al., 1967). Grimby and Hannerz added to this argument that the first motor unit to discharge action potentials could be silenced as the second recruited motor unit continued to discharge action potentials (Grimby & Hannerz, 1968, 1970). They furthered their position later, stating that *"cerebral centres are capable of selecting in advance the recruitment order that is most appropriate for the work intended"* (Hannerz & Grimby, 1973). In contrast, Richard Stein and his colleagues are attributed with this first evidence of the size principle within humans. They detailed strong correlations between the force produced by the motor unit and its recruitment threshold; these findings

concluded that motor units are recruited in an orderly fashion dependent on motor unit force (Gordon et al., 2004; Milner-Brown et al., 1973b).

Motor unit firing behavior acquisition occurs through the decomposition of electromyography (EMG) signals obtained from the muscle. EMG can be captured using two main techniques: indwelling EMG, meaning a small needle is placed within the muscle, or surface EMG, meaning a sensor is placed on the skin. Compared to indwelling EMG, surface EMG offers a non-invasive method of EMG acquisition, enhancing its versatility. Traditionally, motor units have been decomposed from EMG taken during isometric tasks, meaning no change in joint angle during muscle contraction. While data about motor unit properties during isometric tasks can prove useful, the applicability of these results to real-world scenarios is low due to isometric muscle actions being seldom used. The latest iteration, PDIII (De Luca et al., 2015), allows for the decomposition of surface EMG signals obtained during dynamic muscle actions— movements involving a change in joint angle—which are foundational to human movement. Despite recent advancements, there remains limited utilization of surface EMG motor unit decomposition during dynamic muscle actions, posing a knowledge gap that this study aims to explore.

Key characteristics of motor unit firing behavior relevant to our experiment are motor unit firing rate (FR)—the rate at which a motor unit discharges action potentials—and motor unit action potential amplitude ($MUAP_{amp}$)—the magnitude of the summed electrical activity of all the muscle fibers of the motor unit which results from the action potential of the α-motor neuron that innervates them. These variables are dependent on various factors and are intricately modulated by anatomy, current physiological conditions, and task demands. Specifically, these key characteristics are heavily influenced by intensity and biological sex. While the influence of these factors on motor unit firing rate and motor unit action potential amplitude have been detailed

during isometric muscle actions, little is known about the influence of these factors during high-intensity, dynamic muscle actions. Thus, this study aims to explore characteristics of motor unit firing behavior during maximal-intent dynamic muscle actions and how they are influenced by changes in intensity and biological sex.

CHAPTER II: REVIEW OF LITERATURE

2.1 Neuromuscular Anatomy of Motor Output

2.1a The Central Nervous System

Voluntary motor output is a complex, conscious process beginning within the brain. The prefrontal cortex is an area within the frontal lobe of the brain and mainly functions to regulate thoughts and emotions (Arnsten, 2009). The limbic system comprises the hippocampus, cingulate gyrus, amygdala, and hypothalamus; these components collectively are responsible for emotion and memory (RajMohan & Mohandas, 2007). The connection between the prefrontal cortex and the limbic system results in the intent to move (Fuster, 2015; Virameteekul & Bhidayasiri, 2022). It has also recently been shown that the prefrontal cortex contributes to the motor learning circuit, strengthening its role in movement (Kumar et al., 2022).

This intent is then transmitted to the presupplemtary and supplementary motor areas, located within the frontal cortex, which are responsible for planning motor and coordinating complex movements (Nachev et al., 2008). Following the appropriate selection of a motor plan, it is transmitted to the primary motor cortex, a specialized area located in the precentral gyrus, where the majority of the upper motor neurons of the descending motor tracts begin. Each descending pathway carries a specific type of information to a specific area within subcortical structures, acting as a bridge between the intention of the brain and the execution done by the effector. The corticospinal tract is the primary descending tract for motor output, originating in the primary motor cortex, and travels down the brainstem, where the tract decussates at the level of the pyramids in the medulla to the contralateral side (Welniarz et al., 2017). The majority of the axons decussate and form the lateral corticospinal tract, while a small percentage remain on the ipsilateral side and form the anterior corticospinal tract. The corticospinal tract transmits the motor output

signal to the α-motor neuron, with the lateral corticospinal tract carrying voluntary motor actions (Martin, 2005). The decussation of the corticospinal tract into the lateral corticospinal tract results in contralateral representation, meaning the right hemisphere of the brain controls the left side of the body, and the left hemisphere controls the right side of the body (Kuypers, 1981; Mendoza & Foundas, 2008).

While the corticospinal tract transmits and coordinates motor output, it is not the only descending spinal tract that possesses these functions. Recently, the reticulospinal tract has witnessed increased research interest in its role in coordinating voluntary motor output and autonomic functions. The reticular formation is a borderless, web-like network of interneurons and nuclei dispersed among the cortical structure, subcortical structures, and the entire spinal cord (Horn, 2006). The reticular formation is divided into two distinct pathways: the ascending tract—responsible for functions such as motivation, arousal, and alertness—and the descending tract—which projects onto spinal motor neurons and is responsible for the modulation of balance, tone, and coordination of somatic motor movements (Wang, 2009). Thus, the functions of the reticular formation and reticulospinal tract enhance neuromotor physiology and have been shown to promote proficient movement and strength increases (Anzak et al., 2011; Fernandez-Del-Olmo et al., 2014; Škarabot et al., 2022). Interestingly, it has been found that the neural adaptations in strength training arise from adaptations within the reticulospinal tract and primary motor cortex, with minimal credit being given to the corticospinal tract for adaptations in strength (Glover & Baker, 2020). Furthermore, for the force of muscle contraction, the reticulospinal tract shows specificity in overall force output, and the corticospinal tract shows specificity in fine adjustments of force output (Glover & Baker, 2022).

2.1b The α-Motor Neuron and Neuromuscular Junction

The corticospinal tract and reticulospinal tract synapse and exert their effects onto the final component within the neural transmission pathway, the lower motor neuron, residing in the ventral horn of the spinal cord. The lower motor neurons can be classified into three distinct groups: branchial, visceral, and somatic. Branchial motor neurons are located within the brainstem and innervate muscles of the face and neck through the corresponding cranial nerve. Visceral motor neurons are a component of the autonomic nervous system and control smooth muscles and glands. The somatic motor neurons are distributed along the central nervous system and are responsible for transmitting motor output signals to the effector. Somatic motor neurons are further divided into three subtypes: alpha, beta, and gamma (Enjin, 2011; Stifani, 2014). The α-motor neuron is a large neuron with a soma ranging from 50-100 μm (Hultborn & Fedirchuk, 2009) compared to the average mammalian neuron of 20 μm (Ma & Gibson, 2013) with dendrites that can extend several millimeters. α-motor neurons are segmentally clustered along the entirety of the spinal cord, exiting the spinal cord at the ventral root ganglion, which joins with the dorsal root ganglion and exits through the neuroforamen. Each nerve root exiting the neuroforamen maintains a similar stereotyped pattern of sensory feedback and muscle innervation across humans, resulting in a dermatome and myotome, respectively, which are crucial in a neurological clinic setting (Sonoo, 2023; Wilbourn & Aminoff, 1998). Following the exit from the neuroforamen, each α-motor neuron synapses with a varying amount of muscle fibers, resulting in a complex structure known as the neuromuscular junction. The axonal side of the neuromuscular junction stores vesicles containing acetylcholine, a neurotransmitter crucial in generating a contraction within the muscle (Chad, 2003).

2.1c The Muscle

There are about 600 muscles within the human body, each executing a specific function from basic life functions such as breathing and digestion to voluntary motor output. There are three main types of muscle: cardiac, smooth, and skeletal. Skeletal muscle is striated, cylindrical, and multinucleated and connects to the skeleton via tendons, allowing for voluntary motor output. A muscle is composed of several fascicles, each fascicle containing multiple myofibrils. Each myofibril is highly organized into several specific groups. Nuclei reside on the periphery of the myofibril below the sarcolemma. Myofibrils also house the basic contractile unit of a muscle, the sarcomere. Each sarcomere is composed of two main contractile components, actin and myosin. Each sarcomere is surrounded by the sarcoplasmic reticulum, which is responsible for the storage and release of calcium and is an essential component in the excitation-contraction coupling mechanism. Descending into the myofibril are T-tubules, infolding projections that are closely integrated with the sarcoplasmic and contain vital voltage-gated channels utilized during muscle contraction. Excitation-contraction coupling occurs when an action potential is received at the neuromuscular junction and is propagated along the entire sarcolemma and down the T-Tubules, resulting in voltage-gated ion channels stimulating the sarcoplasmic to release calcium ions. These calcium ions bind to troponin on actin, exposing tropomyosin and thus allowing the actin-myosin complex to form and generate a power stroke (Floeter, 2010).

Muscle fibers can be classified depending on their physiological composition. The first method of classification is based on the activity of myosin ATPase and is divided into Type I, IC, IIA, IIB, IIC, IIAC, and IIAB (MacIntosh et al., 2006; Pette et al., 1999; Staron, 1997). A second method of classification is based on the various isoforms of myosin heavy chains (MHC) and is divided into MHC I, IIa, and IIb. The final common classification method of muscle fibers is a

combination of myosin ATPase histochemistry and qualitative histochemistry of certain enzymes within the metabolic pathways and is divided into fast glycolytic (FG), fast-oxidative glycolytic (FOG), and slow oxidative (SO) (MacIntosh et al., 2006; Pette & Staron, 1997). While there is a strong correlation between the classification of Type I and SO, extrapolating this relationship to Type IIA and IIB is more varied (MacIntosh et al., 2006).

One important consideration regarding muscle contraction is that the muscle does not possess the inherent capability to initiate its own contraction, meaning it is the α-motor neuron that is responsible for the response that is realized at the muscular level. Richard Dum and others eloquently exemplify this in a series of two papers. In the first paper, they reinnervated the flexor digitorum longus muscle, a known fast-twitch muscle, with a neuron that innervated the soleus muscle, a known slow-twitch muscle. In the second paper, they did the inverse, they reinnervated the soleus muscle with a neuron that innervated the flexor digitorum muscle. Researchers found that following reinnervation, the slow-twitch muscle fibers that were now innervated by fast-twitch neurons exhibited properties similar to a fast-twitch muscle, and fast-twitch muscle fibers that were now innervated by slow-twitch neurons exhibited properties similar to a slow-twitch muscle (Dum, O'Donovan, Toop, & Burke, 1985; Dum, O'Donovan, Toop, Tsairis, et al., 1985).

2.1d The Motor Unit and its Classifications

This singular α-motor neuron and all the muscle fibers innervated by it result in a motor unit. Motor units can be classified based on their metabolic and mechanical properties (Monti et al., 2001). The simplest classification of motor units was introduced by Henneman and Mendell and is based on their size; a small motor unit innervates fewer and smaller muscle fibers, and a large motor unit innervates more and larger muscle fibers (Henneman & Mendell, 1981). A physiology-based classification method, introduced by Burke, 1999 is based on contractile speed

and fatigability, consisting of slow-twitch and fast-twitch. Fast-twitch motor units are further divided into fatigue-resistant, fatigue-intermediate, and fatigable. A metabolic-based classification method, first introduced by James Peter et al., 1972, is based on the type of muscle fiber innervated by the α-motor neuron that consists of fast glycolytic, fast-oxidative glycolytic, and slow oxidative. The final common classification method is based on the profile of the myosin-heavy chain of the muscle fiber and is divided into types IIa, IIx, and IIb (Schiaffino et al., 1989). While each classification method is unique, each correlates with the others. For example, a motor unit can be classified using Burke's method as fast-twitch, which correlates to Peter's method as being fast-glycolytic. This exemplifies that each classification method has its strengths and weaknesses, thus, a well-rounded classification of motor units using multiple classification methods is ideal.

2.1e Physiology and Key Variables of Motor Unit Firing

Motor units possess unique physiology that helps to define their function and produce force. The first key physiological principle of motor units that results in the modulation of force output is the motor unit action potential (MUAP), which reflects the physical state of the motor unit. An action potential is a fundamental principle of all neurons defined as a rapid change in the voltage across a cell membrane (Grider et al., 2024). A neuron's resting membrane potential is defined as the electrical potential difference across its membrane at rest. The resting membrane potential of α-motor neurons depends on the type and ranges between -72 to -75 mV (Nishimura et al., 2018). The resting membrane potential of a neuron is maintained via Na^+/K^+ ATPase, commonly known as the Sodium-Potassium Pump. Before an action potential, the opening of Na^+ ion channels within the cell membrane results in Na^+ influx, overcoming the resting membrane potential and depolarizing the neuron's cell membrane, resulting in an action potential. Action potentials are governed by the all-or-none principle, which states that depolarization of the cell

membrane will always give a maximal response from the neuron and produce an electrical impulse of a single amplitude (Lucas, 1909). The action potential then travels down the axon and stimulates the muscle fiber at the neuromuscular junction.

There are various factors of the motor unit action potential that can be of interest, such as duration, amplitude, or complexity, with amplitude ($MUAP_{amp}$) being of interest in this review. Motor unit action potential amplitude is defined as the difference in electrical potential between the maximum negative and positive peak (McGill, 2009). Motor unit action potential amplitude has also been shown to be an indicator of muscle fiber type, area, and size. (Colquhoun, Magrini, et al., 2018; Herda et al., 2019; Trevino et al., 2019), total muscle cross-sectional area (Dimmick et al., 2018; Pope et al., 2016; Trevino et al., 2019), and strength (Pope et al., 2016; Sterczala et al., 2020; Trevino et al., 2019). Resistance training has been shown to increase motor unit action potential amplitude in training only high-threshold motor units as these motor units are more likely to reflect changes from resistance training compared to low-threshold motor units (Herda, 2022; Jenkins et al., 2021; Pope et al., 2016). Additionally, decreases in motor unit action potential amplitude have also been associated with muscle fiber atrophy while increases are associated with muscle fiber grouping and hypertrophy (Rodriguez-Carreno et al., 2012).

The second key physiological property of motor units that results in the modulation of force output is firing rate (FR), defined as the rate at which motor units discharge action potentials. Increases in firing rates are one of the mechanisms by which an increase in force output is generated. During isometric contractions, firing rate has been shown to increase as force output, as defined by the %MVC, also increases (Borzuola et al., 2023; Kunugi et al., 2021; Milner-Brown et al., 1973a; Seki & Narusawa, 1996). These findings are also demonstrated during dynamic muscle actions, specifically during the concentric portion (Kallio et al., 2014).

However, the effects of resistance training on neural adaptations at the motor unit level, specifically firing rate, do not show conclusive evidence. One study by Kamen & Knight, 2004 found that exercise increased firing rates in both young and older adults. In contrast, T.W et al., 2011 found that in untrained adult males, resistance training did not provide a statistically significant increase in average motor unit firing rate. Separate reviews conducted by Herda, 2022 and Elgueta-Cancino et al., 2022 further confirm the lack of conclusive evidence on the effect of resistance training on motor unit firing rate and other firing properties. Aging is another factor that can alter motor unit firing properties, specifically resulting in a decrease in firing rate. During isometric muscle actions, a decrease in firing rate has been observed in older adults compared to young adults (Kallio et al., 2014; Kirk et al., 2021). Building upon these findings, Wages and others found that these decreases in firing rate result in clinically significant reductions in leg extensor strength (Wages et al., 2023).

2.1f Motor Unit Recruitment

During voluntary muscle contractions, motor units are recruited based on their size, from small to large, as described by Henneman's "Size Principle" (Henneman & Mendell, 1981). The recruitment threshold is a crucial component within the size principle and is defined as the level of force when a specific neuron first fires. Using recruitment thresholds to define motor units, since small motor units are recruited initially at low force output and large motor units are recruited later at high force output, they are termed low-threshold motor units and high-threshold motor units, respectively. The "Size Principle" was further elaborated on by Carlo De Luca and Zeynep Erim, who introduced the "onion skin phenomenon". De Luca and Erim noted that low-threshold motor units are recruited initially and have a high firing rate during isometric muscle contractions. However, as force output increased, the low-threshold motor units continued to fire at a high rate,

while the high-threshold motor units that were being recruited fired at a lower rate. This resulted in a layering pattern of the motor units, similar to an onion skin (De Luca et al., 1982; Deluca & Erim, 1994). Since this observation, the "Onion Skin" phenomenon has been continuously supported during voluntary muscle contractions, furthering our understanding of how motor units are recruited (De Luca & Contessa, 2012; De Luca & Hostage, 2010; Harmon et al., 2019; Hu et al., 2014).

During the onset of muscle force output, low-threshold motor units are initially recruited, which exhibit high firing rates and low motor unit action potential amplitudes (Reece et al., 2021). These physiological principles of small motor units allow for low fatigability and metabolic requirements; these motor units typically are classified using Peter's classification method as slow-oxidative. Small motor units are also beneficial in fine force modulation and are capable of maintaining a low level of tonic muscle activity. The culmination of these physiological characteristics provides reasons for why smaller motor units are commonly found in muscles responsible for activities such as handwriting, oculomotion, and postural control (Purves, 2018). As the requirement of force output increases, more small motor units are recruited, followed by the recruitment of larger motor units *(high-threshold motor units)*, with these motor units exhibiting low firing rates and high motor unit action potential amplitudes (Reece et al., 2021). Large motor units are highly fatigable and have high metabolic requirements and thus can be classified using Peter's classification method as either fast-oxidative glycolytic or fast-glycolytic. These characteristics of large motor units render them ideal for high-force output tasks. Considering the metabolic and functional requirements of various tasks and the gradient of small to large motor units, this helps explain why they are recruited in the fashion they are. This recruitment pattern allows for the careful modulation of force output and ensures the body is only

expending the necessary energy to complete a desired movement (Conwit et al., 1999; De Luca & Contessa, 2015; Enoka & Duchateau, 2017).

2.2 Electromyography and Motor Unit Decomposition

Electromyography (EMG) is a technique utilized in academic and clinical settings to measure electrical activity within the muscle. Studies of the electrical activity within the muscle and stimulation of the muscle date back to the 18th century, marked by the incidental electrical stimulation of a nerve within a frog leg leading to muscle contraction. Following years of further advancements in electrical stimulation of muscles, there remained a limitation in the ability to assess the electrical properties of the muscle. Carlo Matteucci built upon the work of Luigi Galvani and Alessandro Volta in the electrical properties of frog leg muscles. He invented the "kymographe", an instrument capable of recording and measuring the electricity produced by a muscle during contraction. (Metteucci, 1860). His work influenced Emil Du Bois-Reymond, who, in 1849, invented a sensitive galvanometer, resulting in the first illustration of what is known today as an EMG signal (Du Bois-Reymond, 1848).

Following years of development, in 1929, Adrian and Bronk are credited with the creation of the first robust method of EMG acquisition, indwelling EMG (Adrian & Bronk, 1928, 1929). Indwelling EMG is traditionally done using fine-wire or an intramuscular needle (Kamen & Gabriel, 2010). Indwelling EMG provides benefits such as comprehensive EMG data, especially from deep muscle, but one key limitation is its invasiveness. The act of placing wires or needles within the muscle can be painful, but furthermore, having needles or wires deep within the muscle drastically limits the muscle actions that can be performed, typically being utilized during gait or submaximal fine motor tasks. This limitation of indwelling EMG provided a reason for the development of surface EMG. Surface EMG is a noninvasive method of measuring EMG and is

used on superficial muscle groups. Surface electromyography has been increasingly used in research settings, specifically during submaximal and maximal dynamic muscle actions.

Concerning this study, motor unit properties and yield are key data points that arise from EMG decomposition. The EMG signal is decomposed using an algorithm into individual motor unit action potential trains. Traditionally, in the literature, utilizing the Precision Decomposition I (PDI) algorithm, motor unit decomposition has only been done using EMG signals obtained using indwelling EMG (C. J. De Luca & W. J. Forrest, 1972; De Luca et al., 1982; H. Broman, 1988; Nawab et al., 2008). However, for reasons described previously, indwelling EMG had glaring drawbacks, leaving the need for an alternative. Subsequent upgrades to the PDI algorithm gave rise to the PDII algorithm, and now the most recent algorithm, PDIII. The recent advancements in the PD algorithm make the decomposition of individual motor unit trains from the EMG signals obtained by surface EMG possible. In 2006, Carlo De Luca and others utilized the PDII and PDIII algorithms to successfully decompose surface EMG signals into their respective motor unit action potential trains. During isometric muscle contractions, both surface EMG and indwelling EMG were done simultaneously, with the respective EMG signals being decomposed into motor unit action potential trains. Successful motor unit decomposition from the surface EMG signal was confirmed by comparison that was done from the indwelling EMG signal (De Luca et al., 2006).

Since this publication by De Luca et al. in 2006, motor unit decomposition from surface EMG has only been done during isometric tasks. With further refinement of the PDIII algorithm, De Luca addressed this knowledge gap in 2015 when he and others examined the effectiveness of PDIII in decomposing surface EMG into motor unit action potential trains from surface EMG taken during dynamic muscle contractions. Using surface EMG in different muscle groups (biceps brachii, tibialis anterior, vastus lateralis), motor unit action potential trains were decomposed and

validated using the decompose-synthesize-decompose-compare method (De Luca & Contessa, 2012) and the two-source method (De Luca, 1984). When analyzing the decomposed motor unit action potential trains, researchers found that motor unit properties such as firing rate, motor unit action potential amplitude, and motor unit recruitment all aligned with established neurophysiological principles of motor units. Furthermore, the findings in the variables detailed above also were exhibited by motor units during isometric muscle actions (De Luca et al., 2015). Thus, this was the first publication stating that surface EMG decomposition into motor unit action potential trains is valid and reliable.

Since this publication, there has been a minimal exploration of the use of surface EMG motor unit decomposition during dynamic muscle actions. In a study by Orantes-Gonzalez et al., 2023, they observed changes in motor unit firing properties during changes in the speed of back squat execution. Researchers found that as the speed of execution increased, the motor unit firing rate increased. They also found that when comparing firing properties from the concentric phase and the eccentric phase of the squat, the firing rate was faster during the concentric phase. It is well understood that a squat's concentric phase requires more force compared to the eccentric phase, providing a partial explanation for the increase in firing rate as it is known that the firing rate increases as force requirement also increases (Borzuola et al., 2023; Kunugi et al., 2021). Additionally, Mark Latash and others, in a series of publications, sought to describe the organization of motor units into distinct, force-stabilizing synergies termed motor unit modes, and their control mechanisms. Using cyclical muscle actions, they described that the stability across different muscles *(multifinger and multimuscle)* reflects supraspinal circuitry while stability within a single muscle reflects spinal circuitry (De et al., 2024). Furthermore, they described that the force produced by motor unit modes is stabilized through hierarchical control mechanisms consisting at

the cortical, subcortical, and spinal levels (Benamati et al., 2024). Collectively, these findings illustrate intricate neural control mechanisms during dynamic, cyclical muscle actions.

2.3 Influences on Motor Unit Firing Behavior

2.3a The Muscle and Muscle Action Intensity

As the intensity of a muscle action is elevated, such as with increases in load, to meet this new intensity requirement, neural drive to the working muscle must be elevated. The increase in neural drive is realized at the α-motor neuron, altering firing properties such as motor unit firing rate and Motor unit action potential amplitude. In the literature, these variables have been acquired and described during isometric muscle actions and are plotted as a regression versus recruitment threshold, depicting the firing behavior of the entire motor unit pool contributing to muscle actions.

As it pertains to firing rates, its regression versus recruitment threshold illustrates a significant, strong, and negative relationship, indicating that motor units recruited initially have higher firing rates, while those recruited later have lower firing rates, corroborating the Size Principle and the Onion Skin Phenomenon. Additionally, the recruitment threshold versus firing rate relationship describes the operating point of the motor unit pool. The operating point represents the excitability of the motor unit pool and serves as a modulator of motor unit firing rates (Contessa & Luca, 2013; De Luca & Hostage, 2010). During submaximal isometric muscle actions, as the percent of the maximal voluntary contraction (%MVC) increases, motor unit firing rate (Y-intercept) and slope of the regression increase (Colquhoun, Tomko, et al., 2018; Jeon et al., 2020). This results in an upward and flattening of the recruitment threshold versus firing rate relationship; thus, the motor unit pool operating point elevates. This demonstrates that during these conditions, the neural control mechanism to meet elevated intensity demands is through an increase in motor unit firing rate and recruit additional high-threshold motor units. Furthermore,

the changes in this relationship are muscle-specific due to the variations in muscle fiber composition and functional roles (De Luca & Hostage, 2010). However, as %MVC increases from 80-100%, there is a significant change in Y-intercept but not slope (De Luca & Hostage, 2010). However, this relationship and how it changes with intensity have yet to be investigated during dynamic muscle actions.

As it pertains to motor unit action potential amplitude, its regression versus recruitment threshold reveals a significant, positive, and strong relationship that increases proportionally with %MVC (Kuniki et al., 2024; Miller et al., 2019; Pope et al., 2016; Reece & Herda, 2021; Sterczala et al., 2018; Trevino et al., 2019). The measurement of recruitment threshold during dynamic muscle actions becomes more complex as it fluctuates with force output, fatigue, and even muscle length. Since motor unit action potential amplitude scales with recruitment threshold, it serves as a robust proxy for motor unit size and ultimately, neural drive (Pope et al., 2016). Furthermore, this enables clearer differentiation between low- and high-threshold motor unit strategies, particularly during forceful dynamic contractions. The motor unit action potential amplitude versus firing rate has previously been utilized in the literature to describe motor unit firing behavior, depicting a significant, strong, and negative relationship (Dimmick et al., 2018; Herda et al., 2019; Jenkins et al., 2021; Miller et al., 2019; Parra et al., 2021; Reece et al., 2021; Reece & Herda, 2021).

It is important to note that the recruitment threshold/motor unit action potential amplitude versus firing rate is muscle-specific. While every muscle analyzed in the current literature demonstrates the archetypal recruitment threshold/motor unit potential amplitude versus firing rate relationship as described above, the slope and y-intercept parameters deviate. Specifically, a smaller muscle such as the first dorsal interosseous exhibits a steeper *(more negative)* slope

compared to larger muscles such as the tibialis anterior or vastus lateralis (De Luca & Hostage, 2010). These differences can be attributed to differences in muscle cross-sectional area and muscle fiber composition as muscles such as the first dorsal interosseous and other small hand intrinsic muscles exhibit a smaller muscle cross-sectional area and higher composition of Type I motor units (Enoka & Fuglevand, 2001). This results in fewer high-threshold motor units to recruit and all motor units being recruited at <60%MVC (De Luca et al., 1982, 1996; Duchateau & Enoka, 2022; Kukulka & Clamann, 1981).

2.3b Differences in Biological Sex

Sex differences in maximal strength and performance can be attributed to anatomical and physiological deviations. As it pertains to motor units, the recruitment threshold versus firing rate is maintained between males and females, indicating that both sexes possess the same fundamental motor unit recruitment patterns described by the Size principle and the Onion-skin phenomenon. However, the literature has shown that sex is a moderator for motor unit firing behavior at varying intensities.

During submaximal intensities in varying muscle groups, as the %MVC increases from 20-80%, females exhibit higher motor unit firing rates compared to males (Guo et al., 2022; Inglis & Gabriel, 2020; Kowalski & Anita D., 2020; Nishikawa et al., 2024; Taylor et al., 2022). These findings are likely attributed to anatomical differences between females and males; specifically, females exhibit a greater proportion of Type I muscle fibers, while males exhibit a greater proportion of Type II muscle fibers (Nuzzo, 2024; Trevino et al., 2019). With Type I muscle fibers being innervated by Type I motor units, the physiological principles of these motor units, specifically having higher firing rates, could explain why females tend to exhibit higher motor unit firing rates at these intensities. Of note, at 10% MVC in the first dorsal interosseous, one study has

reported that there is no statistical difference in motor unit firing rate between sexes (Parra et al., 2020) while others have demonstrated a significant difference between the sexes (Guo et al., 2022; Nishikawa et al., 2024).

However, at 100 %MVC, males exhibit higher motor unit firing rates compared to females (Christie & Kamen, 2010; Inglis & Gabriel, 2020). While the influence of sex dimorphisms in muscle cross-sectional area (Nuzzo, 2024), muscle fiber composition (Olmos et al., 2023), muscle pennation angle (Marsala et al., 2025), hormonal influences (Guo et al., 2022; Tenan et al., 2013), menstrual cycle phase (Ansdell et al., 2019; McNulty et al., 2020), and spinal cord anatomy (Yuan et al., 2000) cannot be excluded, sex differences in neuromodulation may modulate the divergence observed at 100 %MVC compared to trends observed during submaximal muscle actions.

Persistent inward currents—a depolarizing current generated by voltage-sensitive channels—amplify and prolong the excitatory input effect on motor units (Orssatto et al., 2021). Specifically, it has been shown that females exhibit significantly more persistent inward currents compared to males in different lower limb muscles. This indicates that at matched intensities, females deploy alternative methods to heighten motor unit firing behavior to complete the task (Jenz et al., 2023). Additionally, females exhibit greater incidences of doublets—a pair of action potentials that occur within a narrow interspike interval that leads to increases in motor unit force output—compared to males, illustrating that females may utilize diverging neuromuscular strategies compared to males to execute a similar task (Inglis & Gabriel, 2020, 2021).

Antagonist co-activation describes the simultaneous contraction of the opposing muscle group to a specific muscle action. Specifically, studies have demonstrated that females exhibit significantly greater antagonist co-activation compared to males in the tibialis anterior (Mendonca et al., 2020), knee extensors (Frey-Law & Avin, 2013; Kaur et al., 2015), and the elbow flexors

(Frey-Law & Avin, 2013; Pincivero et al., 2019). While this mainly functions as a biomechanical protective mechanism for joint stability, it has the potential to modulate the motor unit excitability and firing behavior of the agonist via its interaction with spinal reflexes.

The Hoffman Reflex (H-reflex) is an induced stretch reflex that indicates the excitability and inhibition of the motor neuron pool. It specifically bypasses the muscle spindle and gamma motor neurons, allowing the H-reflex to estimate α-motor neuron excitability independent of presynaptic inhibition and intrinsic excitability (Palmieri et al., 2004). It has been shown that females exhibit significantly lower response time and elevated amplitude of the H-reflex, indicating that their α-motor neurons may be more excitable (M. Hoffman et al., 2018; Mercan & Kuruoğlu, 2024). However, when antagonist co-activation is accounted for, females exhibit a significantly lower H-reflex compared to males, specifically during MVCs (Mendonca et al., 2020). This indicates that female α-motor neurons became less excitable due to antagonist co-activation, providing another potential reason for the divergence in motor unit firing behavior between sexes at maximal intensities. However, it is important to note the conflicting reports stating that there are no sex differences in the H-reflex (M. A. Hoffman et al., 2018; Johnson et al., 2012).

Interestingly, when comparing unweighted, repetitive squats of different cadences between males and females, males exhibited greater motor unit firing rates regardless of cadence (Orantes-Gonzalez et al., 2023). Changes in cadence can be viewed as changes in intensity, as increasing the speed of muscle actions requires a faster motor unit recruitment rate and elevation of motor unit firing properties (Reece et al., 2021). While these findings offer intriguing insights, the methodology of this study had many limitations, such as not controlling for weight, height, or lower limb alignment of the participants; all factors which modulate motor unit firing behaviors.

2.3c *Summary*

In summary, motor unit firing behavior is task-, intensity-, and sex-dependent. While the influences of these variables have been thoroughly detailed during isometric muscle actions, they have yet to be adequately described during dynamic muscle actions. Furthermore, while motor unit recruitment patterns are conserved between sexes, it is evident that each sex deploys differing neuromuscular control strategies to complete similar tasks. Thus, there remains a gap in our understanding of motor unit firing behavior during dynamic muscle actions and sex dimorphisms under these conditions.

CHAPTER III: METHODS

3.1 Experimental Design

This study used an experimental, cross-sectional design to identify changes in motor unit firing behavior during dynamic muscle actions under different loading conditions. Participants were required to visit the laboratory for one visit and complete a strength testing assessment of the dominant elbow flexors while decomposition EMG and surface EMG were captured from the biceps brachii.

3.2 Participants

36 college-aged, resistance-trained participants volunteered to be included in this study. 18 participants were male, and 18 were female. Ethical approval was obtained from the International Review Board at Texas Christian University in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. Participants completed a health questionnaire and signed informed consent before participating in the study. Participants were recruited from the Texas Christian University campus by laboratory members. Participants were eligible to participate if they met the following inclusion criteria: no recent history (<1 year) of surgical interventions or injury of the upper limbs, absence of any neuromuscular disorder or other diseases that may limit physical activity, currently not pregnant, and with no joint pain or inflammation.

Table 1. Participant Characteristics and Motor Unit Metrics Across Loading Conditions

	Female (N = 23)	**Male (N = 12)**
Age (years)	20.8 ± 1.9	22.4 ± 3.2
Height (inches)	65.9 ± 4.06	70.83 ± 3.51
Weight (lbs.)	143.9 ± 21.3	169.2 ± 33.7

1 Repetition Maximum (lbs.)	26.05 ± 6.8	46.2 ± 11.8
Load 1 %1RM	91.3 ± 5.6	88.4 ± 6.06
Load 2 %1RM	99.1 ± 2.5	97.2 ± 5.1
Load 1 motor unit yield (n)	383	273
Load 1 motor unit accuracy (%)	92.3 ± 3.4	94.4 ± 3.2
Load 2 motor unit yield (n)	415	290
Load 2 motor unit accuracy (%)	91.8 ± 2.3	93.8 ± 2.4
Hormonal Contraceptives (n)	13	

3.3 Instrumentation and Procedures

3.3a Maximal Strength Testing

The maximal dynamic strength (1RM) of the elbow flexors was assessed using a traditional biceps curl exercise task. EMG data were simultaneously collected from the biceps brachii, as it is the prime mover during this movement (Basmajian & Latif, 1957). Participants were instructed to stand in the anatomical position, with their backs approximately 2 inches from a wall and their feet aligned with a marker on the floor. Participants were handed a dumbbell with the prescribed load, and two researchers assisted with loading, recording, and observing the participant. A successful repetition was defined as a full concentric contraction of the elbow flexors, completed without postural adjustments that would aid the dumbbell's upward trajectory. Any substantial postural compensations led to a failed attempt. A loadable dumbbell (Rogue Loadable Dumbbell) with microplates of 0.11 kg was used to allow precise adjustments in loading. Testing began with three warm-up sets, starting with an unloaded dumbbell. The load was progressively increased with each warm-up set. Following the warm-up, participants performed maximal strength testing, with a maximum of five attempts allowed to determine their one-repetition maximum (1RM). After each

successful lift, the load was increased based on participant feedback using the OMNI scale and the researcher's judgment of the appropriate load progression based on movement velocity. If an attempt failed, participants could either retry the same load or reduce it, with each attempt counting toward the five maximum attempts. Testing concluded when the participant either reached volitional fatigue, experienced two consecutive failed attempts, or completed five 1RM attempts. The repetitions that were used for comparison were categorized into two tasks: load one (L1) and load two (L2). Load one is defined as the first completed repetition of a lighter load during the 1RM assessment that met the motor unit inclusion criteria (*described below*). Load two is defined as a later repetition during the 1RM assessment that also met motor unit inclusion criteria, and is *always* heavier than load one.

3.3b EMG Signal Acquisition and Processing

Arm length was determined by a measurement from the acromion process to the antecubital space using a standardized metric measuring tape. A mark was placed at 66% arm length using a sterile skin marking pen. Any excess hair was removed using a sterile razor and the skin was prepped using alcohol and a sterile, abrasive gauze. Using a hypoallergenic, double-sided adhesive, a wireless sensor array (Trigno Galileo sensor; Delsys Inc.). The sensor records four differential surface EMG signals in a diamond formation with the electrodes spaced 5 mm apart. The signals were sampled at 2222 Hz with sensor filtering at 20 – 450 Hz and wirelessly streamed to the EMGworks base station. A 1-second Hann window was applied to smooth the firing trajectories of detected motor unit waveforms. The EMG signals were decomposed into motor unit firing trains using the latest PDIII artificial intelligence algorithm (Neuromap v1.2; Delsys, Inc.), which is capable of identifying individual motor units during dynamic muscle actions (De Luca et al., 2015; Nawab et al., 2010). To ensure accuracy, motor unit firing events were validated using

the Decompose–Synthesize–Decompose–Compare test (De Luca & Contessa, 2012; Kline & De Luca, 2014) a method that generates a synthetic signal from the original data and compares decomposition accuracy between the two. Motor units with detection accuracExcluy below 80% were excluded, as this threshold has been established as an important threshold for assessing firing event accuracy during dynamic tasks (De Luca et al., 2015; Madarshahian et al., 2021). Additionally, trials with fewer than five motor units per contraction were excluded. As others have done (Hernandez-Sarabia et al., 2020; Marsala & Christie, 2024), we further attempted to reduce the influence of isolated or erroneous firings on mean motor unit firing rate calculations by excluding motor units trains had fewer than 10 discharges, average inter-pulse intervals (IPI) shorter than 10 ms (doublet discharges), IPI longer than 200 ms, and IPI coefficients of variation > 0.50. For motor units that met inclusion criteria, linear regression was performed on a task- and participant-specific basis to determine the slope and y-intercept of the motor unit action potential amplitude versus firing rate relationship. Additionally, the average firing rate and average motor unit action potential amplitude were calculated for each individual repetition and compared across loads and sexes.

3.4 Statistical Analyses

A two-level multilevel linear model in HLM version 8.2.3.14 using restricted maximum likelihood was used to estimate fixed and random effects. Tests of model fit were calculated using estimates from full information maximum likelihood. Repeated measures (i.e., level one, $N = 152$) were nested within participants (i.e., level two, $N = 35$). There were two models estimated. The unconditional model, a one-way random effects ANOVA, was estimated first. Next, a random intercepts random slopes model was estimated. Condition was entered uncentered in the model as a level one predictor. Sex was entered uncentered (male was coded as one; female as zero) as a

level two predictor for the intercepts and moderator for the slopes. Specifically, the model was formulated as follows:

$$Y_{ti} = \beta_{00} + \beta_{01}Male + \beta_{10}Condition + \beta_{11}Condition * Male + r_{0i} + r_{1i} + e_{ti}$$

Where:

- Y_{ti} is *Motor unit discharge parameter* value for participant *i* at measurement *t*,
- β_{00} is the intercept, representing the overall mean of the outcome,
- β_{01} is the fixed effect of sex (male vs. female),
- β_{10} is the fixed effect of Condition (L1 vs. L2),
- β_{11} is the moderating effect of sex on Condition,
- r_{0i} is the random effect for the intercepts, capturing individual deviations from the overall outcome mean,
- r_{1i} is the random effect for the slopes, capturing individual deviations from the overall slope,
- e_{ti} is the residual error, capturing within-participant variability.

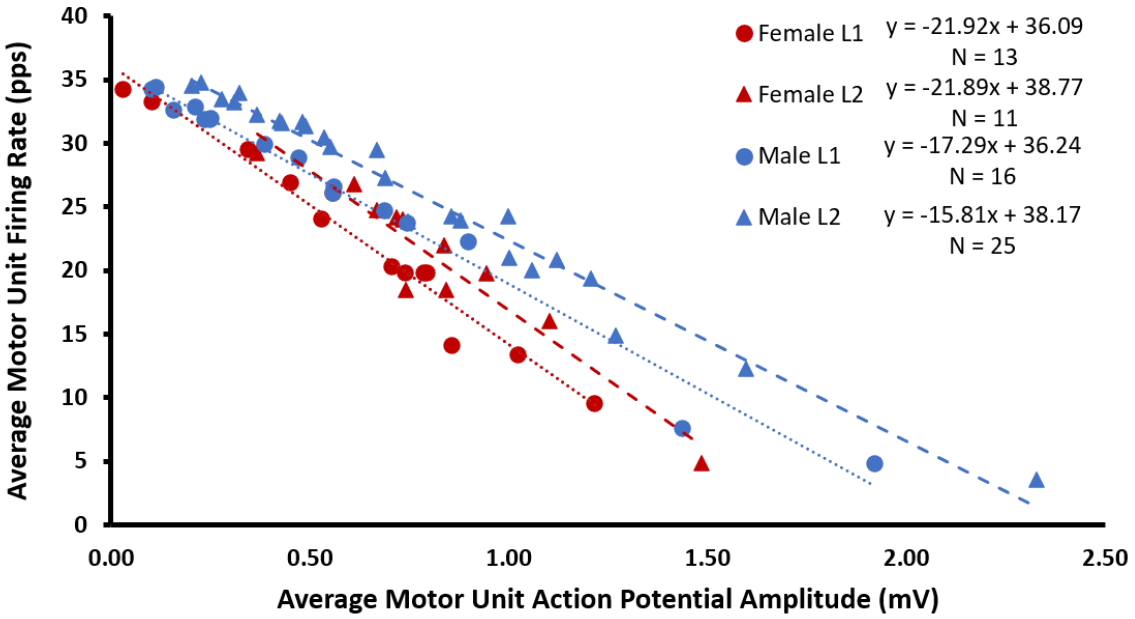

Figure 1. Representative MUAPamp versus firing rate relationship. Depicted in a reference male and female across loading conditions. The regression outcomes (slope and Y-intercept), along with the number of motor units included, are listed next to the legend.

CHAPTER IV: RESULTS

The data, based on the final models, were screened to determine the extent to which the assumptions associated with multilevel modeling were met. These assumptions included: (1) linearity; (2) normally distributed and equal variances of level one residuals; and (3) multivariate normal and homoscedastic level two residuals. Linearity and homogeneity of variance at level one was reviewed by plotting the level one residuals to fitted values and at level two assessed by examining Empirical Bayes residuals to level two predictors. A random display of points suggested this assumption was met for all models for both level one and level two residuals.

Level one normality of residuals was suggested with standardized skewness within an absolute value of two for Y-Intercept, average firing rate, and motor unit action potential amplitude residuals. However, there was slight non-normality with residuals from the slope model. Standardized kurtosis was within an absolute value of two for average firing rates and motor unit action potential amplitude residuals confirming normality. Non-normality was suggested in the kurtosis for Y-Intercept and slope residuals. Shapiro-Wilk's formal test of normality suggested a normal distribution for Y-intercept ($SW = .987$, $df = 152$, $p = .181$), average firing rates ($SW = .991$, $df = 152$, $p = .415$), and average motor unit action potential amplitude residuals ($SW = .985$, $df = 152$, $p = .104$), but suggested non-normality for slope residuals ($SW = .924$, $df = 152$, $p < .001$). The effects were deemed robust to subtle violations and thus, it was reasonable to proceed with the data. Multivariate normality was assessed by a scatterplot of Mahalanobis distance (MDIST) and the expected values of the order statistics (CHIPCT). The points generally adhered to a diagonal line, showing evidence of multivariate normally distributed data.

The hypothesis test for homogeneity of variances at level one suggested that equal variances between participants is plausible for three of the four models (Y-intercept, $\chi 2 = 30.195$, $df = 24$, $p = .178$; Average Firing, $\chi 2 = 22.96$, $df = 24$, $p > .500$; MUAP, $\chi 2 = 13.19$, $df = 24$, $p > .500$). Homogeneity of equal variances was not supported for Slopes ($\chi 2 = 84.65$, $df = 24$, $p < .001$). Homoscedasticity at level one was also examined by plotting Empirical Bayes residuals to the level one predictor. From all models, a random display of points above and below zero suggested that homoscedasticity was reasonable. It is anticipated that some non-normality and heteroscedasticity from the slope model may be due to outliers. Due to the way the data were collected (e.g., by limb), removal of cases would have created imbalance within participant. Additionally, simulation research suggests that fixed effect estimates are relatively robust to violations of normality (Shieh et al., 1999). Thus, model estimation proceeded.

4.1 Y-Intercept of the Motor Unit Action Potential Amplitude versus Firing Rate Relationship

Based on the unconditional model (see Model 1, Table 2), the intraclass correlation coefficient (ICC) was .74, suggesting that about 74% of the variation in Y-intercept is between participants. Thus, it was deemed reasonable to proceed with the multilevel linear model. There was statistically significant variation between participants ($u_0 = 21.241$, $p < .001$), also supporting the need for a multilevel model. Next, a random intercepts random slopes model was estimated (see Model 2, Table 2). Males had statistically significantly higher Y-intercept ($p < .001$) by about seven units higher compared to females. Y-intercept for L2 was statistically significantly greater than L1 ($p = .025$) by nearly 1-1/2 units. Sex was not a statistically significant moderator of the relationship between L2 and Y-intercept ($p = .432$).

Statistically significant variation in average Y-intercept (u_0) between participants still exists as does statistically significant slope variance (u_1). Additional predictors were included in the model to assist in explaining this between-person variability but were not effective in decreasing the variation. Relative to the null model, the proportion reduction in total variance of the outcome has been reduced by 62%. Both AIC and BIC have decreased when reviewing model two relative to the null model, suggesting model fit has improved. Additionally, the deviance test suggests model two has statistically significantly better fit as compared to the null model. The data is visualized in Figure 2.

4.2 Slope of the Motor Unit Action Potential Amplitude versus Firing Rate Relationship

The ICC was .82, suggesting that about 82% of the variation in slopes is between participants, providing support for a multilevel model. There was statistically significant variation between participants (u_0 = 723.70, p < .001). Males had statistically significantly higher slopes (p < .001) by about 40 units higher compared to females. There was not a statistically significant relationship between slopes and L2, suggesting that slopes were similar for L1 and L2 (p = .301). Sex was not a statistically significant moderator of the relationship between L2 and slope (p = .694).

Statistically significant variation in average slopes (u_0) between participants still exists. The slope variance (u_1) was not statistically significant, suggesting the relationship between slopes and L2 was similar across participants. Relative to the null model, the proportion reduction in total variance of the outcome has been reduced by 49%. Both AIC and BIC have decreased when reviewing model two relative to the null model, suggesting model fit has improved. Additionally, the deviance test suggests model two has statistically significantly better fit as compared to the null model.

4.3 Average Firing Rate

The ICC was .52, suggesting that about 52% of the variation in the average firing rate is between participants, providing support for a multilevel model. There was statistically significant variation between participants (u_0 = 9.38, p < .001), further supporting the need for a multilevel model. Males had statistically significantly higher average firing rates as compared to females (p < .001) by about four units higher on compared to females. There was not a statistically significant relationship between average firing rate and L2, suggesting that average firing rate was similar for L1 and L2 (p = .114). Sex was not a statistically significant moderator of the relationship between L2 and Average Firing (p = .449).

Statistically significant variation in the average firing rate (u_0) between participants still exists. The slope variance (u_1) was not statistically significant, suggesting the relationship between average firing rate and L2 was similar across participants. Relative to the null model, the proportion reduction in total variance of the outcome has been reduced by 78%. Both AIC and BIC were decreased when reviewing model two relative to the null model, suggesting model fit has improved. Additionally, the deviance test suggests model two has statistically significantly better fit as compared to the null model.

4.4 Average Motor Unit Action Potential Amplitude

The ICC was .74, suggesting that about 74% of the variation in motor unit action potential amplitude is between participants, providing support for a multilevel model. There was statistically significant variation between participants (u_0 = 0.07, p < .001), further supporting the need for a multilevel model. Males had statistically significantly higher motor unit action potential amplitude (p < .001) by nearly one-half unit higher compared to females. There was not a statistically significant relationship between motor unit action potential amplitude and L2, suggesting that

motor unit action potential amplitude was similar for L1 and L2 (p = .560). Sex was not a statistically significant moderator of the relationship between L2 and motor unit action potential amplitude (p = .183).

Statistically significant variation in mean motor unit action potential amplitude between participants still exists (u_0). The slope variance (u_1) was not statistically significant, suggesting the relationship between motor unit action potential amplitude and L2 was similar across participants. Relative to the null model, the proportion reduction in total variance of the outcome has been reduced by 44%. Both AIC and BIC were decreased when reviewing model two relative to the null model, suggesting model fit has improved. Additionally, the deviance test suggests model two has statistically significantly better fit as compared to the null model.

Table 2. Summary of Fixed and Random Effects for All Models.

Standard errors are presented in parentheses. *p < 0.05, **p < 0.01								
	Y-Intercept		Slope		Average FR		Average MUAP	
Fixed Effects	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2
Mean Outcome	3.39 (0.03)**	3.44** (0.11)	-49.11 (4.69)	-63.54 (4.44)	18.80 (.60)	16.62 (.67)	0.42 (0.05)**	0.25 (0.04)**
L2		1.345* (0.572)		2.68 (2.55)		1.04 (.64)		0.17 (0.03)
Male		6.948** (1.375)		38.94 (7.58)**		5.19 (1.14)		0.41 (0.06)**
Male * L2 (moderator)		0.778 (0.978)		-1.73 (4.36)		-0.84 (1.10)		0.07 (0.05)
Random Effects								
Intercept variance between participants (u_{0_j})	21.242**	11.895**	723.70**	370.56**	9.38**	6.20**	0.07**	0.02**
Slope variance between participants (u_{1_j})	--	2.028*	--	1.52	--	2.08	--	< 0.001
Within participant variance (r_{ij})	7.151	5.639	159.67	160.98	8.45	7.63	0.02	0.02
Model Fit								
-2LL (Deviance Test)	--	χ^2= 47.751, *df* = 5, *p* < .001	--	χ^2= 39.896, *df* = 5, *p* < .001	--	χ^2= 25.061, *df* = 5, *p* < .001		χ^2= 41.068, *df* = 5, *p* < .001
AIC	823.86	786.10	1309.65	1279.75	819.50	804.41	-52.59	-83.66
BIC	832.93	810.30	1318.72	1303.94	828.50	828.60	-43.52	-59.46

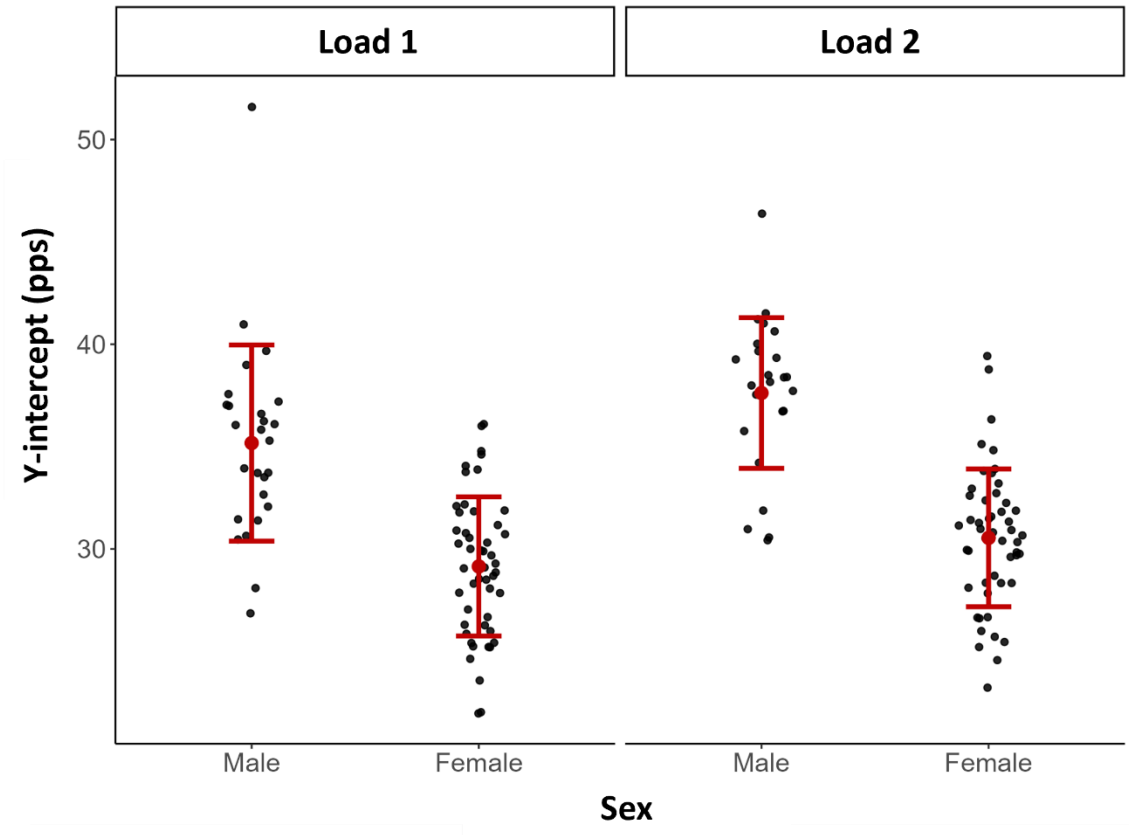

Figure 2. Y-intercept values (pps) across sex and load conditions. Individual data points (black dots) represent Y-intercept values (pps) for each participant, grouped by sex (Male, Female) and load condition (Load 1, Load 2). Red markers indicate group means, with error bars representing standard deviation. The Y-intercept values are significantly greater in males ($p < 0.01$) than females, and greater in Load 2 than Load 1 ($p = 0.025$).

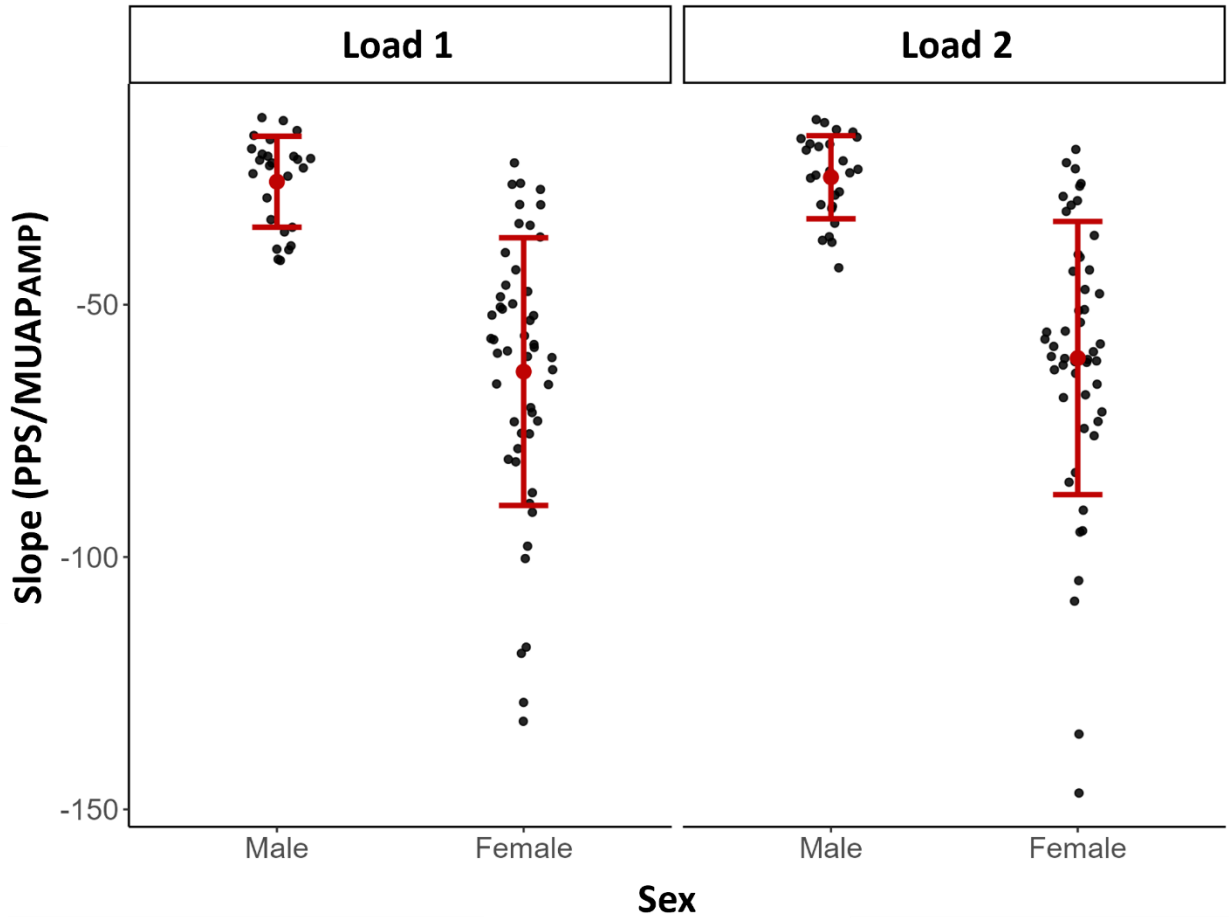

Figure 3. Average $MUAP_{amp}$ Versus FR slope values across sex and load conditions. Individual data points (black dots) represent the slope values ($PPS/MUAP_{amp}$) for each participant, grouped by sex (Male, Female) and load condition (Load 1, Load 2). Red markers indicate group means, with error bars representing standard deviation. The females had significantly lesser (steeper) slopes than the males ($p < 0.01$) with no difference between loading conditions ($p = 0.301$).

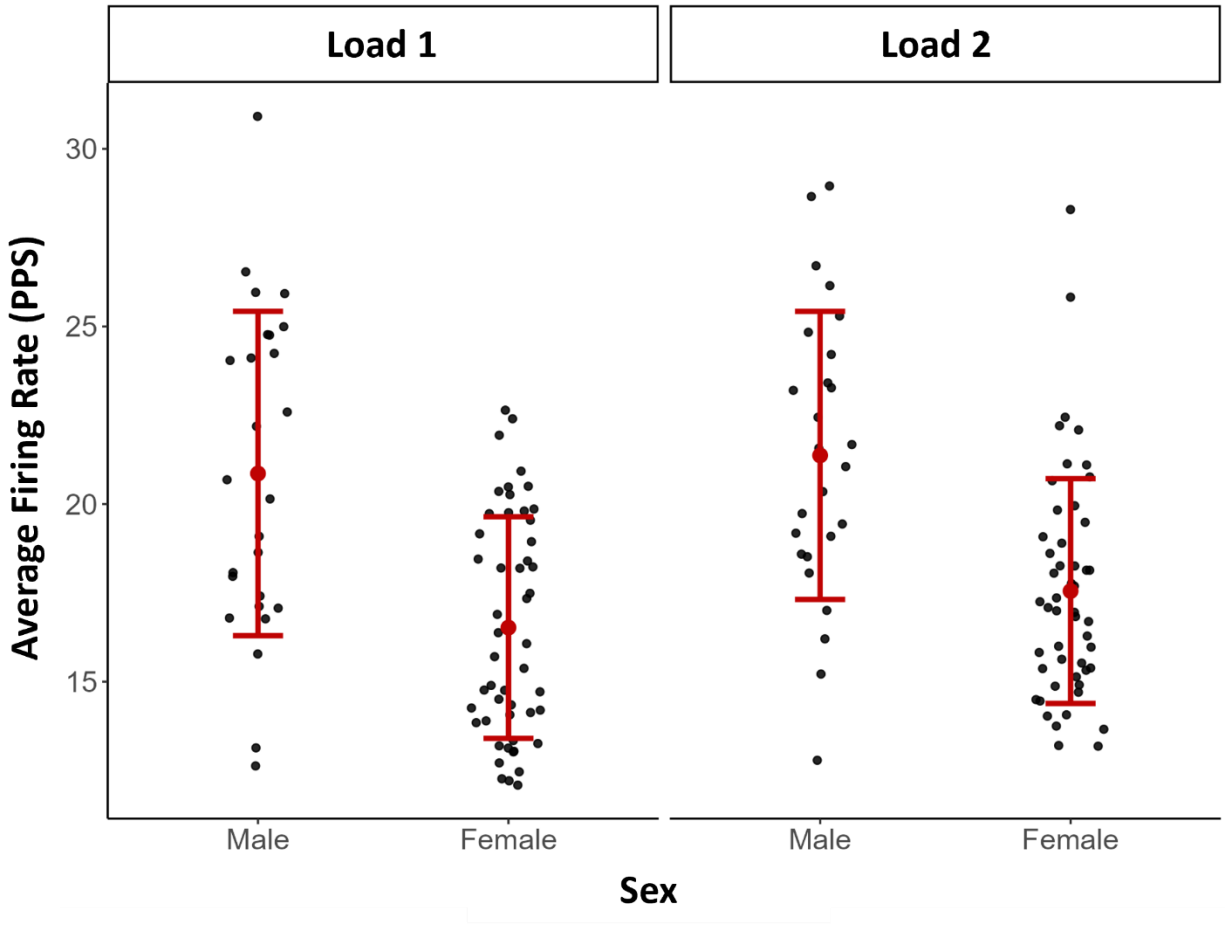

Figure 4. Average FR values (pps) across sex and load conditions. Individual data points (black dots) represent Y-intercept values (pps) for each participant, grouped by sex (Male, Female) and load condition (Load 1, Load 2). Red markers indicate group means, with error bars representing standard deviation. The males had significantly greater FR than the females ($p < 0.01$) with no difference between loading conditions ($p = 0.114$).

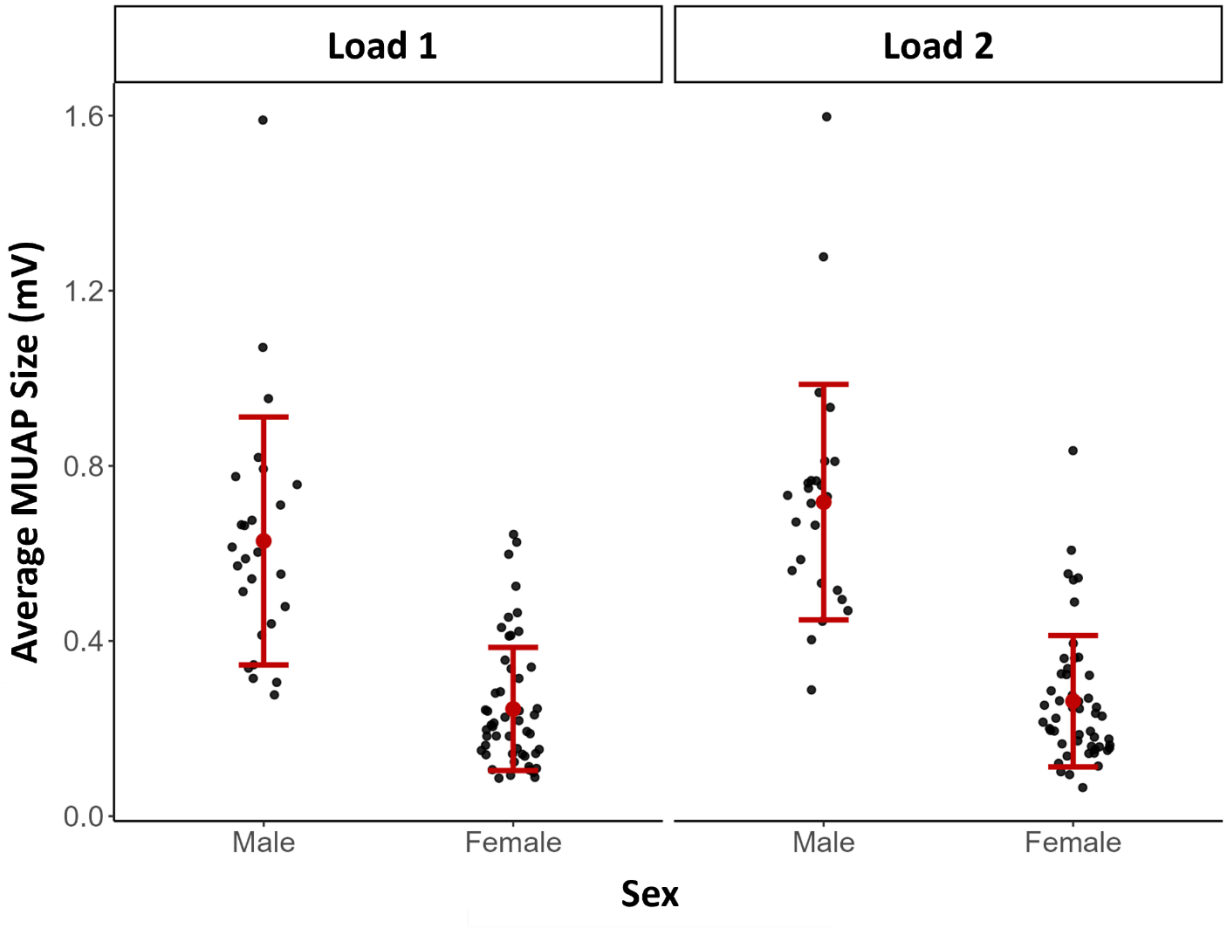

Figure 5. Average $MUAP_{amp}$ values across sex and load conditions. Individual data points (black dots) represent $MUAP_{amp}$ values (mV) for each participant, grouped by sex (Male, Female) and load condition (Load 1, Load 2). Red markers indicate group means, with error bars representing standard deviation. The males had significantly greater MUAP amplitudes than the females ($p < 0.01$) with no difference between loading conditions ($p = 0.560$).

CHAPTER V: DISCUSSION

This study compares the influence of intensity and sex during dynamic muscle actions and compares these parameters between males and females. Furthermore, the use of surface EMG to acquire the motor unit firing behavior during these conditions aims to add to the limited literature utilizing this technique. The main findings suggest increased neural input to the motor unit pool during L2 compared to L1, evidenced by significant increases in the Y-intercept of the motor unit action potential amplitude versus firing rate relationship, despite no significant changes in the average motor unit firing rates. Additionally, this study illustrated significant differences in motor unit firing behavior between sexes, with males showing greater Y-intercepts and slopes of the motor unit action potential amplitude versus firing rate relationship with significantly higher average firing rate and average motor unit action potential amplitude compared to females.

5.1 Load 1 versus Load 2

The depicted motor unit action potential amplitude versus firing rate regression reveals a strong, negative relationship, such as those observed during isometric muscle actions at near maximal intensity (Herda et al., 2019; Jenkins et al., 2021; Miller et al., 2019; Parra et al., 2021; Reece et al., 2021; Reece & Herda, 2021). As load increases from L1 to L2, there is a parallel, upward shift in the motor unit action potential amplitude versus firing rate relationship, aligning with findings observed during isometric muscle actions (De Luca & Hostage, 2010).

Despite no significant changes in average motor unit firing rate between L1 and L2, we found a significant increase in the y-intercept of the motor unit action potential amplitude versus firing rate relationship. Furthermore, there were no significant changes in slope or motor unit action potential amplitude between L1 and L2. These findings demonstrate while at substantially

elevated intensity levels *(~90% and 98% 1RM)* and despite subtle increases in load between conditions (*~1.3kg),* the motor unit pool receives heightened excitatory input, resulting in an elevation of the collective motor unit pool's firing rate, independent of recruitment gain or increases in individual motor unit firing rates. Motor unit firing behavior is clearly influenced by loading conditions and is muscle-specific. This was eloquently illustrated by De Luca & Hostage, 2010, who depicted the recruitment threshold versus motor unit firing rate relationships of various muscles at increasing intensities. They illustrated that as intensity increases from low to moderate, Y-intercept increased while the slope of the relationship flattened *(increased)*. However, the changes in motor unit firing behavior when intensity increased from 80% to 100% was solely a result of increases in Y-intercepts rather than other parameters. This study's findings parallel those of De Luca and Hostage along with others (De Luca & Contessa, 2012), indicating that neural control strategies of motor units are conserved across movement paradigms of maximal intent, a novel finding.

At this high fraction of intensity *(>90% for both L1 and L2),* it can be assumed that all motor units within the biceps brachii were actively contributing to the muscle action since maximum motor unit recruitment within this muscle is reached at ~88% MVC (Kukulka & Clamann, 1981). With no significant difference in motor unit action potential amplitude between loading conditions *(p=0.560)* as detailed, this indicates that L2 was completed in the absence of recruitment gain, paralleling previous work (Kukulka & Clamann, 1981). Additionally, the insignificant differences in motor unit firing rates between L1 and L2 demonstrate that a successful attempt for L2 was not a result of increases in individual motor unit firing rates. It is understood that during submaximal muscle actions, as intensity increases, individual motor unit firing rates can increase accordingly. However, as a given muscle reaches the intensity level requiring

maximum motor unit recruitment, motor unit firing rates may plateau despite further increases in load. This finding was demonstrated in a dramatic example with the anconeus muscle, where at 5% MVC motor unit reached maximum firing rates and with subsequent increases in intensity, there were no significant changes in motor unit firing rates (Le Bozec & Maton, 1987). All motor units exhibit a saturation point, which describes that further increases in a motor unit's firing rate will not provide significant increases in force output by the motor unit. Moreover, further excitatory input on the motor unit at its saturation point will not significantly increase its firing rate, providing an explanation of the motor unit firing rate plateau observed in this study (Bellemare et al., 1983; Brooks et al., 2023; J. Dideriksen & Del Vecchio, 2023; Fuglevand et al., 2015). Furthermore, this concept aligns with the onion-skin phenomenon, where motor unit firing rates will increase and reach a plateau based on their anatomical features (De Luca et al., 1982; Deluca & Erim, 1994). The collective findings in motor unit action potential amplitude and firing rate elaborate on the notion that at near-maximal intensities, elevation in the motor unit pool's operating point is responsible for executing higher load tasks and is not a result of increases in motor unit firing behavior or recruitment.

5.2 Sex Differences

There is consistent evidence that sex differences exist in motor unit firing dynamics. However, as detailed by Lulic-Kuryllo & Inglis, 2022, a wide variety of experimental designs exists, clouding the extent of these divergences. To address the heterogeneity in methodology, recent studies have examined sex differences between lower and higher force output (Nishikawa et al., 2024; Olmos et al., 2023; Parra et al., 2020; Trevino et al., 2019) or with incremental increases across the force spectrum (Inglis & Gabriel, 2021). Few studies have described sex divergences as intensities approach maximums, with no studies assessing subtle increases during

these conditions. This study's novel design addresses this gap, elaborating on sex determinants on performance.

This study demonstrates significant sex dimorphisms in motor unit firing behavior, which corroborates the work of others (Lulic-Kuryllo & Inglis, 2022). Specifically, males exhibited higher y-intercepts and greater slopes *(flatter)* of the motor unit action potential amplitude versus firing rate relationship, average motor unit firing rate, and average motor unit action potential amplitude compared to females. These findings parallel the current literature demonstrating that during high-intensity muscle actions, males recruit larger, higher threshold motor units opposed to females who may deploy different neural control strategies by relying on greater relative firing rate. This divergence is likely a compensatory mechanism for smaller muscle fiber territories, reduced twitches, and differences in muscle fiber composition (Inglis & Gabriel, 2020; Lecce et al., 2024; Olmos et al., 2023; Trevino et al., 2019).

The most established explanation for sex-based differences in motor unit firing behavior is attributed to divergence in anatomical features as it is well understood that females exhibit significantly smaller muscle cross-sectional area, differing muscle fiber composition that favors Type I muscle fibers, and smaller Type II/Type I muscle fiber composition ratio compared to males (Nuzzo, 2024; Olmos et al., 2023). Accounting for Type I muscle fibers being innervated by Type I α-motor neurons, it seems logical to infer that regardless of intensity, females should exhibit greater motor unit firing rate, contrasting our findings. This inference was demonstrated by Colquhoun, Magrini, et al., 2018, where individuals with greater Type II muscle fiber compositions *(typically males)* exhibited lower Y-intercepts and greater *(flatter)* slopes.

This is demonstrated during submaximal muscle actions (Guo et al., 2022; Inglis & Gabriel, 2020; Kowalski & Anita D., 2020; Nishikawa et al., 2024; Taylor et al., 2022), however,

this relationship reverses at maximal intensities with males exhibiting greater motor unit firing rate and Y-intercepts as outlined in this study and others (Christie & Kamen, 2010; Inglis & Gabriel, 2020). For the Y-intercept, it is important to note that these findings from previous studies utilized the recruitment threshold versus firing rate relationship compared to the motor unit action potential amplitude versus firing rate deployed in this study. Given that both sexes operated at near maximal intensities *(~90-98% 1RM)* and that all motor units within the biceps brachii are recruited at ~88% MVC (Kukulka & Clamann, 1981), it can be assumed that the largest, highest-threshold motor units were active in both sexes. Thus, since males express a greater proportion of Type II to Type I muscle fibers and muscle cross-sectional area, they likely recruited more large, high-threshold motor units that fired at elevated rates compared to females. These findings are further explained by the work of Lecce et al., 2024, where they characterized sex difference in low- and high-threshold motor units, illustrating that female lower-threshold motor units exhibit greater neural drive and motor unit firing rate while the higher-threshold motor units of males exhibit greater neural drive and motor unit firing rate. The findings for females can explain why during submaximal muscle actions, females exhibit significantly greater motor unit firing rates. Conversely, the findings for males can explain why the motor units of males exhibit higher motor unit firing rates during near-maximal muscle actions, as presented in this study and others.

Apart from differences in muscle cross-sectional area and muscle fiber composition, anatomical divergences in α-motor neurons can contribute to the observed sex differences in motor unit firing behavior. In anesthetized nonhuman animal models, males exhibit larger and more motor neurons accompanied by larger muscle fibers and a greater number of muscle fibers innervated by a motor neuron (Celichowski & Drzymała, 2006; Celichowski & Drzymała-Celichowska, 2007; English & Widmer, 2003). Human post-mortem spinal cord histological

analysis details that males exhibit parallels the findings from nonhuman animal models, detailing that male spinal cords exhibit larger motor neurons (Yuan et al., 2000). These differences in motor neurons can modulate their synaptic input, excitability, and firing behavior, thus providing another avenue of how anatomical differences can explain sex differences in motor unit firing behavior.

While the influence of anatomical differences cannot be understated, the influence of differences in neuromodulation cannot be excluded, particularly at high-intensities (Škarabot et al., 2023). During intensity-matched tasks, females exhibit larger magnitudes of persistent inward currents. This finding indicates that females may deploy strategies that aid in maintaining sustained contractions versus males, who possess inherent anatomical advantages (Jenz et al., 2023). Additionally, females exhibit a greater incidence of doublet firing during isometric muscle actions across each contraction intensity from 20-100% MVC (Inglis & Gabriel, 2020, 2021). One hypothesis for this observation is to increase the tautness of the muscle-tendon unit due to greater tendon flexibility and laxity in females (Jakobi et al., 2018a; Smart et al., 2018). Doublets also modulate force development; specifically, those occurring at the onset of motor unit firing result in a significant increase in motor unit force generation (Cheng et al., 2013; J. L. Dideriksen et al., 2020; Mrówczyński et al., 2015). These findings demonstrate that females may exhibit increased doublet firing incidence as a compensatory mechanism to mitigate anatomical disadvantages to meet the task requirements of maximal intensity muscle actions. Additionally, females exhibit a greater magnitude of antagonist co-activation in many muscle groups, specifically the biceps brachii (Frey-Law & Avin, 2013; Pincivero et al., 2019). One key function of antagonist co-activation is to improve joint stability, explaining why females may exhibit greater magnitudes due to their propensity to exhibit greater joint laxity, including at the elbow joint (Gardner et al., 2021). As a result, antagonist co-activation can modulate motor unit firing behavior through

modulating spinal reflexes or inhibitory synaptic input onto the α-motor neuron, reducing its overall excitability from descending neural drive. While female α-motor neurons are more excitable (M. Hoffman et al., 2018; Mercan & Kuruoğlu, 2024), when antagonist co-activation is accounted for, this discrepancy is eliminated. This illustrates that females exhibit greater inhibitory synaptic input on their α-motor neurons, providing another explanation for sex differences in motor unit firing behavior (Mendonca et al., 2020). Moreover, recent evidence demonstrates that at higher levels of force output, females exhibit greater recruitment thresholds (Lecce et al., 2024; Nishikawa et al., 2024). This may be a result of greater antagonist co-activation or female's reliance on differing neural control strategies outlined above, nonetheless, this contributes to the sex differences observed in motor unit firing dynamics. Thus, the culmination of these aforementioned anatomical and neuromodulatory sex dimorphisms contributes to a symphony of modulatory influences in motor unit firing behavior.

5.3 Muscle Contraction and Electromyography Types

The decomposition of EMG signals into their respective motor unit action potential trains offers a window into the neural control strategies of the central nervous system and the functional behavior of skeletal muscle. While decomposition of EMG signals obtained from indwelling EMG has been considered standard of practice since its inception, its invasiveness raises inherent limitations, restricting the conditions that this technique can be utilized for to isometric, low-intensity, or slow muscle actions (Bawa et al., 2014; Desmedt & Godaux, 1977; F et al., 1983; Stotz & Bawa, 2001). While the implications of indwelling EMG studies provide the foundation for motor unit understanding, their applicability is limited as real-world human movement is dynamic in nature. The introduction of surface EMG in conjunction with the advent of advances in motor unit decomposition algorithms offers a non-invasive, reliable method of motor unit

acquisition under dynamic conditions (De Luca et al., 2015; Kline & De Luca, 2014). Additionally, surface EMG increases motor unit acquisition across the recruitment gradient, mitigating the historic disproportionate underrepresentation of high-threshold motor units and advancing the horizon of possible understanding in motor unit firing dynamics.

Under dynamic conditions, neuromechanical constraints interact in complex ways, which still pose challenges, specifically during high force and high velocity due to increased variability from rapid motor unit recruitment and firing rates (Del Vecchio et al., 2019). Despite these obstacles, the strides to overcome them are substantial. From the work of Orantes-Gonzalez et al., 2023 demonstrating differences in motor unit firing rate based on contraction type that aligns with previous isometric studies (Del Valle & Thomas, 2005; Kallio et al., 2013), to the work of Latash and others (Benamati et al., 2024; De et al., 2024) describing the role of the central nervous system in forming and modulating force-stabilizing synergies, the momentum of surface EMG-derived motor unit decomposition grows. This current investigation contributes findings of motor unit recruitment and firing parameters during dynamic, maximal-intent muscle actions that parallel previous work of isometric methodology. Collectively, our work demonstrates that motor units detected from surface EMG decomposition during dynamic maximal muscle actions corroborate established physiological principles of motor unit control while advancing the collective understanding of motor unit firing behaviors in an unknown area.

5.4 Methodological Concerns

This study had several limitations that warrant consideration. Primarily, we relied solely on the decompose-synthesize-decompose-compare method without applying secondary validation criteria for motor unit firing, such as spike-triggered averaging of motor unit action potential waveforms or utilizing the two-source method. The decompose-synthesize-decompose-compare

method first introduced by Nawab et al., 2010, and improved by De Luca & Contessa, 2012, assesses accuracy of motor unit decomposition through a series of steps: (1) decompose EMG signal into individual motor unit action potential trains, (2) synthesize a new EMG signal using only the decomposed motor unit spike trains and corresponding action potential templates, (3) add Gaussian noise to synthetic EMG signal, (4) decompose synthetic EMG signal, (5) compare motor units decomposed from synthetic EMG signal to original EMG signal. This method is frequently used to validate motor unit decomposition and is comparable to direct validation methods with the two-source method (Kline & De Luca, 2014).

Spike-triggered averaging is a waveform-averaging model where multiple segments of a recorded signal are time-aligned based on α-motor neuron firings *(the trigger).* Then, the time epoch about these firings is averaged across all the events to mitigate interference from other motor units. This method has been shown to improve the accuracy of motor unit decomposition from surface EMG (Hu et al., 2013a, 2013b; McManus et al., 2016; Thompson et al., 2018). However, other studies have indicated the accuracy of motor unit firing behavior relationships derived from surface EMG that only utilize the decompose-synthesize-decompose-compare method are reliable and are not improved with the addition of spike-triggered averaging (Beausejour et al., 2023; Herda et al., 2020; Parra et al., 2021). The two-source method utilizes the simultaneous collection of EMG and subsequent comparative analysis of data derived from surface EMG and indwelling EMG (Mambrito & De Luca, 1984). While this is a robust method that validates motor unit decomposition derived from surface EMG, it has been shown that surface EMG is a reliable and valid method and can be utilized independent of the two-source validation method (Holobar et al., 2009, 2011). Furthermore, it has been shown that when strict inclusion criteria are used, the motor unit action potential amplitude versus firing rate relationship is unaffected by potential

inaccuracies of motor unit decomposition derived from surface EMG (Hernandez-Sarabia et al., 2020). Considering that this study's methodology exhibited high accuracy of motor unit action potential trains *(Average ≥ 92%)* while applying robust inclusion criteria (Marsala & Christie, 2024), this furthers the methodological choice of omitting secondary validation.

It is important to note that in the initial investigation by De Luca et al., 2015 detailing the PDIII algorithm's ability to accurately decompose motor units obtained during dynamic muscle actions, data was acquired from cyclical, dynamic muscle actions. Furthermore, the authors stated the motor unit decomposition yield and accuracy increased with greater amounts of cyclical contractions *(eight contractions)*. This methodology allows the PDIII algorithm to account for intracycle shape changes and similarities, enhancing its decomposition ability. While this may seem to reduce the validity of this study's methodology, the ability of the PDIII algorithm to accurately decompose motor unit firing behavior from a singular muscle action, as detailed by well-established physiology, speaks to its ability and reliability to be used for motor unit firing dynamics analysis during dynamic muscle actions.

Different contraction intensities and desired probability levels are dependent on motor unit yield. Specifically, as both of these factors increase, the necessary motor unit yield increases (Marsala et al., 2024). In the context of motor unit yield, there is ongoing conversation on the influence of sex on motor unit yield (Lulic-Kuryllo & Inglis, 2022). These differences in motor unit yield on the basis of sex may be attributed to anatomical differences in factors such as subcutaneous tissue size and content (Hug et al., 2021; Lulic-Kuryllo et al., 2021) or elevated recruitment thresholds (Peng et al., 2018). To account for this, our sampling favored an increased proportion of female compared to male participants. Hesitancies about this unproportional distribution were addressed by our statistical approach, which employs multi-level modeling to

account for the hierarchical structure of the data, nesting motor units within individuals. This approach allows us to model both within-subject and between-subject variability, reducing the impact of individual differences on population-level inferences (Tenan et al., 2014).

Lastly, strength matching has been utilized in the context of sex differences to account for the deviations in muscle size and strength. As demonstrated by Inglis & Gabriel, 2020, the findings of males exhibiting significantly greater motor unit firing rates at 100% MVC resolved when participants were strength-matched. While superficially this seems to reduce the significance of our findings due to methodological differences, strength-matching possesses significant limitations. Specifically, this methodology often leads to comparisons between below-average males and above-average females relative to population norms. This makes the distinction between whether differences are a result of biological sex or disparities in fitness and physical activity levels inconclusive (Jakobi et al., 2018b; Lulic-Kuryllo & Inglis, 2022).

5.5 Conclusion

This study demonstrates that motor unit firing behavior during dynamic, maximal-intent contractions is modulated in a load-dependent manner, confirming the hierarchical control mechanism of motor units in a novel setting. Our findings indicate that despite modest increases in load *(~1.3kg)* at near maximal intensities, increases in neural drive elevate the operating point of the motor unit pool independent of recruitment gain or individual motor unit firing behavior. Additionally, we show that during these conditions, males exhibit greater motor unit action potential amplitudes, average firing rates, and motor unit behavior that favors generating high contraction forces (e.g., *flatter slope of the motor unit action potential amplitude versus firing rate relationship*) compared to females. This is likely as a function of unique muscle fiber compositions and motor unit firing behavior, specifically in high-threshold motor units. These

differences have implications for motor control, training adaptations, and neuromuscular rehabilitation, emphasizing the need for sex-specific considerations of motor unit behavior that account for the disparities as previously described. This study emphasizes the increasing momentum in the use of modern motor unit decomposition techniques in flexible movement patterns, more accurately reflecting the human condition.

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APPENDICES