Ph.D. Dissertation of Sport Science

Neuromuscular Mechanism on Enhancement of Voluntary Muscle Force Production

: Regulation of muscle activation pattern at level of motor units

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Graduate School of
Seoul National University
Department of Physical Education
Human Movement Science Major

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Abstract

The generation of voluntary muscle force relies on the intricate interplay between the neuromuscular system and motor unit activation. The motor unit, operating within this complex neuromuscular mechanism, serves as the primary link between the central nervous system (CNS) and the execution of movement. It acts as a neuromechanical transducer, converting sensory information and descending neural inputs into the necessary forces required for coordinated muscle actions. This dissertation quantifies the recruitment of motor units and firing rates, which are coding factors contributing to muscle force in the neuromuscular mechanism of human voluntary muscle force production. It investigates the interplay between the neuromuscular system and motor unit activation through three key experimental studies. Firstly, the relationship between joint angle and motor unit recruitment regulation is examined, revealing the role of the neuromuscular mechanism in coordinating muscle contractions based on body configuration. Secondly, investigates the effects of various interventions on neural adaptations. Specific focus on the short-term impact of the neuromuscular mechanism of warm-up exercises by quantifying the properties of recruited motor units, such as firing rate and recruitment threshold. Thirdly, the dissertation focuses on the long-term effect of neuromuscular strength training, which leads to increased muscle strength and expanded recruitment thresholds. This training optimizes motor unit activation and control, resulting in improved force production. In vivo, research further demonstrates that targeted interventions can enhance voluntary force production by regulating motor unit activation patterns. Overall, this research significantly advances our understanding of the complex interplay between the CNS and muscle contractions, providing valuable insights into how various interventions impact motor unit activation and ultimately influence muscle performance.

Keyword: Neuromuscular mechanism, Voluntary muscle force production, Motor unit activation, Neural adaptation, Neuromuscular strength training, Muscle activation
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Table of Contents

List of Table

List of Figures

Chapter 4

Chapter 5

Chapter 1. General Introduction

1.1. Problem Statement

Numerous studies and scientific perspectives have shed light on the mechanistic and physiological aspects of human movement control and adaptation (Zatsiorsky, 2002; Enoka, 2008; De Luca & Mambrito, 1987; Martin & Schovanec, 1999; Basmajian, 1985; Keynes, Aidley & Huang, 2001). Despite the diversity of these interpretations, they converge on the understanding that human movement patterns continually evolve and adapt in response to a range of factors. At the core of this complex process is the central nervous system (CNS), which governs the intricate human motor system. The CNS exhibits remarkable neural adaptation and plasticity to accommodate internal and external changes, including alterations in body configuration, temperature, and training (Enoka, 1997; Duchateau & Enoka, 2006; Enoka, 2008; Racinais & Oksa, 2010; Watanabe & Akima, 2011; Zatsiorsky, 2003; Zatsiorsky, 2008; Zatsiorsky, Kraemer & Fry, 2020). These distinct characteristics highlight the exceptional capabilities of the human neuromuscular system.

The neuromuscular system is a sophisticated integration of muscles and nerves, playing a pivotal role in facilitating voluntary movement and force production. It serves as a crucial communication pathway between the brain and muscles, enabling the transmission of signals that orchestrate motor function. This intricate interplay between nerves and muscles allows for the execution of precise and coordinated movements, as well as the regulation of essential bodily functions. The neuromuscular system represents a remarkable example of the intricate connections and mechanisms that underlie human motor control and performance.

The coordination of movement and control of bodily functions relies on the collaborative functioning of nerves and muscles within the neuromuscular system. Voluntary movement and the production of force necessitate muscle contraction, which is initiated by the activation of motoneurons in the spinal cord. Each muscle is innervated by multiple motor neurons, and the magnitude of muscle force generated is determined by the recruitment of these motor neurons and their firing rate. Significant studies conducted by Adrian & Bronk (1929), Bigland & Lippold (1954), Milner-Brown et al. (1973), Henneman & Mendell (1981), De Luca (1997), Enoka & Duchateau (2008), and Kandel et al. (2012) have firmly established the importance of motor neuron recruitment and modulation of firing rate in the production of muscle force. A comprehensive understanding of the intricate interplay between motoneurons and muscle contraction is crucial for elucidating the underlying mechanisms governing voluntary movement and force generation.

In order to comprehend the mechanisms behind improvements in muscle strength and human movement performance, it is crucial to consider not only the kinetics (e.g., joint torque, force) and kinematics (e.g., joint angle, velocity) but also the activity of motor units (Liddell & Sherrington, 1925; Sherrington, 1925). Motor units serve as the primary output of the central nervous system (CNS), converting sensory and descending neural inputs into the forces required for movement, making them key neuromechanical transducers. Despite the recognition of motor units as the final common pathway (Liddell & Sherrington, 1925; Sherrington, 1925; De Luca et al., 1982b; De Luca & Erim, 1994), our understanding of the neuromuscular mechanism remains relatively limited due to a lack of comprehensive knowledge regarding how the nervous system controls the activity of multiple motor units to generate voluntary force production.

Therefore, there is a significant need to further investigate motor unit behavior and quantify variables associated with the neuromuscular mechanism in order to acquire the knowledge required for a comprehensive understanding of the enhancement and control of human movement performance. Such findings have practical implications as they can be applied to strategies aimed at improving movement performance, designing effective strength training programs, and developing rehabilitation tools. By advancing our understanding of the neuromuscular system, these insights can benefit a wide range of individuals seeking to optimize their physical capabilities and overall quality of life.

The current dissertation will specifically address the following topics: 1) *Neuromuscular mechanism of a joint angle on torque and motor unit recruitment regulation.* The amount of force generated by a muscle reacts differently depending on the motor unit activity pattern and the muscle fiber and muscle-tendon complex mechanical properties (Haffajee, Moritz & Svantesson, 1972; Latash et al., 2010;). It has been well discovered that changing the angle of a joint, that is, the length according to a change in position, significantly affects the maximum force that a muscle can generate (Hansen et al., 2003; Leedham & Dowling, 1995; Linnamo et al., 2006; Koo et al., 2002). However, there is unclear what effect joint angle has on motoneuron excitation patterns. Consequently, it is unclear how motor unit activity, or the relationship between the motor unit and force, is altered by the joint angle. 2) *Neuromuscular mechanism of warm-up effect.* The properties of motor units within muscles such as the firing rate and recruitment threshold regulated by the central nervous system (CNS) play a key role to adjust muscle force (Bigland & Lippold,1954). It has been well discovered that the increment of body temperature has a positive effect on the magnitude of muscle force. However, there is scant evidence of the exact neuromuscular mechanism of the body temperature on the regulation of muscle force. 3) *Neuromuscular strength training based on neural adaptation to improve muscle force with motor unit recruitment and rate coding*. Neuromuscular strength training focuses on the neural adaptations that occur in the neuromuscular system to enhance muscle force. It is widely acknowledged that neuromuscular factors play a crucial role in improving muscle strength. Specifically, motor unit recruitment and rate coding are essential components that link neural activation to the mechanical force generated by muscle fibers. Despite previous studies, there is still limited understanding of the specific neuromuscular changes occurring at the motor unit level that contribute to the increase in muscle force following strength training. Duchateau and Enoka (2002), Herda (2022), and Duchateau et al. (2006) have highlighted this knowledge gap. Therefore, the primary objective of this study is to quantify the effect of neuromuscular strength training on neural adaptations.

1.2. Study Objectives

The overarching objective of this dissertation is to provide a comprehensive description of how motor unit function arises from the properties of motor neurons and muscle units. Additionally, the study aims to elucidate the neuromuscular mechanisms by which motor unit activity regulates muscle force production.

Furthermore, the dissertation seeks to identify and investigate factors that have the potential to enhance the performance of human movement.

1) To quantify the neuromuscular mechanism of a joint angle on torque and motor unit recruitment regulation (chapter 3).

2) To attempt to uncover the neuromuscular mechanism of the warm-up exercise through motor unit behavior quantification (chapter 4).

3) To quantify the effect of neuromuscular strength training based on neural adaptations (chapter 5).

1.3. Organization of Dissertation

The current dissertation consists of series of sub-studies that are systematically linked (Figure 1.1).

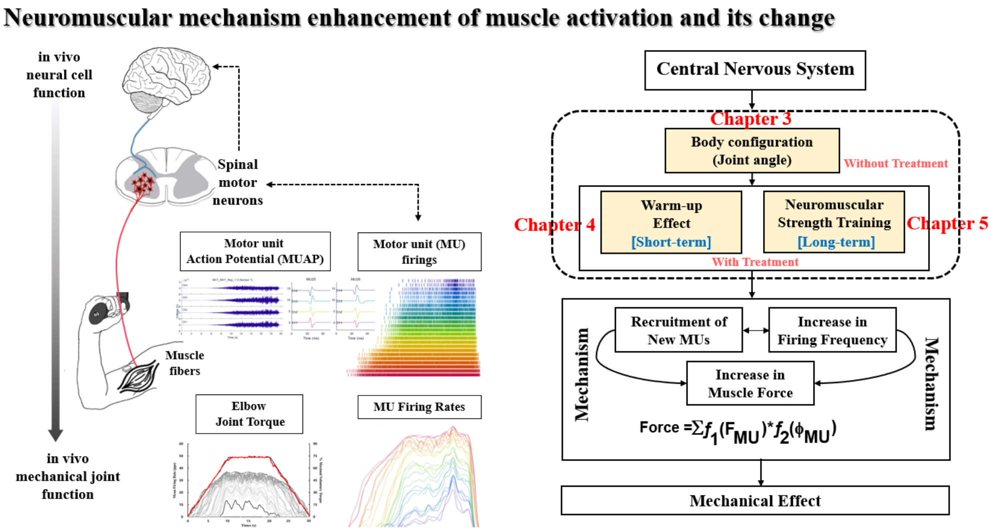


Figure 1.1. Organization of dissertation

1) Study 1 (chapter 3): The effect of an elbow joint angle on torque and motor unit recruitment regulation relationship in human elbow flexor and extensor muscles.

2) Study 2 (chapter 4): To quantify the Neuromuscular Effect of Warm-Up on Regulation of Motor Unit Properties during Isometric Torque Production Tasks.

3) Study 3 (chapter 5): To quantify the effect of neuromuscular strength training based on neural adaptations.

Chapter 2. Background of Literature Review

2.1. Motor Unit

The motor unit (MU) is indeed considered the basic and smallest functional unit of the neuromotor system. It acts as the common final pathway of the motor system, comprising a motor neuron located in the ventral horn of the spinal cord or brainstem, its axon, and the specific muscle fibers that it innervates (Liddell & Sherrington, 1925; Sherrington, 1925). To initiate voluntary muscle contraction, the central nervous system (CNS) orchestrates the transmission of a control signal from the brain to the spinal cord. This neural command is subsequently received by alpha motor neurons, which are responsible for innervating specific groups of skeletal muscle fibers. These innervated muscle fibers collectively constitute a "motor unit" (MU), representing the fundamental building block of the neuromotor system. Notably, the coordinated firing of muscle fibers within the MU results in synchronous contractions, underscoring the integral role of the MU as the basic functional unit. Upon activation, a single MU generates an electrical signal termed a motor unit action potential (MUAP) and produces a force output known as force twitch. As muscle contractions require the concerted activity of multiple MUs, it is evident that the neuromotor system functions as a neuromechanical transducer, translating neural signals into mechanical force during muscle contraction.

2.1.1. Motor unit types

Motor units have been classified into three primary types based on their response to sag and fatigue tests (Burke et al., 1999). Motor units that do not exhibit sag during prolonged contractions are categorized as slow-twitch contracting units (Type S). Conversely, motor units that display sag are identified as fast-twitch contracting units (Type F). Further categorization within the fast-twitch units differentiates between those that fatigue rapidly (Type FF) and those that exhibit fatigue resistance (Type FR) when subjected to a standardized stimulus protocol. This classification of motor units aligns with the classification of muscle fibers. Type S motor units correspond to Type I muscle fibers, Type FR motor units innervate Type IIa fibers, and Type FF motor units contain Type IIb (similar to Type IIx) muscle fibers. This classification scheme has been widely employed to characterize the characteristics of various muscles across different species and to examine the alterations that arise in response to various natural and induced interventions. By linking motor unit types with specific muscle fiber types, this classification system offers a comprehensive framework for studying the functional properties and adaptations of muscles in diverse contexts.

2.2. Motor unit recruitment during voluntary contraction

Extensive research has established that the nervous system governs voluntary actions by modulating the contribution of individual motor units and the overall number of motor units activated for a given task (Henneman & Mendell, 1981; De Luca, 1985; Enoka & Duchateau, 2008; Kandel et al., 2012; Heckman & Enoka, 2012). This capability to engage multiple motor units simultaneously is known as motor unit recruitment. Seminal studies by Adrian and Bronk (1929) and Seyffarth

(1940) have provided empirical evidence demonstrating that as the intensity of muscle contraction escalates, additional motor units are recruited, accompanied by an augmentation in the firing rates of the activated motor units. Further advancing our understanding of motor unit recruitment, Henneman (1957) made a significant observation that has become known as the Henneman Size Principle. According to this principle, in response to increasing excitation, motoneurons are recruited in a specific order based on their size. In essence, during a voluntary contraction, numerous motor units are activated, and their recruitment follows a hierarchical pattern of increasing size. This principle is closely associated with the arrangement of motor neurons based on their size distribution. Specifically, smaller motor neurons predominantly innervate slow-twitch muscle fibers, while larger motor neurons innervate fast-twitch muscle fibers. Consequently, as the force requirement of the muscle increases, the motor units are recruited in a sequential manner, starting from the smaller motor neurons that innervate slow-twitch fibers and progressing toward the larger motor neurons that innervate fast-twitch fibers.

Furthermore, Milner-Brown et al. (1973) conducted a study that revealed a noteworthy relationship between motor unit recruitment thresholds and contraction times. They found that motor units with higher recruitment thresholds exhibited faster contraction times, typically ranging from 30 to 100 milliseconds, in comparison to motor units with lower recruitment thresholds. This suggests that motor units with higher recruitment thresholds possess characteristics that allow for more rapid contractions.

In the context of relative force production during maximal voluntary contraction (MVC), the recruitment threshold of a motor unit provides insights into the relative size of that motor unit within the overall motor unit population contributing to muscle force generation. Consequently, changes in the force capacity of low-threshold motor units due to fatigue can have implications for the recruitment thresholds of larger motor units. This phenomenon implies that even though larger motor units may have minimal involvement in a specific task, fatigue-induced alterations in the force capabilities of low-threshold motor units can lower the recruitment threshold of the larger motor units (Baudry et al., 2009; Farina et al., 2009). Notably, the order of motor unit recruitment is relatively resistant to change and is not significantly influenced by various interventions such as physical training (Van Cutsem et al., 1998), aging (Fling et al., 2009; Klass et al., 2008), or muscle fatigue (Adam & De Luca, 2003). This stability in recruitment order implies that despite alterations in the force capacity of individual motor units, the hierarchical recruitment pattern remains largely unchanged.

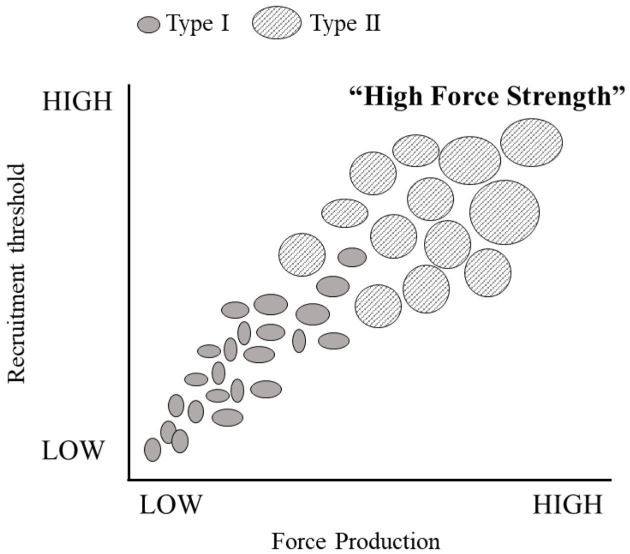


Figure 2.3. Size Principle of motor unit recruitment threshold. The motor neurons are arranged according to their size. Dark gray circles are type I motor units, light gray circles are type II motor units, and large circles indicate larger motor units containing more fibers. The line of orderly recruitment, the heavier resistance recruits more and more motor units

and associated muscle fibers.

Despite the widespread agreement on the size principle as the basis for motor unit recruitment during voluntary contractions (Feiereisen, Duchateau & Hainaut, 1997; Jones, Lyons, Bawa & Lemon, 1994; Scutter & Turker, 1998), there have been suggestions that specific conditions may require some flexibility in this recruitment scheme. One such condition is related to changes in muscle length during movement (Mattei et al., 2003; Seyffarth, 1940). The synaptic input received by the motor nucleus is influenced by both isometric and non-isometric contractions (Tax et al., 1989; Tax et al., 1990; van Bolhuis, Medendrop & Gielen, 1997), and as a result, the recruitment order of motor units may be altered during muscle shortening and lengthening. Desmedt and Godaux (1979) conducted experiments on the First Dorsal Interosseous (FDI) muscle and observed potential alterations in the recruitment order of motor units across three types of contractions: low isometric contractions, ballistic isometric contractions, and slow and ballistic shortening contractions. These findings suggest that the recruitment order of motor units can be influenced by the specific characteristics of the contraction being performed.

2.3. Rate Coding of Motor Unit Discharge

The control of force generation during voluntary muscle contractions involves the recruitment of motor units and rate coding mechanisms (Bigland & Lippold, 1954; Gydikov & Kosarov, 1974; Milner-Brown et al., 1973; Monster & Chan, 1977; Person & Kudina, 1972; De Luca, 1985; Enoka & Duchateau, 2008; Kandel et al., 2012; Heckman & Enoka, 2012). The relative contribution of a recruited motor unit to a specific task is determined by the rate at which it generates action potentials, a process known as rate coding. Each motor unit possesses a force-frequency relationship, indicating the relationship between its discharge rate and the resulting muscle force. However, the discharge rate observed in a motor unit can vary depending on the nature of the task being performed. For instance, as the discharge rate gradually increases, muscle strength exhibits a linear increase, with a pronounced relationship between the rate of discharge rate increment and force (Seyffarth, 1940; Person & Kudina, 1972; Tanji & Kato, 1973).

Desmedt and Godaux (1977) were the first to propose a description of motor unit discharge in the tibialis anterior muscle during ballistic contractions. They reported that the motor unit exhibited a high instantaneous discharge rate (60-120 Hz) at the onset of ballistic contraction, which gradually decreased during subsequent discharges. This observation may reflect the early stage of discharge rate adaptation observed during repetitive activation of motor neurons (Sawczuk et al., 1995; Miles et al., 2005). A similar discharge pattern was also observed in the first dorsal interosseus (Desmedt & Godaux, 1977) and the masseter (Desmedt & Godaux, 1979). These elevated rates of motor unit discharge appear to have an impact on the strong excitatory inputs required for generating ballistic contractions.

2.4. Joint Angle and Voluntary Force Production

It is widely recognized that altering joint angle or muscle length has a substantial influence on the voluntary force generation capacity of a muscle (Hansen et al., 2003; Leedham and Dowling, 1995; Linnamo et al., 2006; Koo et al., 2002).

Furthermore, the length of muscle fibers and the rate of length change directly impacts maximal voluntary force production, as elucidated by the established force-length and force-velocity relationships of muscle (Zajac, 1989). During isometric contractions, both muscle length and joint angle must be taken into account as determinants of maximal voluntary muscle force production.

The adjustment of joint angle has been observed to elicit alterations in neural activity during isometric contractions, including modulation of motoneuron stimulation rate (Rack and Westbury, 1969; Harridge and White, 1993) and the integration of afferent feedback from sensors within the muscles and joints of the human body (Stein and Kearney, 1995; Vander Linden et al., 1991; Suter and Herzog, 1997). Notably, the force generation capacity of a muscle relies not only on the neural commands originating from the central nervous system (CNS) but also on its length. Consequently, muscle length has the potential to modify motor unit recruitment thresholds (Miles et al., 1986).

2.5. Warm-up Effect (Short-term effect)

The motor system is characterized by its remarkable adaptability, capable of undergoing both structural and functional modifications in response to acute stress. In this section, we examine the acute adaptations of the motor system and its response to stress induced by warm-up exercises. Specifically, we investigate the techniques and mechanisms underlying the observed changes in muscle potentiation and the impact of arousal on performance. This dissertation centers around the study of human movement, with a particular emphasis on exploring how a warm-up exercise influences the muscle's capacity to generate force, perform work, and produce power.

An important benefit of a warm-up is the increase in muscle temperature, which positively impacts the biomechanical performance of the motor system. Activities such as vertical jumps or throws typically show improved performance following a warm-up, primarily due to the influence of increased muscle temperature on contraction speed and power production. Elevated temperature levels enhance both the maximal velocity of muscle shortening and peak muscle power. The improvement in jump performance can be attributed to the effect of muscle temperature on contraction speed. Within the physiological temperature range, changes in temperature specifically affect the maximal velocity of muscle shortening while leaving maximal isometric force unchanged. Previous studies have demonstrated that alterations in contraction speed result in an increase in peak power output. Therefore, the increase in muscle temperature during a warm-up contributes to improved muscle performance by enhancing contraction speed and power production (Binkhorst et al., 1977; Cheung & Sleivert, 2004; de Ruiter et al., 1999; de Ruiter & de Hann, 2000).

Significant changes in muscle temperature have been found to alter the force capacity of muscles, indicating the influence of temperature on muscle performance (Ranatunga et al., 1987; Steinen et al., 1996). For instance, Bergth and Ekblom (1979) observed an increase in maximal isometric torque of the knee extensor muscle, from 262 Nm to 312 Nm, when the muscle temperature was raised from 30.4°C to 38.5°C (a 2.4% increase). This increase in maximal torque was associated with a 44% improvement in vertical jump height and a 32% increase in power production during cycling. The underlying physiological mechanisms for these improvements in exercise performance following warm-up are primarily attributed to temperature-related mechanisms (Asmussen & BØJe, 1945; Bergth & Ekblom, 1979). Elevated muscle temperature has been linked to increases in muscle metabolism (Gray et al., 2011) and muscle fiber conduction velocity (MFCV) (Pearce et al., 2012). Additionally, enhancements in VO2 kinetics (the rate of oxygen uptake) (Poole & Jones, 2012) and improvements in muscle contractile performance following prior contractile activity have been reported (Sale, 2002). These physiological responses further support the notion that warm-up induced increases in muscle temperature contribute to improved muscle function and performance in various exercise tasks.

An active warm-up involves increasing muscle temperature through muscle activity. The extent of temperature increase during an active warm-up is dependent on the intensity of muscle contraction. Saugen and Vollestad (1995) conducted a study in which subjects performed isometric contractions (lasting 8-20 seconds) with the quadriceps femoris muscles. They found that the greatest increase in temperature in the vastus lateralis muscle occurred when the contraction was within the range of 30% to 70% of maximum voluntary contraction (MVC) force. That temperature did not increase further with stronger contraction. The increase in temperature ranged from 3.1 mk/s at 10% MVC to 14mk/s at 70% MVC (mk=millikelvin). As a result, an active warm-up improves the execution of a brief performance (<10) more than a passive warm-up and can attenuate lactate accumulation in subsequent intense activity.

2.6. Neural Adaptation and Strength Training (Long-term effect)

The neuromuscular system exhibits remarkable adaptability in response to external demands and environmental stimuli. This adaptability is evident in the immediate changes observed in the structure and function of the neuromuscular system following strength training. In the past, it was commonly believed that muscle size, as measured by cross-sectional area, was the primary determinant of strength. Consequently, weight training was used to induce muscle hypertrophy, aiming to increase strength. However, research since the 1980s, conducted by authors such as Vladimir Zatsiorsky and Roger Enoka, has shifted the focus to the neural aspects of strength expression.

It has been recognized that effective strength training involves not only muscle hypertrophy but also improvements in the neural elements of strength expression. Two key qualities of effective strength training are the ability to recruit more motor units during contractions and the ability to contract motor units at a faster rate. While hypertrophy is typically accompanied by increased strength due to adaptation to training stress, enhancing the neuromuscular system is a primary mechanism for increasing strength and power without necessarily increasing muscle size.

2.6.1. Neural adaptation to Strength Training

The gradual increase in electromyography (EMG) amplitude observed during strength training suggests that the improvement in strength is accompanied by heightened motor unit activity, potentially resulting from augmentation in peak discharge rate. Notably, the relationship between strength training and adaptations in motor unit activity is most prominently demonstrated in rapid muscle contractions (Vila-Chã, Falla & Farina, 2010). Prior investigations have compared the initial discharge rate of the tibialis anterior motor unit before and after a 12-week training period involving rapid contractions with moderate loads (up to 35%). The training regimen resulted in increased torque generation and enhanced EMG response during rapid maximal contractions (Duchateau, Semmler & Enoka, 2006). By examining the instantaneous discharge rates of the first four action potentials, researchers evaluated the fundamental alterations in motor unit activity that underlie the accelerated rise in surface EMG. Notably, the average instantaneous discharge rate rose from 69 pulses per second (pps) to 96 pps following training, with a significant increase in the number of motor units firing in the brief interval between successive action potentials. Consequently, the ability to enhance torque production at a faster rate was associated with adaptations in motor unit discharge rate.

2.6.2. Motor unit recruitment and rate coding changes with strength training

In previous investigations examining alterations in the maximal discharge rate of human motor units, particularly in response to training interventions, Van Cutsem et al. (1998) conducted a study involving ballistic contractions of ankle dorsiflexor muscles over a period of 3 months using moderate loads (30-40% MVC). The findings revealed a substantial 82% enhancement in maximum rate of force development (RFD) during these ballistic contractions. Notably, while no changes were observed in the order of motor unit recruitment, the average rate of discharge for the first four action potentials increased by 38% following the training period.

Additionally, the training regimen also resulted in an increase in the number of motor units (ranging from 5% to 33%) exhibiting discharges surpassing 200 Hz at the onset of activation. The notable enhancement in rate of force development (RFD) observed during ballistic contraction predominantly stemmed from the adaptation of motor unit discharge rates, considering that the mean time to maximum force in motor unit mechanical response remained unchanged in a statistically significant manner. Plausible mechanisms accounting for these modifications in motor unit discharge rates may involve various segments along the corticospinal pathway. While certain changes could potentially occur at supraspinal levels (Schubert et al., 2008), it is likely that a portion of the adaptations is attributed to alterations in the intrinsic properties of motor neurons, as observed in rat models following endurance training (Gardiner et al., 2006).

It has been estimated that the maximum force capacity of a motor unit can undergo changes of up to 50 times (Enoka, 1995). Consequently, the forces generated during movement are influenced by the recruitment of specific motor units. The recruitment of high-threshold motor units, which is consistently required for achieving maximum power generation, proves advantageous for force production as it innervates a relatively large number of muscle fibers capable of generating high forces (Enoka & Fuglevand, 2001). Thus, the rapid recruitment of high-threshold motor units significantly impacts maximal strength. Various theories of adaptation in motor unit recruitment have been proposed in response to training. One hypothesis suggests that training can lead to increased motor unit recruitment, preferential recruitment of high-threshold motor units, and lower thresholds for motor unit activation (Sale, 1988, 2003). These potential adaptations collectively serve to enhance agonist activation, thereby increasing muscle tension development and subsequently improving overall output.

Chapter 3. Neuromuscular Mechanism of a Joint Angle on Torque and Motor Unit Recruitment Regulation

3.1. Introduction

Motor units represent the fundamental and smallest functional units within muscles (Liddell & Sherrington, 1925; Sherrington, 1925). Muscles consist of multiple motor units that typically work together during muscle contraction (Fritz, 2003; Calancie & Bawa, 1990). Moreover, the force generated by a muscle varies depending on the activity pattern of motor units, as well as the mechanical properties of the muscle fibers and the muscle-tendon complex (Linnamo et al., 2006; Koo et al., 2002). Notably, altering the joint angle, which affects muscle length based on positional changes, significantly influences the maximum voluntary force that a muscle can exert (Hansen et al., 2003; Leedham and Dowling, 1995). Muscle fiber length and the rate of length change directly impact the maximal voluntary contraction, as described by the well-established force-length and force-velocity relationships of muscles (Zajac, 1989). During an isometric contraction, muscle length and joint angle should be considered decisive factors for maximal voluntary contraction. These are important considerations as the relationships between force, motor unit properties and joint angle are necessary when estimating the neuromuscular mechanism. Because it is possible that the joint angle could affect motor unit recruitment or motor unit firing rate-coding strategies of the muscles (Miles et al., 1986).

However, there is unclear what effect joint angle has on motoneuron excitation patterns. Consequently, it is unclear how motor unit activity, or the relationship between the motor unit and force, is altered by the joint angle. Therefore, this study aimed to examine the effect of various elbow joint angles on the torque and motor unit recruitment regulation relationship in human flexor and extensor muscles. And we hypothesized that the change in the body configuration, that is, the joint angle, will show a different maximum joint torque that the muscle can generate and the motor unit recruitment threshold and firing rate properties during the voluntary contractions.

3.2. Methods

3.2.1. Subjects

Twenty healthy subjects (age: 28 ± 2.31 years, height: 175 ± 1.4 cm, weight: 78±5.32 kg, bicep fat thickness: 1.1 ± 0.2 mm) participated in this study. The exclusion criteria for the subject recruitment included balance disorders such as dizziness and musculoskeletal injuries, neurological disorders, or uncorrected visual acuity deficits and dysfunction. The manual muscle testing (MMT) of all the participants was under grade 5, and the body mass indices (BMIs) were within a normal range (i.e., 18.5 to 24.9). All participants gave informed consent in accordance with the recommendations of the Seoul National University Institutional Review Board (IRB No. 2004 /002-016).

3.2.2. Apparatus

Force/Torque measurement. Humac Norm dynamometer (Humac/Norm Testing and Rehabilitation System., MA, USA;) were measured at five (i.e. 10°, 30°, 60°, 90°, and 120°) elbow angles during isometric flexion and extension at torque levels from 0%-100% of maximum voluntary torque (MVT). This dynamometer was used to record biomechanical signals (torque, and position) in this study. In addition, each subject's weight and other necessary features were inputted into the Humac Norm dynamometer and the participants' information was input before the experiment.

Muscles. We chose to conduct this experiment on the biceps brachii (BB) and triceps brachii (TB) muscles because (1) it generally has a relatively high number of muscle spindles (i.e., motor units); and (2) elbow joints are joints with one degree of freedom (sagittal plane motion) and have distinct agonist and antagonist muscle relationships. For this reason, it has the advantage of quantifying the relationship between the change in force/torque produced by the muscle across the joint and the measured electrical potential of the muscle.

Motor unit recording (dEMG recoding decomposition technology). To determine the modulation of the motor neuron pool, we used the Delsys decomposition system that could identify and record the action potentials from multiple motor units using a specialized surface EMG electrode (Decomposition EMG; Trigno Galileo sensor, Delsys, USA). The dEMG is made up of five pins (0.5 mm diameter) and records four surface EMG signals. The EMG signals were sampled at 2000Hz and bandpass filtered at 20-450Hz before being stored on computer. This dEMG sensor was measured biceps brachill (BB) and Triceps brachii lateral head (TB) muscles. The EMG signals were then decomposed into single motor unit action potentials using the Delsys decomposition algorithm, which has been shown to be reliable during isometric contractions (Nawab et al. 2010). Surface electromyography (sEMG) decomposition technology have greatly improved the ability to examine motor control strategies. On the other hand, early studies of motor unit function used intramuscular EMG methods to record single motor unit activities, such as needle and fine-wire electrodes. The disadvantages of these methods are that they are invasive, they can only detect the activities of a few motor units, and they are restricted to low-level muscle contractions. However, the sEMG decomposition technology developed by De Luca et al. (2006) is noninvasive and capable of detecting the activities of up to 40 motor units during strong contractions. It is also important to note that the accuracy of this decomposition algorithm is generally greater than 95% (De Luca & Nawab, 2011; Nawab et al., 2010).

3.2.3. Experimental Procedure

The subjects visited the laboratory for two consecutive days. On the first day, the subjects had a practice session to become familiar with the experimental setup and environment. Further, the practice could rule out the learning effect during actual data acquisition. On the second day, each subject had a short practice session and performed the given experimental tasks.

All the experiment participants performed the maximal voluntary torque (MVT) tasks during the elbow flexion and extension efforts with five elbow joint angles including five elbow joint angles (10°, 30°, 60°, 90° and 120°) according to the visual feedback trajectory given by the monitor. We confirmed that the participants required to match the template torque on the screen with the produced torque by the elbow joint. The template consisted of zero torque followed by a slanted line from 0% to 100% MVT for the corresponding conditions at a rate of 10% MVT/s. Elbow joint angle was defined using degrees of flexion, where a fully extended elbow corresponds to 0°. The order of the joint angles in each experiment was varied randomly. At each joint angle, a series of maximal voluntary contractions was performed for elbow flexion and extension. A rest period of 5 minutes was provided between joint angles, and care was taken throughout the protocol to avoid fatigue. Subjects placed the supine position on the upper Body exercise and testing table (UBXT) to face the ceiling and then rotated the axis of rotation of the lateral epicondyle of the subject's elbow joint. The chest and abdomen were fixed with a belt so that it could be aligned with the axis of rotation, and other parts of the pelvis and lower extremity muscles could not be moved during the examination. Besides, the elbow joint was exercised correctly by adjusting the length of the forearm using an elbow adapter and holding the elbow adapter handle to extend and flex the elbow joint. The examiner set the subject has set anatomical zero and set the range of motion from 0 ° to 130 °

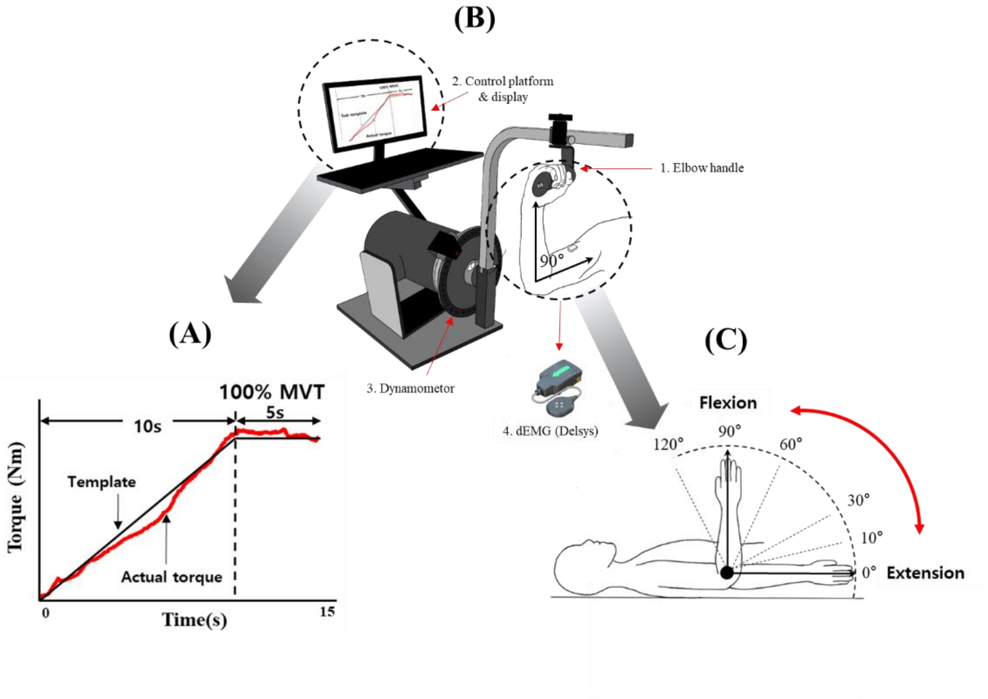


Figure 3.2. The experimental setup and measurement procedure are illustrated as follows: (A) An example of the maximum voluntary torque (MVT) task, (B) Introduction to the HUMAC NORM device, with labeled components including 1) elbow handle, 2) control platform and computer display, 3) dynamometer, and 4) Decomposition EMG (dEMG), and (C) The definition of the range of movement associated with the elbow joint.

3.2.4. Data Analysis

Both torque and dEMG data were analyzed offline using customized code (MATLAB, MathWorks, Natick, MA, USA) were written. The torque data acquired with the HUMAC NORM device from the MVT task was filtered by a zero-lag fourth-order Butterworth low pass filter with a cutoff frequency of 1Hz. The dEMG data were acquired with EMGworks Software version 4.8.0 and decomposed into motor units with Neuromap software 1.2.2. We analyzed both torque and motor unit data over the 15-s until finished MVT task. All the variables were computed before and after the warm-up exercise of each condition.

Maximal Voluntary Torque (MVT). MVT was chosen as the maximum torque value of an isometric maximum voluntary contraction of each condition that is represents the muscle strength of the participants. The rate of torque increase was 10% MVT/s followed by a sustain at 100% MVT for the 5-s.

Decomposition of dEMG signals. The surface EMG signals were decomposed into multiple motor unit action potentials (MUAPs) using the Delsys decomposition algorithm. The outcome of this algorithm provided the time train of motor units recruitment including 1) the number of motor units, 2) the action potential shapes of each identified motor unit, and 3) the firing instances (spikes) of action potentials of each identified motor unit. This outcome was validated using the Decompose-Synthesize-Decompose-Compare test (Nawab et al. 2010). The firing rate trajectory of each motor unit was computed by low-pass filtering the impulse train with a unit-area Hanning window of 1-s duration. The average accuracy of the firing instances tested was an average of 91%. The values for the individual contraction conditions and the average number of motor units are presented in Table 1. For each motor unit, three parameters were extracted from the mean firing rate data: the recruitment threshold, firing rate at recruitment and peak firing rate at the MVT production level.

The recruitment threshold was calculated as the torque level at which the motor unit began to fire. The firing rate at recruitment was estimated from the inverse of the average of the first three inter-pulse intervals and the peak firing rate was computed as the average value of the mean firing rate trajectory during the duration of the constant MVT torque. If no constant mean firing rate region could be identified in the higher-level contractions at 10% MVC/s, the maximum value of the mean firing rate trajectory was taken as the peak firing rate. Linear regressions were performed on the firing rates at recruitment and peak firing rates versus the recruitment threshold. The algorithms use artificial intelligence techniques to separate superimposed action potentials and allocating it to an individual train belonging to a specific motor unit. The technique generally identifies all the firings of 20–30 motor unit action potential trains per contraction. The algorithm produces a file containing the number of motor units observed and the instances of their firings.

3.2.5. Statistics

The statistical analysis was performed using SPSS 24. 0 (IBM, Armonk, NY, USA). Descriptive statistics were used; the data are presented in the text as means ± standard errors. Two-way repeated ANOVA was used with factors including *Angle* (Five level: 10°, 30°, 60°, 90° and 120°) and *Direction* (two levels: flexion and extension). For each MVT task, the relationship between the mean firing rate (pulse per second, pps) and the recruitment threshold (Nm) was examined using linear regression analyses. A paired t-test was used to confirm the difference of the one-to-one correspondence between each elbow joint angle condition (10°, 30°, 60°, 90° and 120°). The significance level of all statistical analyses was set at $\alpha = 0.05$.

3.3. Results

3.3.1. Isometric torque strength. The maximal voluntary torque (MVT) task exhibited an inverted 'U' relationship in relation to each elbow joint angle and direction, with the order of 10° < 30°< 120° < 60° < 90°. These findings were supported by a two-way repeated measures ANOVA, considering the factors Elbow angle (five levels: 10°, 30°, 60°, 90°, and 120°) and Direction (two levels: flexion and extension). The analysis of the absolute values of MVT (i.e., the magnitude of MVT) revealed significant main effects of Elbow angle ($F_{[4,76]} = 61.139$, $p<0.0001$, $\eta p^2=0.763$), along with significant interactions (interaction=Elbow angle × Direction; $F_{[4,76]} = 6.906$, p = 0.000, $\eta p^2=0.267$). Specifically, significant differences were observed between the 10° and 90° angle conditions ($p<0.0001$). The MVT decreased at more extended or flexed joint angles (e.g., at 10°) compared to less extreme joint angles (e.g., at 90°). Consequently, the elbow angles that exhibited a significant difference in MVT production were 10° and 90° ($p<0.01$), respectively, with an average difference of 29%.

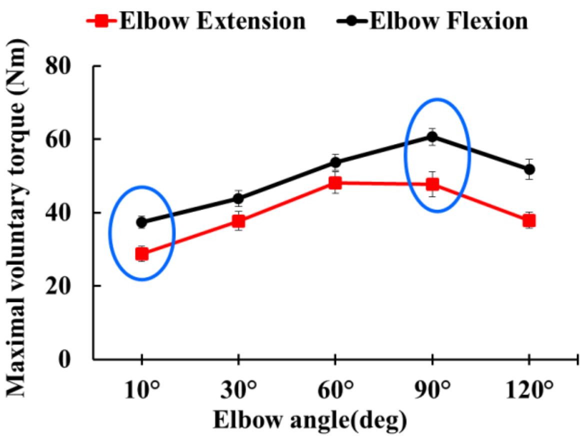


Figure 3.3. The relationship between joint angle and MVT for flexion (top) and extension (bottom) of the elbow joint. The mean averaged over all subjects is presented, where vertical error bars represent on standard error (SE).

Total Number of Accepted Motor Units

As presented in Table 3.1, there were no significant differences observed in the mean numbers of motor units across all joint angle conditions. The results of the two-way repeated measures ANOVA, based on the data of motor unit numbers, also indicated a lack of significant main effect for *Elbow angle* ($F_{[4,76]} = 1.508$,

p<0.208, ηp^2=0.763).

Table 3.1. Distribution of the analyzed number of motor units by agonist and antagonist muscles during MVT task.

Number of Motor Units per Contraction (Average number of motor units (MUs)) (Accuracy 95% above)											
Direction		Flexion					Extension				
Angle (deg)		10°	30°	60°	90°	120°	10°	30°	60°	90°	120°
# of MU	Agonist	23	23	24	25	23	22	19	18	18	19
	Antagonist	11	10	9	9	9	12	13	11	9	8

Effect of angle on motor unit mean firing rate (MFR) and recruitment threshold (RT). We conducted an analysis to examine the relationship between the mean firing rate (MFR) and recruitment thresholds (RT) of motor units during the maximal voluntary torque (MVT) task. The recruitment threshold for each motor unit was determined as the percentage of MVT at which the first firing of the motor unit occurred. Figure 3.5 illustrates an example of a linear regression depicting the relationship between motor unit MFR and RT for a representative subject in the 10° and 90° elbow angle conditions. The MFR versus RT relationship is typically best described by a linear model, as reported by Harmon et al. in 2019. In our study, we analyzed these relationships on an individual contraction basis. Notably, in the 90° elbow angle condition, the linear slopes exhibited an increase with decreased y-intercepts, indicating a significant effect of elbow angle (as shown in Figure 3.4). Additionally, we performed two-way repeated-measures ANOVAs with the factors Elbow angle (five levels: 10°, 30°, 60°, 90°, and 120°) and Direction (two levels: flexion and extension) on the MVT. The analysis revealed a significant main effect of Elbow angle ($F_{[4,76]}$ = 3.45, p<0.01) with no significant factor interactions.

Specifically, post-hoc pairwise comparisons confirmed that the 10° and 90° elbow joint angles were significantly different conditions (p<0.03).

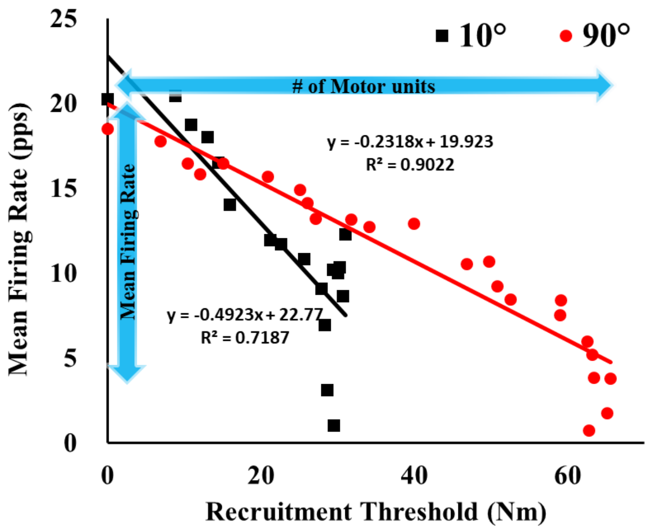


Figure 3.4. The relationship between recruitment threshold (RT) and mean firing rate (MFR) at 10° and 90° elbow joint angle.

The recruitment threshold of each motor unit was recorded as the torque level achieved, measured in MVT, at the instance when the first firing of the motor unit occurred. As illustrated in Figure 3.5, the motor unit recruitment threshold exhibits variations with changes in the elbow angle. Specifically, at an elbow angle of 10°, the observed recruitment primarily consisted of low-threshold motor units. In contrast, at an elbow angle of 90°, there was a relatively higher recruitment of high-threshold motor units.

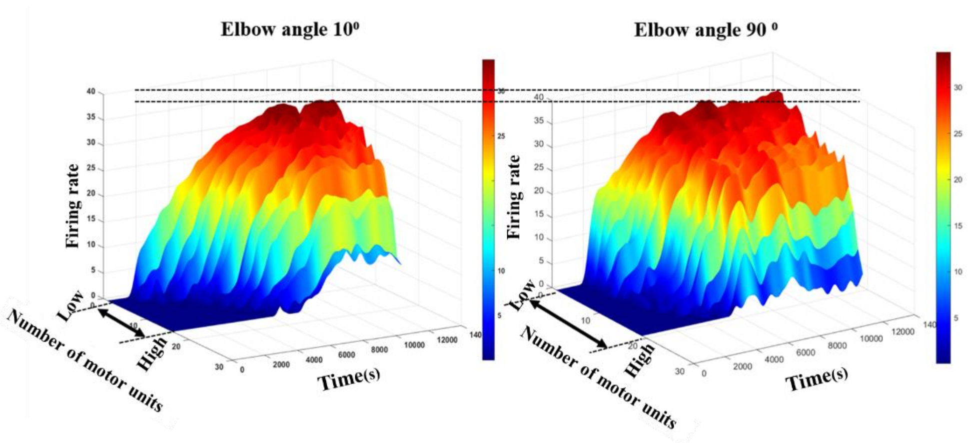


Figure 3.5. The comparison between joint angle and the decomposition of motor unit (MU) information revealed the mean firing rate of motor units achieving over 95% accuracy at both 10° and 90° elbow joint angles.

3.4. Discussion

The present study aimed to examine the effect of various elbow joint angles on the torque and motor unit recruitment regulation relationship in human flexor and extensor muscles. The findings of this study contribute to our understanding of the neuromuscular mechanisms underlying muscle force production and provide insights into motor unit recruitment and rate-coding strategies.

Our results demonstrated an inverted 'U' relationship between MVT and elbow joint angle, consistent with previous research (Kulig et al., 1984; Leedham and Dowling, 1995; Linnamo et al., 2006; Prodoehl et al., 2003). Specifically, MVT decreased at more extreme joint angles (e.g., 10°) compared to less extended or flexed angles (e.g., 90°), indicating the influence of the length-tension relationship and force-length properties of the muscle on force generation. This finding suggests that the length-tension relationship of the muscle, along with the force-length and force-velocity relationships (Edman & Reggiani, 1987; Zajac, 1989), play significant roles in determining the maximal force-generating capacity of the muscle (Herzog & Leonard, 2002).

The observed differences in MVT across joint angles can be attributed to variations in motor unit recruitment patterns. Our analysis of motor unit recruitment thresholds revealed a distinct pattern with respect to joint angle. At 10°, we predominantly observed the recruitment of low-threshold motor units, while at 90°, there was a relatively higher recruitment of high-threshold motor units. These findings indicate that the neuromuscular system modulates motor unit recruitment based on joint angle, potentially optimizing force production by activating motor units with varying force capabilities (Miles et al., 1986).

To further understand the neuromuscular mechanisms underlying the observed torque differences, the study investigated the relationship between recruitment thresholds (RT) and mean firing rate (MFR) of motor units. The relationship between RT and MFR provides further insights into the impact of joint angle on neuromuscular control. The findings from linear regression analysis between RT and MFR revealed that in the 90° elbow angle condition, the slopes increased while the y-intercepts decreased, indicating a significant influence of joint angle on motor unit firing rates. Specifically, in the 90° joint angle condition, as muscle force output increased, the slope of the linear regression line representing this relationship progressively flattened, indicating the recruitment of motor units with higher thresholds. This observation implies that the activation patterns of motor units are adjusted to accommodate the varying mechanical characteristics of the muscle-tendon complex at different joint angles (Enoka, 1995; Pasquet et al., 2005).

The findings from our study have significant implications for understanding neuromuscular mechanism and optimizing performance in tasks involving joint movements. The ability to adapt motor unit recruitment and firing rates according to joint angle may contribute to efficient force generation and coordination during various functional movements. Moreover, our results provide a foundation for developing targeted rehabilitation interventions and training protocols tailored to specific joint angles to enhance motor control and functional outcomes.

3.5. Conclusion

Our study highlights the significant impact of the elbow joint angle on both maximal voluntary torque and the regulation patterns of motor unit recruitment. The observed changes in muscle length corresponding to the elbow joint angle suggest the involvement of the central nervous system in detecting alterations in body posture and coordinating muscle contraction. Specifically, the findings indicate that the elbow joint angle influences the strategies employed for motor unit recruitment and the coding of motor unit firing rates within the muscles. Moreover, the angle-dependent variations in motor unit recruitment thresholds and firing rates provide valuable insights into the adaptability and optimization of motor unit regulation strategies. These findings significantly contribute to our understanding of neuromuscular mechanisms and have broad implications in various fields, such as performance enhancement and motor control. They provide a foundation for further research and the development of targeted interventions and training protocols tailored to specific joint angles, which can enhance performance and optimize functional outcomes.

Chapter 4. Neuromuscular Effect of Warm-Up on Regulation of Motor Unit Properties during Isometric Torque Production Tasks

One outstanding characteristic of the motor system is its neural adaptation. When subjected to short-term effects, it can adapt by modifying both its structural and functional properties. Chapter 4 delves into the acute adjustments of the motor system in response to stress associated with a bout of warm-up exercise.

4.1. Introduction

A warm-up exercise is commonly employed as a preparatory measure to induce transient and temporal effects on muscular functions (Bishop, 2003). The functional significance of muscles, as proposed by Hill, lies in their ability to convert chemical energy into mechanical work and heat (Hill, A.V., 1938; Hill, A.V., 1949), which is directly associated with muscular force production. Hill's muscle model utilizes mechanical concepts such as stiffness, damping, and inertia mass to elucidate the relationship between muscle force and its length, velocity, and acceleration. From a physiological standpoint, Hill's muscle model revealed that the heat generated within active muscles is proportional to the work performed by the muscle (Hill, A.V., 1963).

It has been widely documented that the warm-up exercise leads to a substantial enhancement in the capacity for force generation in skeletal muscles (Bergh & Ekblom, 1979). Notably, the underlying principle of the warm-up effect is attributed to the temperature-related mechanism (Asmussen & BØJe, 1945; Bishop, 2003), which elucidates the peripheral alterations in muscle physiology, including muscle metabolism (e.g., blood flow) (Gray et al., 2011), conduction velocity of muscle fibers (Pearce et al., 2012), increased muscle fiber performance (Gray et al., 2008), and electrical activity (Sale, 2002), induced by the elevation of muscle temperature. Noteworthy, passive warm-up, involving the elevation of body temperature through external heat sources, demonstrates a similar effect to active warm-up (Bishop, 2003; Davies & Young, 1958). Collectively, these studies consistently assert that a primary outcome of the warm-up exercise is the augmentation of resultant forces through modifications in peripheral aspects of muscle activation.

However, considerable research attention has been dedicated not only to peripheral changes in muscle function but also to central adaptations, which are referred to as neuromuscular adaptations (Enoka, 1988; Sale, 1988). These investigations have explored the effects of the warm-up exercise on both muscle strength and neural processes. Several studies on strength training have demonstrated improvements in both muscle strength and variables related to neural processes through effective muscle group activation and coordination (Pucci et al., 2006; Vila-Chã & Falla, 2016; Del Vecchio et al., 2019). Hence, the warm-up exercise enhances muscle strength by engaging both peripheral and neural aspects of muscle physiology and mechanics.

The size principle, also known as Heinemann's principle (Henneman, 1957), elucidates the relationship between motor neurons and the muscle fibers they innervate, collectively referred to as motor units. Motor neurons with larger cell bodies tend to innervate fast-twitch, high-force, and less fatigue-resistant muscle fibers, whereas motor neurons with smaller cell bodies tend to innervate slow-twitch, low-force, and fatigue-resistant muscle fibers. The size principle specifically addresses the recruitment order of motor unit pools, where motor neurons with smaller cell bodies are recruited before those with larger cell bodies. Consequently, the warm-up is likely to modulate the patterns of motor unit recruitment. The patterns of motor unit recruitment are determined by the firing rate and activation threshold of the recruited motor units. These properties, regulated by the central nervous system (CNS), play a crucial role in adjusting muscle force as per demand (Bigland & Lippold, 1954).

Recently, the advanced techniques and analytical tool for the identification of motor unit action potentials (MUAPs) using multi-channel surface electromyography (sEMG) has been developed by De Luca and colleagues (De Luca et al.,2006; Nawab et al., 2010; De Luca & Nawab, 2011), which is a so-called 'decomposition EMG (dEMG)'. A classical method to identify individual MUAPs is indwelling EMG, which could detect a few motor units within a target muscle, while the dEMG method is noninvasive as the sEMG is, and it is capable of detecting up to around 40 MUAPs during relatively strong muscle contractions. Of course, suspicious opinions have been raised since the motor units via dEMG is not from direct measure, but from a decomposed quantity on the surface EMG. However, the decomposition algorithm has been proven to be valid and reliable, especially at the isometric contraction (Deluca et al, 2006; Newab et al, 2010; Deluca & Hostage, 2010; Deluca & Contessa 2012). Thus, with the high accuracy and a large number of motor units being detected from various intensity of isometric contractions, this technology can be an acceptable candidate to examine the effect of warm-up exercise with both peripheral and central perspectives (De Luca & Erim, 1994; De Luca, LeFever, McCue, & Xenakis, 1982a, 1982b).We have known that the force exerted by a muscle during a voluntary contraction depends on the number of motor units recruited for the action and the rates at which they discharge action potentials. The current study attempts to uncover the neuromuscular mechanism of the warm-up exercise by quantifying the properties of the recruited motor units, including firing rate and recruitment threshold.

In the context of muscle function, the nervous system plays a crucial role in regulating muscle force through the modulation of motor unit recruitment and rate coding. Therefore, understanding the activity of motor units is essential for comprehending the underlying neuromuscular mechanisms that govern voluntary control of muscle strength and human movement performance. A recent study by De Luca and Hostage (2010) used linear regression analyses to examine this relationship in three different muscles with various levels of isometric contractions, thereby indicating that there was an inverse relationship between the average motor unit firing rate and the recruitment threshold for each muscle at each force level. This finding is consistent with the ‘‘onion skin’’ organization of motor unit firing rates described in previous studies (De Luca & Erim, 1994), which states that at any specified force level, the firing rates of earlier recruited (i.e., low-threshold) motor units are larger than those of later recruited (i.e., high-threshold) motor unit.

Furthermore, it has been proposed that the relationship between firing rate and recruitment threshold represents an "operating point" of the motor neuron pool that undergoes shifts in response to excitation (De Luca & Hostage, 2010). As force output increases, the slope of the linear regression line depicting this relationship becomes progressively flatter, indicating the recruitment of motor units with higher threshold values. These findings suggest that the recruitment of additional motor units is necessary to achieve higher force outputs. In addition to the slope of the linear regression line, the y-intercept is also an important variable when examining motor control strategies. For example, an increase in the y-intercept but without any change in the slope of the linear regression line indicates increased firing rates by all of the detected motor units. Therefore, we may determine how various interventions influence the motor control strategy by examining the changes in the linear slope and the y-intercepts of the relationship between the average motor unit firing rate and the recruitment threshold.

While the validity of the computational procedure of dEMG has been confirmed through experimental outcomes, limited attention has been directed towards understanding the neuromuscular mechanism of warm-up exercise. Specifically, there is a lack of knowledge regarding the alterations in the relationship between average motor unit firing rate and recruitment threshold induced by warm-up exercise. Therefore, the present study aims to uncover the neuromuscular mechanism of warm-up exercise by quantifying the properties of recruited motor units, including firing rate and recruitment threshold. We formulated the hypothesis that warm-up exercise enhances muscle strength by inducing significant neuromuscular changes in motor unit recruitment threshold and firing rate characteristics during voluntary muscle contractions.

4.2. Methods

4.2.1. Subjects

Fifteen healthy male subjects (age: 32 ± 4.1 years, biceps fat thickness: 1.2 ± 0.2 mm, MMT grade 5, BMI: 18.5 to 24.9) participated in the experiment. Subject recruitment involved excluding individuals with medical histories of musculoskeletal injuries, neurological disorders, or uncorrected visual acuity deficits and dysfunction. Prior to the experiment, participants were fully informed about the study's procedures and potential risks. They provided written consent, which was approved by the Institutional Review Board (IRB No. 2004/002-016) at Seoul National University. The original signed consent form was retained in the experimental records, while a copy was provided to each participant.

4.2.2. Apparatus

Ergometric Apparatus. The Human Norm (Computer Sports Medicine Inc., CSMI, USA) dynamometer was utilized to measure joint torque during the experiment, specifically in the constrained and fixed arm configuration, as depicted in Figure 4.1. The participants were positioned in a supine position, and the frame length of the dynamometer was adjusted to accommodate individual variations in arm anatomy. They were instructed to rotate the elbow joint along an axis aligned with the lateral epicondyle of the elbow joint. Once the desired joint angle was set, the experimental frame was locked, ensuring a static (i.e., isometric) condition. The elbow joint angle was defined with 0° corresponding to a fully extended elbow joint. The chest, abdomen, pelvis, and lower extremities were stabilized using a belt to isolate the elbow joint. Visual feedback of the voluntary torque exerted by the participants was provided on a computer screen.

Motor Unit Recording. Prior to attaching EMG electrodes, the skin over the muscle was cleansed with rubbing alcohol. The Delsys decomposition EMG system was used to identify multiple motor units using a specialized surface EMG electrode (Decomposition EMG; Trigno Galileo sensor, Delsys, USA). The dEMG electrodes were placed on the biceps brachill (BB) and triceps brachii (TB) muscles with the recommendations described SENIAM guideline (Hermens.H.J et al, 2000). In particular, the dEMG electrode heads were placed at near the centroid of the muscle to detect the maximum amount of EMG activity. The EMG signals were sampled at 2000Hz and bandpass filtered at 20 ~ 450Hz.

Muscles. We chose to conduct this experiment on the biceps brachii (BB) and triceps brachii (TB) muscles because: (1) it generally has a relatively high number of muscle spindles (i.e., motor units), which may allow us to observe a large treatment effect on muscle following the warm-up intervention; and (2) elbow joints are joints with one degree of freedom in the sagittal plane, and have distinct agonist and antagonist muscle relationships.

4.2.3. Experimental Protocol

The participants visited the laboratory on two consecutive days for the experiment. The first day involved a practice session aimed at familiarizing the subjects with the task protocol and experimental setup. This practice session was crucial to ensure that the measured maximal voluntary contraction (MVC) level closely reflected the subject's strongest effort and to minimize the potential influence of a learning effect during actual data collection.

On the second day, the participants performed the main tasks of the experiment. The primary objective of the experiment was to generate maximal voluntary torque

(MVT) in elbow flexion and extension efforts at two different elbow joint angles: 10° and 90°. The elbow joint angle was defined such that a fully extended elbow joint corresponded to 0° (Figure 4.1C). The procedure included two trials for each condition, and the order of joint angles and torque directions was randomized. The highest value obtained from the two trials was selected as the MVT. These experiments were conducted both before and after the warm-up protocol. Before starting the main task, two brief maximal contractions, each lasting approximately 3 seconds, were performed with a rest period of 3 minutes between trials. The maximum value obtained from the two trials was recorded as the MVT. Subsequently, the participants were instructed to track a series of ramp torque templates displayed on a computer screen using the torque dynamometer output. The torque template lasted for 15 seconds and consisted of an increasing slanted line from 0% to 100% of MVT for the corresponding conditions at a rate of 10% MVT/s, followed by a sustained period at 100% MVT for 5 seconds. In a single trial, the feedback screen displayed both the prescribed torque template and the produced torque (Figure 4.1A).

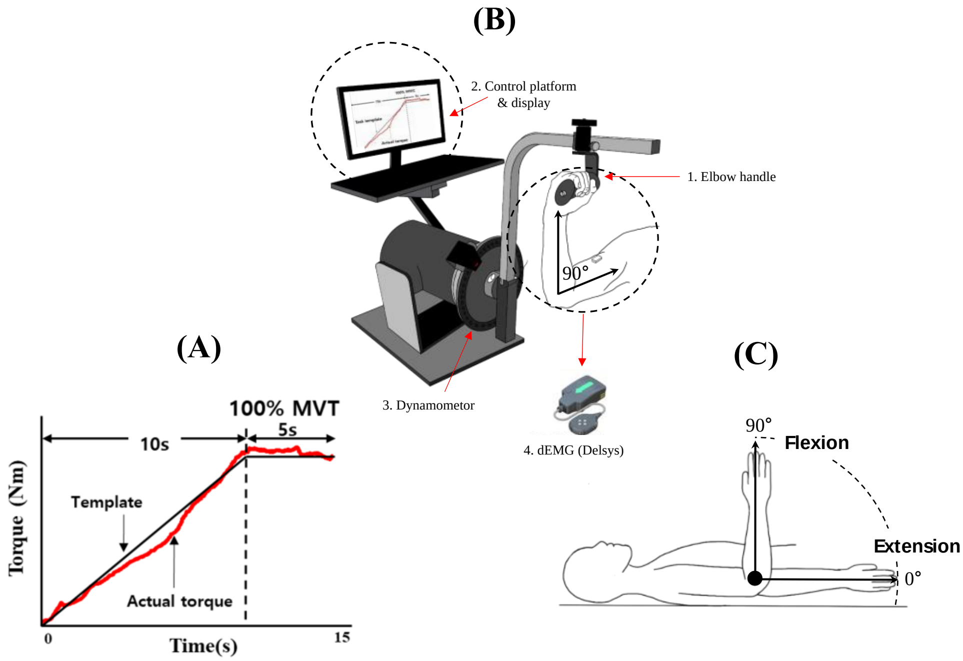


Figure 4.1 The experimental setup and measurement procedure are illustrated as follows: (A) An example of the maximum voluntary torque (MVT) task, (B) Introduction to the HUMAC NORM device, with labeled components including 1) elbow handle, 2) control platform and computer display, 3) dynamometer, and 4) Decomposition EMG (dEMG), and (C) The definition of the range of movement associated with the elbow joint.

Warm-up protocol. The total duration of the warm-up protocol was approximately 20 minutes. The frequency of movement during Steps 2 and 3 was precisely controlled using a metronome to ensure a specific time and number of repetitions. This adjustment was made to regulate the frequency of movements in Steps 2 and 3. The primary objective of the warm-up protocol was to elevate the body temperature, which has been shown to have beneficial effects (Asmussen & Boje, 1945; Binkhorst, Hoofd, & Vissers, 1977; Bishop, 2003). The protocol consisted of three distinct steps. **Step 1** *Aerobic exercise*: Jogging with light intensity for 5 minutes and moderate intensity for 5 minutes was performed on a treadmill followed by ACSM guidelines (Swain et al., 2007). The intensity was constantly controlled based on each subject's %heart rate reserve (i.e., %HRR30 to 60) in real-time using an optical heart rate monitor (i.e., Polar OH1) (Pescatello, Riebe& Thompson, 2014). **Step 2** *Form rolling*: Foam rolling was in order on the biceps, triceps, back, and shoulder muscles, considering the origin, insertion, and action of the biceps brachii (BB) and triceps brachii (TB), with the used multilevel rigid roller. (i.e., trigger-point grid foam roller). For each section of the body, gently rolled the foam roller, about one inch per second for about 30 to 60 seconds total (Wiewelhove et al., 2019). **Step 3** *Upper body active warm-up*: The total types of 8 upper body active warm-ups were performed for 5 minutes (about 30s for each type) as a method recommended in previous studies (Page & Ellenbecker, 2019; Christensen et al., 2020; Chen et al., 2020; McCrary et al., 2015). The active warm-up was performed 10-12 repetitions each using Thera Band®. 1) Biceps curl, 2) Triceps extension, 3) External shoulder rotations, 4) Band pull apart, 5) Arm circles, 6) Arm swings, 7) Wall slides, 8) Band face pulls.

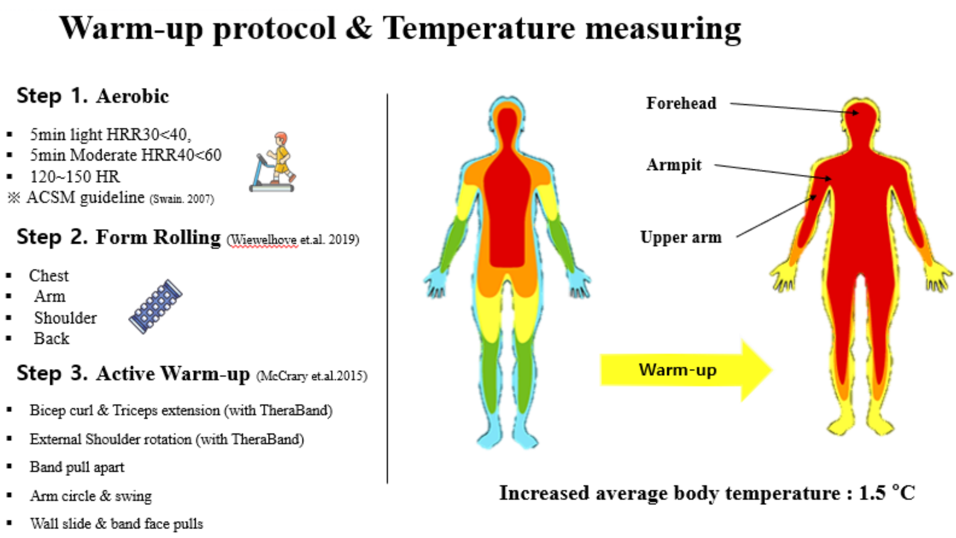


Figure 4.2. Warm-up exercise protocol and body temperature measuring

Measurement of body temperature. Warm-up exercise has been shown to increase muscle temperature, which in turn affects skin temperature. While there may be a disparity between skin and intramuscular temperature, previous studies have established a nearly linear relationship between the two (Hopf and Maurer, 1990). Hence, in the present experiment, it was hypothesized that muscle temperature would be significantly correlated with body surface temperature (De ruiter et al., 1999). To assess this, temperatures were measured at three locations (forehead, armpits, and upper arm) using digital thermometers (Eco Temp Basic; Omron Healthcare Inc.) and a non-contact infrared thermometer (Fluke Corp, Washington, USA) before and after the warm-up exercise. The completion of the warm-up was determined based on the criterion that the average temperature increase reached 1.5°C (Bergh & Ekblom, 1979; Racinais & Oksa, 2010)

4.2.4. Data Analysis

Both torque and dEMG data were analyzed offline using customized code (MATLAB, MathWorks, Natick, MA, USA) were written. The torque data acquired with the HUMAC NORM device from the MVT task was filtered by a zero-lag fourth-order Butterworth low pass filter with a cutoff frequency of 1Hz. The dEMG data were acquired with EMGworks Software version 4.8.0 and decomposed into motor units with Neuromap software 1.2.2. We analyzed both torque and motor unit data over the 15-s until finished MVT task. All the variables were computed before and after the warm-up exercise of each condition.

MVT. MVT was chosen as the maximum torque value of an isometric maximum voluntary contraction of each condition that is represents the muscle strength of the participants. The rate of torque increase was 10% MVT/s followed by a sustain at 100% MVT for the 5-s.

Decomposition of dEMG signals. The surface EMG signals were decomposed into multiple motor unit action potentials (MUAPs) using the Delsys decomposition algorithm. The outcome of this algorithm provided the time train of motor units recruitment including 1) the number of motor units, 2) the action potential shapes of each identified motor unit, and 3) the firing instances (spikes) of action potentials of each identified motor unit. This outcome was validated using the Decompose-Synthesize-Decompose-Compare test (Nawab et al. 2010). The firing rate trajectory of each motor unit was computed by low-pass filtering the impulse train with a unit-area Hanning window of 1-s duration. The average accuracy of the firing instances tested on a set of 120 contractions was an average of 92%. The values for the individual contraction conditions and the average number of motor units are presented in Table 1. For each motor unit, three parameters were extracted from the mean firing rate data: the recruitment threshold, firing rate at recruitment and peak firing rate at the MVT production level.

The recruitment threshold was calculated as the torqu level at which the motor unit began to fire. The firing rate at recruitment was estimated from the inverse of the average of the first three interpulse intervals and the peak firing rate was computed as the average value of the mean firing rate trajectory during the duration of the constant MVT torque. If no constant mean firing rate region could be identified in the higher-level contractions at 10% MVC/s, the maximum value of the mean firing rate trajectory was taken as the peak firing rate. Linear regressions were performed on the firing rates at recruitment and peak firing rates versus the recruitment threshold. The algorithms use artificial intelligence techniques to separate superimposed action potentials and allocating it to an individual train belonging to a specific motor unit. The technique generally identifies all the firings of 20–30 motor unit action potential trains per contraction. The algorithm produces a file containing the number of motor units observed and the instances of their firings.

Motor unit selection. After decomposition and verification of the motor units, the number of recorded motor units varies randomly with trials and conditions, so we selected five motor units. Therefore, the following five recorded motor units were selected from each condition and trial: 1) the first recruited motor unit (MU1) represents the smallest motor unit in the pool.; 2) the last recruited motor unit (MU5) represents the largest motor unit in the pool.; 3) the motor unit recruited in the middle (MU3, middle between MU1 and MU5) represents the average motor unit recruited during the task; 4) the motor unit in the between MU1 and MU3 (MU2) represents the lower-threshold motor units; and 5) The motor unit in the between MU3 and MU5 (MU4) represents the higher-threshold. This approach reduces the influence of discharge rate and maximizes the reliability of the comparisons. Therefore, the sum of the selected five motor units was our approach to compare motor unit pool activity across trials, conditions, and populations. We used five motor units for normalization for two reasons: 1) all trials had recordings of at least five motor units. 2) Farina and colleagues demonstrated that five motor units accurately represent the motor unit pool (Negro & Farina 2011; Negro et al. 2009; Gallego et al. 2015;). The selected five MUs were individually analyzed.

Quantification of motor unit activity: Inter-spike interval analysis. We computed the activity of a single motor unit discharge and multiple motor unit discharges. The single motor unit activity was quantified from the spikes of individual motor units. The activity of multiple motor units was quantified from the sum of spikes from the selected five motor units. The analysis section is from 1 s after the start of elbow torque to 1 s before the end of MVT because it is the section where task execution is performed most stably, and data is collected. The integral of the power within each frequency band was calculated for each trial and condition and then averaged for each subject. The mean discharge rate was quantified as the average of the interspike interval, which reflects the time between two consecutive spikes. Discharge rate variability was quantified as the coefficient of variation of the interspike interval (SD of interspike intervals/mean discharge rate×100). Moreover, we quantified the normalized power, before frequency-domain analyses, the interspike interval was transformed into a continuous signal by interpolating the interspike interval. A finite Fourier transform was applied to quantify the power spectrum of the multiple motor units (Mottram et al. 2005). The power spectrum of the discharge rate was divided into the following four frequency bands: 0-4Hz(delta), 4-10Hz(alpha), 10-35Hz(beta), and 35-60 Hz(gamma). Specifically, modulation of motor units between 0-4 Hz(delta) has been associated with common drive (De Luca and Erim 2002), and modulation between 4 and 10 Hz (theta and alpha bands) has been associated with working memory, short-term memory, and emotional arousal (Jensen and Lisman 2005; Knyazev 2007) and force control in tonic contraction (Mima et al. 2000). Oscillations between 10 and 35 Hz(beta)have been linked with motor function and maintenance of steady motor output (Chakarov et al. 2009; Engel and Fries 2010) and precision in motor output (Kristeva-Feige et al. 2002), and oscillations between 35 and 60 Hz(gamma) have been associated with strong voluntary contractions

(Chakarov et al. 2009: Brown et al. 1998).

4.2.5. Statistical Analyses

Descriptive statistics were used; the data are presented in the text as means ± SE and in the figures. Three-way repeated ANOVA was used with factors including *Warm-up* (2 levels: before and after) and *Angle* (two level: 10° and 90°) and *Direction* (two levels: flexion and extension). For each MVT task, the relationship between the average firing rate (pulse per second (PPS)) and the recruitment threshold (MVT(Nm)) was examined using linear regression analyses. Also, we used a mixed-model three-way ANOVA (2 warm-up groups × 2 elbow angles × 4 Frequency band) with repeated measures on phase to compare the normalized power from the multiple motor units across two phases and four frequency bands (0-4Hz(delta), 4-10Hz(alpha), 10-35Hz(beta), 35– 60 Hz(gamma)). Significant main effect from the ANOVA were followed by appropriate post hoc analyses. A paired t-test was used to confirm the difference of the one-to-one correspondence between before warm-up and after warm-up in each angle condition (10° and 90°). The significance level of all statistical analyses was set at p<.05. Analyses were performed with the IBM SPSS 24. 0 (IBM, Armonk, NY, USA).

4.3. Results

Torque production. The magnitudes of maximal voluntary torque (MVT) was increased with the warm-up exercise for all experimental conditions. In particular, the magnitude of MVT was larger in the flexion than in the extension condition, and larger at 90° as compared to 10° of the elbow angles. These findings were supported by three-way repeated measures ANOVA with factor *Warm-up* (two levels: before and after), *Angle* (two level: 10° and 90°), and *Direction* (two levels: flexion and extension) on the absolute values of MVT (i.e., the magnitude of MVT), which showed significant main effects of *Warm-up* ($F_{[1,14]}$ = 31.89, p < 0.0001), *Direction* ($F_{[1,14]}$ = 11.80, p<0.004), and *Angle* ($F_{[1,14]}$ = 185.89, p<0.0001,) with no factor interactions.

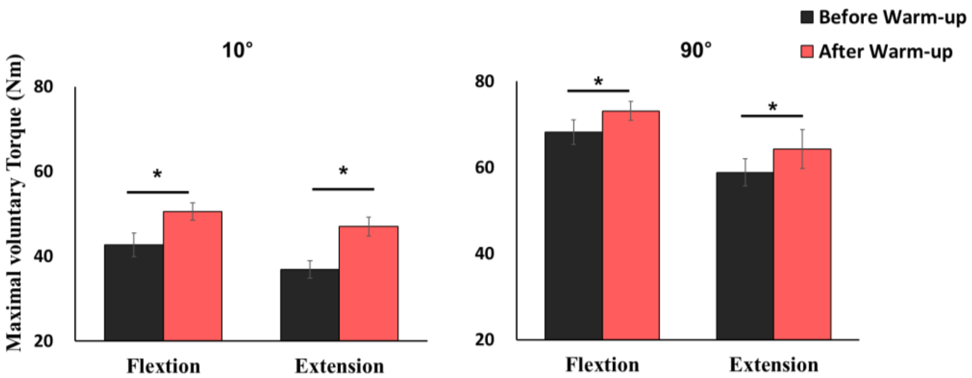


Figure 4.3. Average maximal voluntary torque (MVT) (Nm) before and after warm-up exercise intervention.

Total Number of Accepted Motor Units. As shown in Table 2, the total and mean numbers of motor units used in the data analyses were significantly increased after the warm-up intervention. The results of the three-way repeated measures ANOVA based on the number of motor units data showed that there was significant main effect of Warm-up ($F_{[1,14]}$ = 22.21, p<0.0001), with no factor interaction.

Table 4.1. Distribution of the analyzed number of motor units was compared before and after the warm-up intervention.

		Average number motor units per contraction (Average Accuracy of Decomposition)							
Condition		Before warm-up				After warm-up			
Direction		Flexion		Extension		Flexion		Extension	
Elbow angle°		10°	90°	10°	90°	10°	90°	10°	90°
# of MU	Agonist	16 92%	15 92.6%	18 93%	17 91.4%	20.8 92%	17.7 91.8%	20.8 91.8%	19.7 92%
	Antagonist	10 91%	9 92%	9 92%	9 92%	9 93%	11 91%	10 92%	7 91%

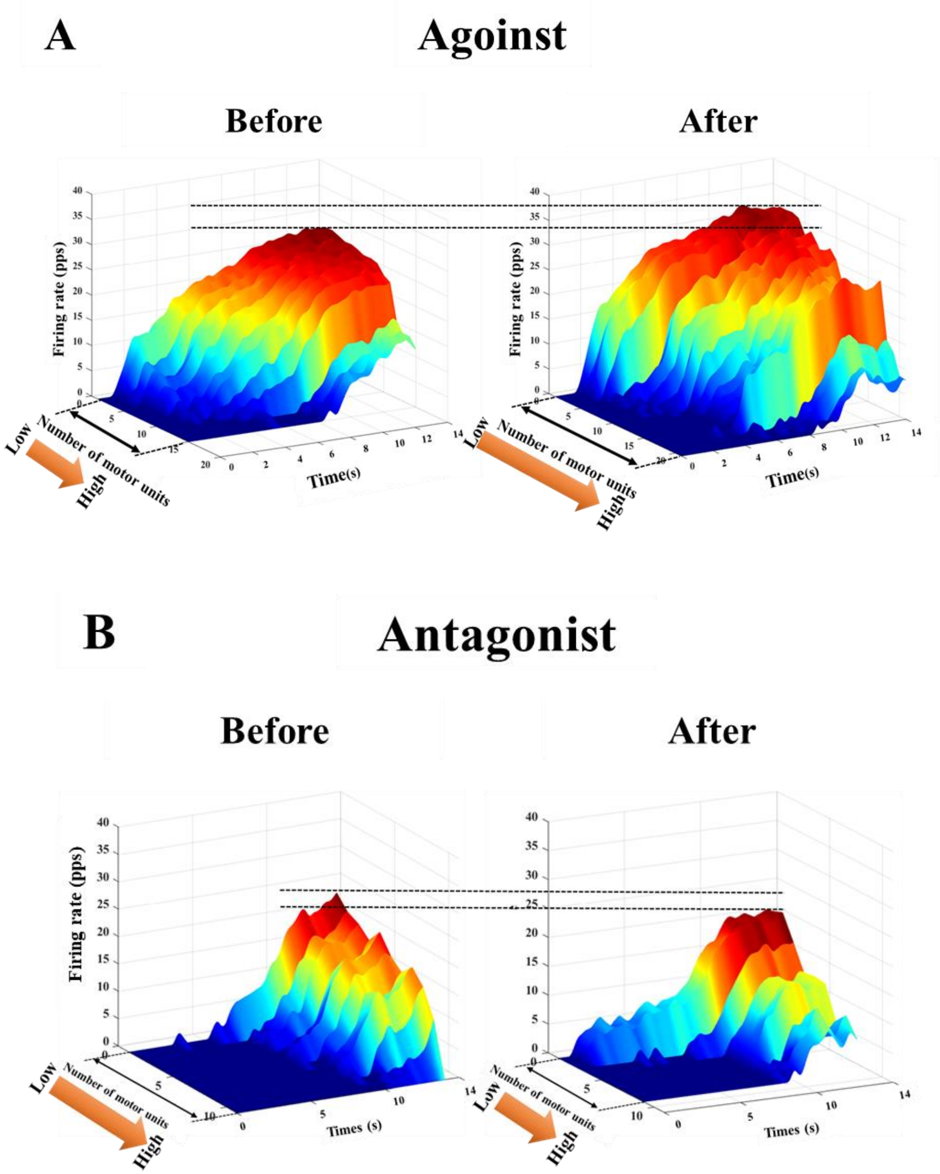


Figure 4.4. Before and after warm-up, a three-dimensional plot is created with the following axes. The data used for the plot are obtained from single trials performed by a representative subject, both before and after the warm-up intervention, focusing on the agonist (A) and antagonist (B). The motor units are decomposed from the decomposition electromyography (EMG) signal acquired from the biceps brachii (BB) muscle at a 90° elbow angle. Each bar in the plot represents the firing time of an action potential.

Correlation Between Mean Firing Rate (MFR) and Recruitment Thresholds (RT). We analyzed the relationship between the mean firing rate (MFR) and the recruitment thresholds (RF) of motor units observed during the MVT. The recruitment threshold of each motor unit was recorded as the force level achieved, measured in percent MVT at the instance at which the first firing of the motor unit occurred. Figure 4.6 shows an example of a linear regression of the relationship between the motor unit MFR and the RF for a representative subject before and after the warm-up intervention. The MFR versus RF relationship is typically best fit with a linear model (Harmon, Kylie K., et al 2019). In the current study, we analyzed relationships examined on an individual contraction basis. After the warm-up intervention, linear slopes were decreased with increased y-intercepts, with a significant effect on warm-up intervention (Figure 4.6). The three-way repeated-measures ANOVAs with factors Warm-up (two levels: before and after), Angle (two levels: 10° and 90°), and Direction (two levels: flexion and extension) on the MVT torque, which showed significant main effects of Warm-up $F_{[1,14]}=5.52$, $p<0.03$) and Direction ($F_{[1,14]}=69.60$, $p<0.0001$) with no factor interactions. In particular, the Warm-up effect (i.e., increased motor units after warm-up) was significantly increased motor units after warm-up conditions confirmed by post-hoc pairwise comparisons ($p<0.03$).

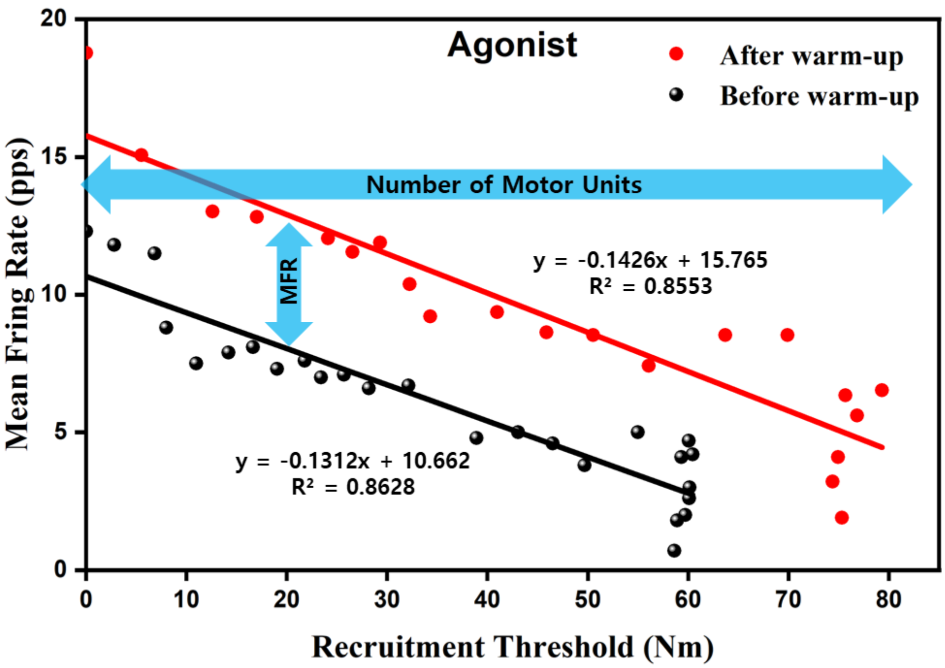


Figure 4.5. The average value of the motor unit firing rates is plotted as functions of recruitment threshold, separately for contractions sustained at MVT before and after the warm-up exercise. An example of a linear regression line is presented to depict the relationship between the mean firing rate and recruitment for subject 3, both before and after the warm-up intervention, specifically at the 90° elbow flexion angle of MVT. pps: pluse per second.

The number of recruited motor units and their mean firing rate. The mean discharge rate of multi-motor motor units (Table 4.1) varied with the warm-up, angle, and direction. For the mean discharge rate, there was a significant main effect of Warm-up ($F_{[1,14]}$=13.23, p<0.003). Specifically, after warm-up intervention, the mean discharge rate increased compared to before warm-up all of the conditions.

Table 4.2 Modulation of motor unit

Condition	Before warm-up				After warm-up			
Direction	Flexion		Extension		Flexion		Extension	
Elbow angle°	10°	90°	10°	90°	10°	90°	10°	90°
Mean discharge rate, pps	79±3.2	79±4.8	100±7.0	84±5.4	100±8.7	88±5.8	102±7.7	100±7.1
Discharge rate variability, pps	90±5.6	112±8.4	86±5.0	79±4.7	92±4.9	88±6.3	96±7.9	89±8.6

Values are mean ± standard error

However, there was no significant increase in discharge rate variability for all the conditions (*Warm-up*: $F_{[1,14]} = 0.004$, $p<0.949$). There was no statistical difference for warm-up effect in MU1 and MU2, which are relatively small motor units whereas, in MU3, MU4, and MU5, the main effect by *Warm-up* ($F_{[1,14]}$ = MU3:12.38, $p<0.003$; MU4:11.731, $p<0.004$; MU5:12.55, $p<0.003$). In particular, it showed a statistically large increase at 35-60 Hz (gamma) after warm-up in all conditions. For the relative power in five motor units discharge, there was a significant main effect for *Warm-up* ($F_{[3,42]}=23.328$, $p<0.0001$) and frequency band ($F_{[3,42]}=75.562$, $p<0.0001$). Particularly, post-hoc analysis indicated that after warm-up compared with before warm-up exhibited greater relative power from 35- 60Hz (t =-2.72, $p=0.001$) (see Figure 4). Specifically, after warm-up participants exhibited increased power in all frequency bands, (delta(0-4Hz):32%; alpha(4-10Hz):21%; beta(10-35Hz): 21%; gamma(35-60Hz): 35%).

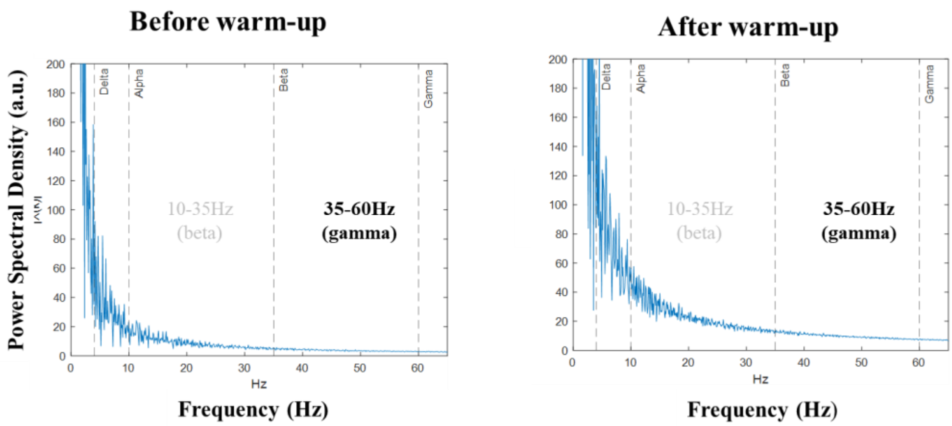


Figure 4.6. The power spectrum of the discharge rate was divided into the following four frequency bands: 0-4(delta), 4 -10(alpha), 10-35(beta), and 35-60(gamma)Hz. Power spectral density of the biceps brachii (BB) muscle motorneuron pool for before and after warm-up exercise with elbow 10° flexion. Before warm-up (A) and after warm-up(B).

4.4. Discussion

In this study, we aimed to uncover the neuromuscular mechanism of the warm-up exercise by quantifying the properties of the recruited motor units, including firing rate and recruitment threshold. The main finding of the present study was that isometric elbow flexion and extension torques were increased significantly after the warm-up exercise for both 10° and 90° of elbow angle), which were associated with the recruitments of higher threshold motor units after the warm-up exercise. Also, the firing rates of motor units observed in the same threshold were larger with the warm-up exercise (i.e., scaled-up and elongated regression line after the warm-up exercise). These results were further associated with significant increments of power spectral densities of the gamma band (35-60 Hz), especially in the relatively large motor units.

Relationship Between the Mean Firing Rate (MFR) and Recruitment Thresholds (RT)

De Luca and Hostage (2010) utilized this relationship to examine the motor control strategies in different muscles at various force levels (20%, 50%, 80%, and 100% of MVC). They found that more motor units were recruited as force levels increased, which was indicated by the motor unit detection at higher recruitment thresholds in subsequent contractions. The firing rates of motor units recruited near the same threshold were greater, which is reflected by the increasing y-intercept of the firing rate regressions.

In the present study, consistent with previous research (De Luca & Erim, 1994; De Luca et al., 1982b), all subjects demonstrated an inverse relationship between motor unit firing rate and recruitment threshold before and after the warm-up protocol. This finding aligns with the notion that motor units recruited at higher thresholds tend to exhibit lower average firing rates during contractions (De Luca & Contessa, 2012; De Luca & Hostage, 2010). However, following the warm-up, there was an increase in MVT levels compared to before the warm-up. This was accompanied by the recruitment of additional motor units, indicated by their detection at higher recruitment thresholds during subsequent contractions. Specifically, there was an enhanced recruitment of higher-threshold motor units associated with greater force generation, such as fast-twitch muscle fibers (Type II muscle fibers). Furthermore, the firing rates of motor units recruited near the same threshold were higher after the warm-up, as evidenced by the increased y-intercept of the firing rate regressions. Additionally, the mean discharge rate of agonist muscles showed a significant increase after the warm-up, as indicated in Table 4.2.

The observed increase in MVTs after the warm-up intervention could be attributed to changes in neural factors, mechanical factors, or a combination of both (Pucci et al., 2006; Vila-Chã & Falla, 2016; Del Vecchio et al., 2019). While this study did not directly quantify the changes in the muscle-tendon complex related to mechanical factors following the warm-up protocol, we did observe alterations in neural factors such as motor unit mean firing rate and recruitment threshold. Specifically, the results demonstrated a significant increase in the mean y-intercept of the linear relationship between mean firing rate and recruitment threshold after the warm-up, accompanied by a progressively flatter (less negative) slope of this relationship (De Luca & Contessa, 2012; De Luca & Hostage, 2010). These findings suggest that the warm-up intervention enhanced central output to motor neurons and effectively activated new motor units, thereby contributing to the achievement of higher force output.

Neuromuscular Mechanism of Warm-up (Motor unit properties with neuromuscular mechanism)

Based on previous studies examining the optimal performance achieved through the warm-up effect, it has been observed that an increase in muscle temperature leads to enhanced blood flow, which in turn improves exercise performance. This improvement can be attributed to changes in both viscosity and stiffness within the muscle (Buchthal et al., 1944; Bergh & Ekblom, 1979). Moreover, it is understood that the physiological mechanism underlying these outcomes involves an increase in electromyographic (EMG) activity through stimulation of the neuromuscular system (Stewart, Macaluso & De Vito, 2003; Petrofsky & Lind, 1980). However, there remains limited evidence regarding the precise neuromuscular mechanism through which the warm-up influences muscle force regulation. The positive effects of warm-up on the muscular system can be attributed to central mechanisms. One such mechanism involves an increase in muscle strength and power through enhanced activation of motor units (Patten et al., 2001; Duchateau, Semmler & Enoka, 2006; Vila-cha et al., 2010). The significant increase in motor unit firing rate and recruitment observed in the agonist muscle following warm-up supports this central mechanism.

In this study, inter-spike interval analysis using fast Fourier transform was conducted on the inter-spike interval data of five selected representative motor units.

The data was divided into four frequency bands: delta (0-4 Hz), alpha (4-10 Hz), beta (10-35 Hz), and gamma (35-60 Hz). The results revealed a significant increase in power within the gamma frequency band (35-60 Hz) following warm-up. These findings align with previous studies that reported changes in the gamma frequency band during strong voluntary muscle contractions (Brown et al., 1998; Chakarov et al., 2009). Moreover, the increase in power within the gamma frequency band was associated with heightened high-frequency oscillations in muscle activity, which have been linked to improved force control (Ulloa, 2022). These results provide novel evidence supporting the notion that the warm-up effect modulates muscle activation through the nervous system and enhances joint torque control.

From a neuromuscular mechanism perspective, the warm-up effect can be understood as a robust signal sent directly from higher centers, such as the brain, to motor neurons, facilitating movement execution. This direct signaling pathway enhances the excitability of motor units (MUs) that are capable of generating stronger contractions. Consequently, larger MUs are recruited, accompanied by an increase in firing rate. Notably, these effects were particularly pronounced in relatively large motor units, including MU#3, MU#4, and MU#5, resulting in a significant improvement in MVT. This observation suggests that the warm-up effect specifically activates fast-twitch muscles, characterized by Type II muscle fibers, which possess the capacity for explosive strength and speed during brief bursts of activity.

4.5. Conclusion

In this study, we aimed to uncover the hypothesis that warm-up exercise enhances muscle strength by inducing significant neuromuscular changes in motor unit recruitment threshold and firing rate characteristics during voluntary muscle contractions. Our findings support this hypothesis, as we observed that warm-up exercise led to notable alterations in the neuromuscular components of motor units within the muscles. Specifically, the firing rate of the recruited motor units increased following warm-up exercise. Furthermore, our results suggest that warm-up exercise is associated with the recruitment of large motor units, particularly Type II fast-twitch motor units. These motor units exhibited higher power spectral densities in the frequency band corresponding to voluntary contractions (35-60 Hz). By identifying these neuromuscular mechanisms underlying the warm-up effect, our study contributes to the understanding of how warm-up exercise can influence muscle performance. The findings also provide valuable insights for the design of warm-up strategies in human movement.

Chapter 5. Neuromuscular Strength Training based on Neural adaptation to Improve Muscle Force Underlying Motor Unit Recruitment and Rate Coding

In Chapter 4 of our studies, we focused on investigating the short-term effects of a warm-up exercise on the motor system. Through our research, we aimed to uncover the potential neuromuscular mechanisms that underlie these short-term effects and understand how they can impact performance in human movement. Building upon the findings from Chapter 4, Chapter 5 delves into the topic of neuromuscular strength training and explores how motor unit recruitment and rate coding change over the course of training. Our objective is to investigate the long-term effects of the neuromuscular system in response to strength training, specifically examining the neural adaptations that take place.

5.1. Introduction

The role of neuromuscular factors in enhancing muscle strength is widely acknowledged. Previous research indicates that increases in muscle strength following strength training sessions with strong voluntary contractions are primarily attributed to minor changes in the contractile apparatus (Blazevich et al., 2007; Seynnes et al., 2007; Weier et al., 2012). Consequently, it is believed that a significant portion of the improvement in muscle force can be attributed to changes in neuromuscular factors resulting from strength training. Recordings of individual motor units (i.e., needle EMG) (Van Cutsem et al., 1998; Vila-Cha˜ et al., 2010) and recordings of electromyogram (EMG) activity (Hakkinen & Komi, 1983; Aagaard et al., 2002a; Balshaw et al., 2016; Del Vecchio et al., 2018b) have been used to suggest the types of neuromuscular factor changes elicited by strength training.

When there is a noticeable increase in muscular strength without significant hypertrophy (i.e., muscle size increase), it suggests that neural mechanisms are involved in the process of gaining strength. Surface electromyographic (sEMG) techniques have been utilized to investigate this phenomenon. Studies utilizing sEMG have demonstrated that in the initial phase of a training program, strength gains are accompanied by an increase in the amplitude of sEMG activity (Narici et al., 1989; Aagaard et al., 2000; Aagaard et al., 2002b; Häkkinen et al., 2000). This increase in sEMG amplitude is typically interpreted as an augmentation in neural drive. Neural drive refers to the magnitude of efferent neural output from the central nervous system (CNS) to the active muscle fibers. In other words, it signifies an increase in the neural signals sent from the CNS to the muscles involved in producing force. The findings from these studies suggest that neural adaptations, such as an increased neural drive, contribute to the early phase of strength gains during training, even before substantial muscle hypertrophy occurs. This highlights the importance of neural mechanisms in the acquisition of muscular strength and underscores the significance of neural adaptations in the early stages of strength training.

Indeed, it is crucial to acknowledge the limitations associated with sEMG and needle electromyography (needle EMG) techniques when examining motor unit activity. sEMG, despite its utility, has limitations in accurately capturing individual motor unit behavior due to its lack of spatial resolution (Yue et al., 1995; Felici & Del Vecchio, 2020). As a result, the information obtained from sEMG may provide an incomplete understanding of motor unit activity and dynamics. On the other hand, needle EMG is an invasive procedure that can capture motor unit activity more directly. However, it also has limitations in terms of sampling a comprehensive representation of motor units and may cause discomfort to participants (Rubin, 2019). Due to the invasiveness and potential discomfort associated with needle EMG, its application in research studies may be limited, and the sample size of motor units assessed may not be as extensive as desired. Therefore, while both sEMG and needle EMG offer valuable insights into motor unit behavior, it is essential to recognize their limitations and consider alternative methods or complementary approaches to gain a more comprehensive understanding of motor unit recruitment and firing patterns.

One such advancement is the introduction of Decomposition EMG (dEMG), which has significantly enhanced our ability to study motor unit activity. The dEMG allows for the separation of individual motor unit activity from the recorded signal, overcoming the limitations associated with surface and needle EMG techniques (De Luca et al., 2006; Nawab et al., 2010; De Luca & Nawab, 2011). By utilizing dEMG, researchers can obtain a more precise understanding of motor unit firing patterns, recruitment behavior, and synchronization. This technique enables the identification and analysis of individual motor units, providing insights into their firing rates, recruitment thresholds, and coordination within a muscle (Enoka et al., 2019; Del Vecchio et al., 2020). These detailed measurements contribute to a better understanding of the complex neuromuscular mechanisms involved in motor control.

Indeed, despite extensive research, the specific neuromuscular changes at the motor unit level that underlie the increase in muscle force after strength training remain largely unknown (Duchateau et al., 2005). Furthermore, there is a lack of consensus regarding the optimal training protocol to effectively improve neuromuscular strength. The nervous system regulates muscle force throughout the operating range of a muscle by adjusting both motor unit recruitment and rate coding through various neuromuscular mechanisms. Motor unit recruitment refers to the activation of additional motor units as force requirements increase, while rate coding involves modulating the firing rates of active motor units. Understanding the intricate interplay between motor unit recruitment and rate coding is crucial for comprehending the adaptive responses of the neuromuscular system to strength training.

Therefore, in this study, neuromuscular strength training was performed based on neural adaptation for 4 weeks to find out the long-term effect of the neuromuscular system according to maximize the activation of the motor unit. The core of neuromuscular strength training is defined as a form of exercise training that specifically targets the neuromuscular system to enhance muscle performance and function. This form of training seeks to maximize the recruitment and firing of motor units within a muscle, leading to enhanced force production and improved motor performance. Unlike traditional strength training approaches that primarily focus on muscle hypertrophy, neuromuscular strength training places emphasis on optimizing the neuromuscular adaptations that occur within the neural and muscular systems. So, we hypothesize that the increase in muscle force produced after the neuromuscular strength training would be accompanied by a significant increase in the motor unit firing rate, an increment in the number of recruited motor units, a significant increase in the discharge rate, and a decrease in variability of discharge rate.

5.2. Methods

5.2.1 Subjects

Twenty-eight healthy adults will be enrolled as participants of the current study. Subjects will assign to an intervention (INT, n=15) or to a control (CON, n = 15) group, which were matched for anthropometric characteristics, physical activity habits and baseline levels of muscle strength. The exclusion criteria for the subject recruitment included balance disorders such as dizziness and musculoskeletal injuries, neurological disorders, or uncorrected visual acuity deficits and dysfunction. The manual muscle testing (MMT) of all the participants was under grade 5, and the body mass indices (BMIs) were within a normal range (i.e., 18.5 to 24.9). All experiment will proceed after all participants are asked to fill out an informed consent in accordance with the recommendations of the Seoul National University Institutional Review Board (IRB No.2303/004-010).

- Flow of individuals through study

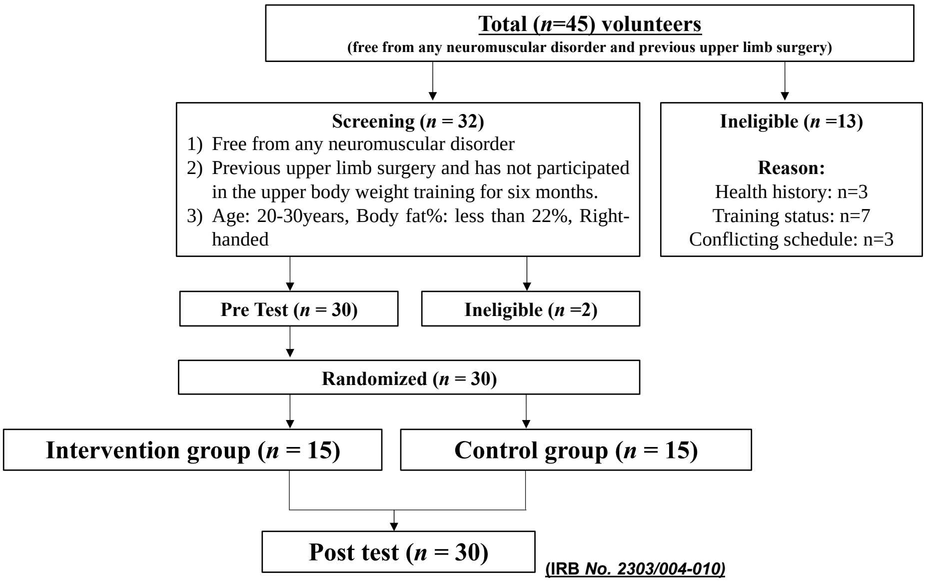


Figure 5.1. Subject recruitment flow chart

5.2.2. Apparatus

Ergometric Apparatus (Torque signal recording). The Humac Norm (Computer sports Medicine Inc., CSMI, USA;) dynamometer will be to measure joint torque at the constrained and fixed arm configuration. The subjects will be in supine position, and the frame-length was adjusted to accommodate individual difference in the arm anatomy and then will be ask to rotate the elbow joint about an axis of rotation, which was aligned with the lateral epicondyle of the elbow joint. Once the joint angle is set at a particular angle, the experimental frame for rotation will be lock; thus, the subjects will be in isometric condition. The elbow joint angle is defining such that a fully extended elbow joint has corresponded to 0°. In this study, only the 90° elbow joint angle will be measured. The chest, abdomen, the pelvis and lower extremity were fixed using a belt to isolate the elbow joint. Visual feedback of the voluntary torque will display on a computer screen. The joint torque signals sampling rate was

100Hz, and the zero-lag fourth-order Butterworth low pass filter with a cutoff frequency of 15Hz.

Motor Unit Recording. The Delsys decomposition EMG system will be used to identify multiple motor units using a specialized surface EMG electrode (Decomposition EMG; Trigno Galileo sensor, Delsys, USA). The dEMG electrodes are place on the biceps brachill (BB) and triceps brachii (TB) muscles with the recommendations described SENIAM guideline (Hermens.H.J et al, 2000). Prior to attaching EMG electrodes, the skin over the muscle is prepare by removal of superficial dead skin with adhesive tape and sterilized with an alcohol swab. In particular, the dEMG electrode heads are place at near the centroid of the muscle to detect the maximum amount of EMG activity. The EMG signals are sampled at 2000Hz and bandpass filtered at 20 ~ 450Hz.

Muscles. We chose to conduct this experiment on the biceps brachii (BB) and triceps brachii (TB) muscles because: (1) it generally has a relatively high number of muscle spindles (i.e., motor units), which may allow us to observe a large treatment effect on muscle following the strength training; and (2) elbow joints are joints with one degree of freedom in the sagittal plane, and have distinct agonist and antagonist muscle relationships.

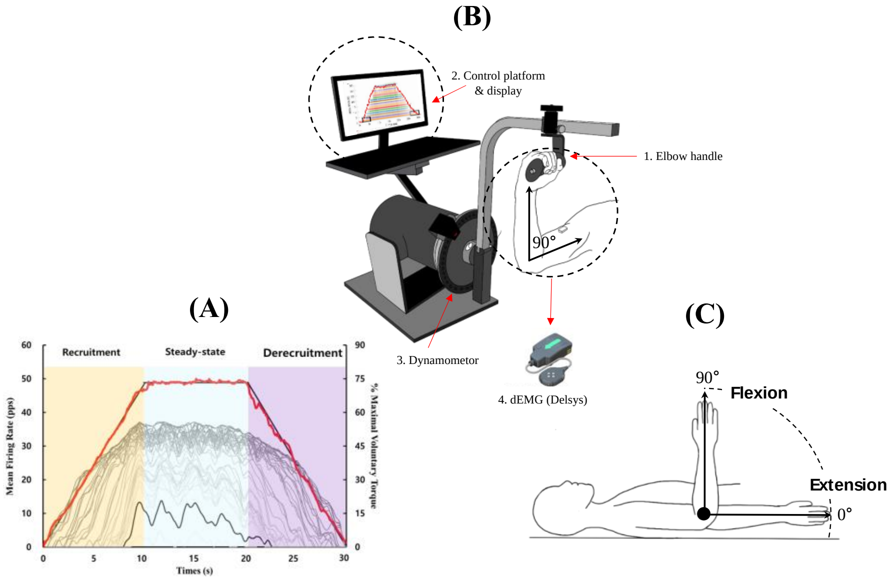


Figure 5.2. The figure presents an illustration of the experimental setup, including: (A) a representative submaximal trapezoidal contraction task with the actual torque signal displayed in red and torque templates shown on a computer screen, (B) an introduction to the HUMAC NORM device, with labeled components such as the 1) elbow handle, 2) control platform and computer display, and 3) dynamometer, and (C) the definition of the range of movement associated with the elbow joint.

5.2.3. Overview of the Experimental

Subjects are asked to be available for 15 laboratory visits within a 7-weeks period. In weeks 1 and 2, participants visit the laboratory on two occasions, 3–5 days apart. The first visit thoroughly explained experimental procedures, training protocol, and familiarized with maximal voluntary torque (MVT) task and submaximal trapezoidal contraction task of the dominant arm. No measurements were made during the first visit. The second visit was used to obtain before (pretest) measurements, which included the recordings of isometric elbow flexion torque during MVT task and submaximal trapezoidal contraction task and decomposition EMG (dEMG) recordings from the biceps brachii (BB) and triceps brachii (TB) muscles. Weeks 3–

6 comprised the 4 weeks (three times a week) of unilateral isometric neuromuscular strength training of elbow flexors and arm strength training. Participants of the CON group maintained their physical activity habits during the 4 weeks. In week 7, subjects repeated the after(posttest) measurements.

5.2.4. Experimental Protocol

The measurements will be performed in the second week (before) and the seventh week (after) within 7 days before the start of the training and 2–3 days after the final training session, respectively. The subjects are asked to refrain from high-intensity training and caffeine consumption in the 48 and 24 h prior to the measurement sessions, respectively. Also, diurnal variability in muscle contractility was minimized by performing the two sets of measurements at the same time of day (Racinais et al., 2005). After a standardized warm-up (i.e., chapter 4 warm-up protocol), the main task involved the recordings of muscle force and dEMG from the biceps brachii (i.e., agonist) and triceps brachii (i.e., antagonist) muscles of the dominant arm during MVT task and submaximal trapezoidal contraction task. As established in the familiarization session, the subjects are asked to focus on the movement of the elbow flexors and to isolate the activation of BB as much as possible during the warm-up contractions.

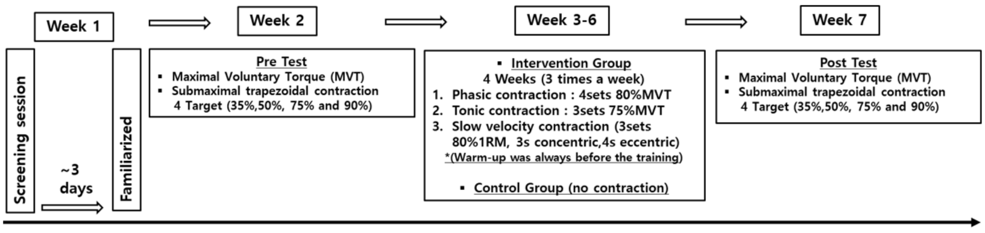


Figure 5.3. Diagram of measurement and neuromuscular strength training plan.

Maximal voluntary torque (MVT) task. Subjects perform maximal voluntary torque (MVTs) under 90° elbow joint angle with isometric elbow flexion. We instructed to increase the torque constantly at a rate of 10% MVT/s from 0% to 100% in order to unify the timing of generating the MVT to apply equally to all subjects. At the same time, subjects were instructed to 'as hard as possible' for strong verbal encouragement to achieve the maximum during each contraction. It was performed three times, with a 3–5-minute break between trials. MVT will denote the greatest torque recorded during any of the MVTs and will use as a reference to determine the target torque for the submaximal contractions.

Submaximal trapezoidal contraction task. The submaximal trapezoidal contraction consisted of a 10s linear torque increase, a 10s steady-state torque plateau, and a 10s linear torque decrease. Two trials will perform at each of the four target torque levels (35%, 50%, 75%, and 90% of MVT). The submaximal trapezoidal contractions will perform randomly and are separated by 3min of recovery. Only the 90° elbow joint angle will be measured in this study.

5.2.5. Training Protocol

To maximize neural adaptation, the neuromuscular strength training intervention combines phasic and tonic contraction (Balshaw et al., 2016; Enoka et al., 2006; Van Cutsem et al., 1998; Del Vecchio, 2020) and slow velocity contraction, as reported previously (Piazzesi et al., 2007; Bishop et al., 2018; Scott & Hussey, 2018; Mavros, et al.,2017; King et al., 2015). The 4-week intervention training comprised 12 supervised training sessions (~60 min each) that were separated by 48–72 hours.

Each training session begins with a standardized warm-up protocol in Chapter 4 (study 2), followed by MVT to determine the submaximal training intensities.

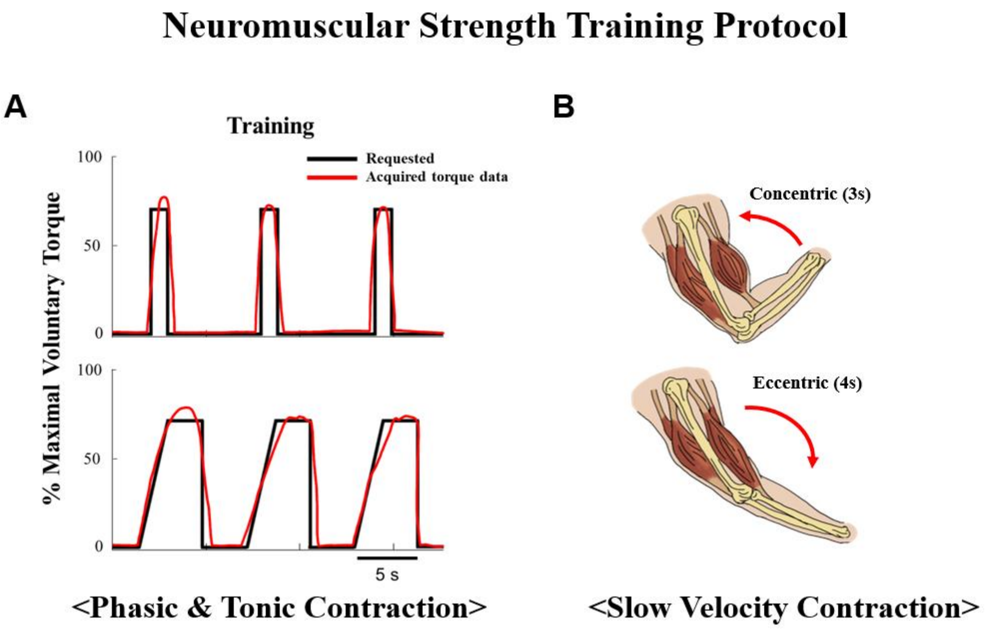


Figure 5.4. Neuromuscular Strength Training protocol. A: The top panel of the figure presents data regarding phasic contractions, showcasing the torque-time curve. The bottom panel demonstrates the corresponding data for tonic contractions. B: Information on slow velocity contractions.

After the MVTs, subjects will perform 40 isometric phasic contractions (Van Cutsem et al., 1998) with the elbow flexors of the dominant arm (four sets of 10 repetitions). Like the pretest measurements, subjects will be instructed to avoid pre-tension or counter-movement actions and to exceed a horizontal target on a monitor positioned at 80% of their MVT ‘as quickly as and as hard as possible’ for ~1 s and rest for 5 s between contractions. After the phasic contractions, the subjects will perform 30 isometric tonic contractions (three sets of 10 repetitions). Each series lasted 60 s with 2 min of recovery between sets. The target torque during the tonic contractions is

75%MVT, and the steady-state phase is 3s. After the plateau phase, the subjects are instructed to relax with a 2 s rest between contractions. And then, subjects performed slow velocity contraction. They are required to perform each repetition with a repetition timing of 3-second concentric and 4-second eccentric barbell curls or hammer curls by undertaking flexion–extension movements of the elbow with three sets of 6–8 repetitions at 80% 1RM with a 2-minute recovery period between sets.

5.2.6. Data Analysis

Both torque and dEMG data will be analyzed offline using customized code (MATLAB, MathWorks, Natick, MA, USA) were written. The torque data acquired with the HUMAC NORM device from the MVT and submaximal ramp torque task will be filtered by a zero-lag fourth-order Butterworth low pass filter with a cutoff frequency of 1Hz. The dEMG data will acquire with EMGworks Software version 4.8.0 and decomposed into motor units with Neuromap software 1.2.2. We will analyze both torque and motor unit data until finish MVT and submaximal ramp torque task. All the variables were computed before and after the neuromuscular strength training of each condition.

Decomposition of dEMG signals. The surface EMG signals will be decomposed into multiple motor unit action potentials (MUAPs) using the Delsys decomposition algorithm. The outcome of this algorithm provides the time train of motor units recruitment including 1) the number of motor units, 2) the action potential shapes of each identified motor unit, and 3) the firing instances (spikes) of action potentials of each identified motor unit. This outcome will be validated using the Decompose-Synthesize-Decompose-Compare test (Nawab et al. 2010). The firing rate trajectory of each motor unit will compute by low-pass filtering the impulse train with a unit-area Hanning window of 1-s duration. For each motor unit, three parameters will extract from the mean firing rate data: the recruitment threshold, firing rate at recruitment and peak firing rate at the MVT and submaximal ramp torque level.

The recruitment threshold will calculate as the torque level at which the motor unit began to fire. The firing rate at recruitment is estimated from the inverse of the average of the first three interpulse intervals, and the peak firing rate was computed as the average value of the mean firing rate trajectory during the duration of the constant torque at the target torque. If no constant mean firing rate region could be identified in the higher-level contractions at 10% MVC/s, the maximum value of the mean firing rate trajectory was taken as the peak firing rate. Linear regressions will perform on the firing rates at recruitment and peak firing rates versus the recruitment threshold. The algorithms use artificial intelligence techniques to separate superimposed action potentials and allocate it to an individual train belonging to a specific motor unit. The technique generally identifies all the firings of 20–30 motor unit action potential trains per contraction. The algorithm produces a file containing the number of motor units observed and the instances of their firings.

Motor unit selection. After decomposition and verification of the motor units, the number of recorded motor units varies randomly with trials and conditions, so we will select five motor units. Therefore, the following five recorded motor units will selected from each condition and trial: 1) the first recruited motor unit (MU1) represents the smallest motor unit in the pool.; 2) the last recruited motor unit (MU5) represents the largest motor unit in the pool.; 3) the motor unit recruited in the middle

(MU3, middle between MU1 and MU5) represents the average motor unit recruited during the task; 4) the motor unit in the between MU1 and MU3 (MU2) represents the lower-threshold motor units; and 5) The motor unit in the between MU3 and MU5 (MU4) represents the higher-threshold. This approach reduces the influence of discharge rate and maximizes the reliability of the comparisons. Therefore, the sum of the selected five motor units is approach to compare motor unit pool activity across trials, conditions, and populations. We will use five motor units for normalization for two reasons: 1) all trials had recordings of at least five motor units. 2) Farina and colleagues demonstrated that five motor units accurately represent the motor unit pool (Negro & Farina 2011; Negro et al. 2009; Gallego et al. 2015;). The selected five MUs were individually analyzed.

Quantification of motor unit activity: Inter-spike interval analysis. We will compute the activity of a single motor unit discharge and multiple motor unit discharges. The single motor unit activity is quantified from the spikes of individual motor units. The activity of multiple motor units is quantified from the sum of spikes from the selected five motor units. The analysis section is from 1 s after the start of elbow torque to 1 s before the end of submaximal ramp torque task because it is the section where task execution is performed most stably, and data is collected. The integral of the power within each frequency band was calculated for each trial and condition and then averaged for each subject. The mean discharge rate will be quantified as the average of the interspike interval, which reflects the time between two consecutive spikes. Discharge rate variability quantified as the coefficient of variation of the interspike interval (SD of interspike intervals/mean discharge rate×100). Moreover, we will quantify the normalized power, before frequency-domain analyses, the interspike interval is transformed into a continuous signal by interpolating the interspike interval. A finite Fourier transform will be applied to quantify the power spectrum of the multiple motor units (Mottram et al. 2005). The power spectrum of the discharge rate is divided into the following four frequency bands: 0-4Hz(delta), 4-10Hz(alpha), 10-35Hz(beta), and 35-60 Hz(gamma). Specifically, modulation of motor units between 0-4 Hz(delta) has been associated with common drive (De Luca & Erim 2002), and modulation between 4 and 10 Hz (theta and alpha bands) has been associated with working memory, short-term memory, and emotional arousal (Jensen and Lisman 2005; Knyazev 2007) and force control in tonic contraction (Mima et al., 2000). Oscillations between 10 and 35 Hz(beta)have been linked with motor function and maintenance of steady motor output (Chakarov et al., 2009; Engel and Fries 2010) and precision in motor output (Kristeva-Feige et al., 2002), and oscillations between 35 and 60 Hz(gamma) have been associated with strong voluntary contractions (Chakarov et al., 2009: Brown et al. 1998).

5.2.5. Statistics

All statistical analyses will conduct using SPSS 24.0 (IBM, Armonk, NY), and the data are presented as means and standard errors (SE). Two-way repeated ANOVA was used with factors including Training (2 levels: Before and After) and group (2 levels: INT and CON). When significant interactions are found, a Bonferroni correction will be applied to account for multiple comparisons. For each MVT task and submaximal ramp task, the relationship between the average firing rate (pulse per second (PPS)) and the recruitment threshold (%MVT) will be examined using linear regression analyses. Also, we will use mixed-model three-way ANOVA (2 training ×2 group×4 Frequency band) with repeated measures on phase to compare the normalized power from the multiple motor units across two phases and four frequency bands (0-4Hz(delta), 4-10Hz(alpha), 10-35Hz(beta), 35– 60 Hz(gamma)). Significant main effects from the ANOVA will follow by appropriate post hoc analyses. A paired t-test will use to confirm the difference of the one-to-one correspondence between before and after training in each group (INT and CON). The significance level of all statistical analyses is set at α= 0.05.

5.3. Results

Anthropometrics. The two groups had no statistical differences concerning age, body mass, skeletal muscle mass, percent body fat, and peak torque during maximal voluntary torque with elbow flexion (Figure 5.5).

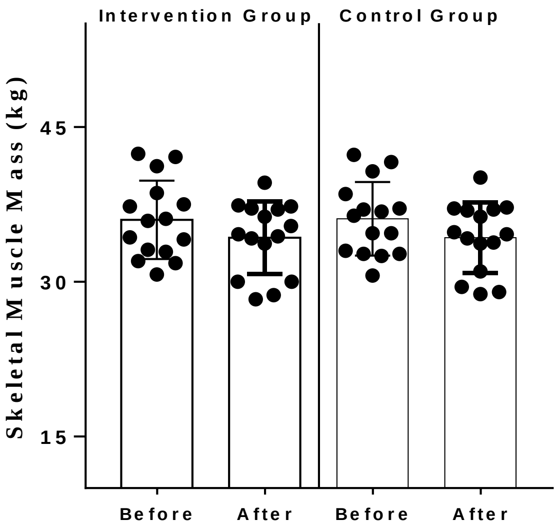


Figure 5.5. Comparison of before and after skeletal muscle mass between the intervention

group and the control group.

Neuromechanical changes after strength training. After four weeks of neuromuscular strength training, the elbow flexor muscle with isometric contraction increased the magnitudes of maximal voluntary torque (MVT) from 67 ± 15 to 85 ± 20 Nm (interaction = intervention × group; $F_{[1,14]} = 32.138$ $p = 0.000$, $\eta p^2 = 0.697$), where no changes were observed for the control group (from 66 ± 13 to 61 ± 10 Nm).

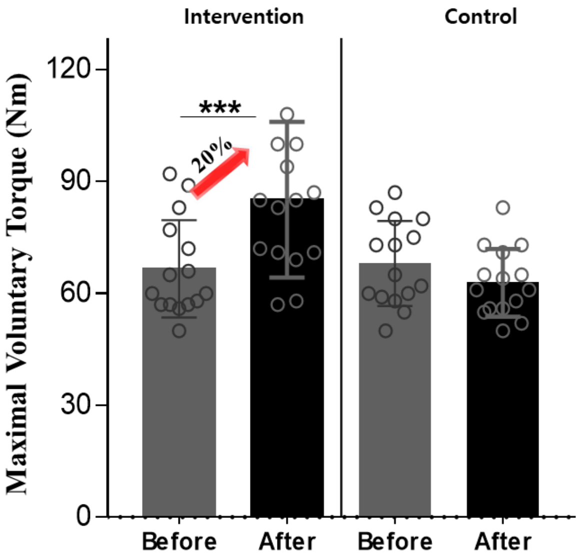


Figure 5.6. Comparison of before and after MVT change in the intervention group and the control group.

These findings were supported by two-way repeated measures ANOVA with factor *Intervention* (two levels: before and after) and *Groups* (two levels: intervention and control) on the absolute values of MVT(Nm) (i.e., the magnitude of MVT) on the absolute values of MVT (i.e., the magnitude of MVT), which showed significant main effects of *Intervention* ($F_{[1,14]} = 10.729$, $p<0.006$, $\eta p^2 = 0.434$), *Groups* ($F_{[1,14]} =$ 7,778, $p<0.014$) with significant factor interactions (interaction = intervention ×

group)

Total Number of Accepted Motor Units. Table 5. presents the results of the data analyses related to the motor unit recruitment in the intervention group after the neuromuscular strength training. It indicates that there were significant increases in both the total number and mean number of agonist motor units used during the analyzed tasks. This suggests that the neuromuscular strength training led to an enhanced recruitment of motor units in the agonist muscle. A three-way repeated measures ANOVA supported these findings with factors *Intervention* (two levels: before and after) and *Groups* (two levels: intervention and control) and *Torque levels* (four levels: 35%, 50%,75% and 90%), which showed that there was significant main effect of *Intervention* ($F_{[1,14]} = 9.422$, $p<0.008$, $\eta p^2=0.34$) and *Torque levels* ($F_{[1,14]} = 36.563$, $p<0.000$, $\eta p^2=0.723$) with significant *Intervention × Groups* reflected the fact that that the effect of group was intervention group only. Post-hoc pairwise comparison confirmed that the 50%,75% and 90% of intervention group.

Table 5.1 Distribution of the analyzed number of motor units before and after the Control and Intervention group.

		Average Number of Motor Units(MU) per Torque level (Average Accuracy of decomposition)							
Muscle		**Agonist (BB)**				**Antagonist (TB)**			
Group		**Control**		**Intervention**		**Control**		**Intervention**	
Torque level		**Before**	**After**	**Before**	**After**	**Before**	**After**	**Before**	**After**
# of Motor Units	**35%**	29(91%)	19(90%)	21(90%)	24 (91%)	6(91%)	7(91%)	8(91%)	11(91%)
	50%	23(91%)	23(91%)	22(91%)	**29***(90%)	10(91%)	10(91%)	12(91%)	15(91%)
	75%	25(91%)	25(90%)	25(90%)	**30***(90%)	15(91%)	16(91%)	14(91%)	18(91%)
	90%	26(91%)	27(90%)	25(91%)	**31***(91%)	16(91%)	18(91%)	16(91%)	20(91%)

*Significant number of MU shown in bold. BB, Biceps Brachii; TB, Triceps Brachii. The number in brackets represents th e average of the decomposed firing instances of the set of motor units per contraction level.

The number of recruited motor units and their inter-pulse interval average.

The average inter-pulse interval of multi-motor motor units (Table 5.3) varied with the intervention, group, and torque levels. For the average inter-pulse interval, there was a significant main effect of *Intervention* ($F_{[1,14]}$ = 14.43, p<0.004).

Table 5.3. Changes in motor unit mean discharge rate for all conditions

Condition Groups Target torque	Control Group			Intervention Group		
	Before	After	P Value	Before	After	P Value
35%	118.6±7.3	111.2±6.4	< 0.446	112.2±7.8	136±9.12	**< 0.002***
50%	126±11.1	110.3±6.5	< 0.096	106.1±5.4	132.2±8.6	**< 0.028***
75%	93.2±6.44	84.1±5.16	**< 0.037***	80.9±4.26	111.3±9.6	**< 0.008***
90%	106±9.44	95.7±7.42	< 0.068	79.9±8.73	93.9±10.7	**< 0.019***

Data are presented as means ± SE; n=15 subjects for the both group. *Significantly higher torque values in intervention group (IG) than control group (CG)

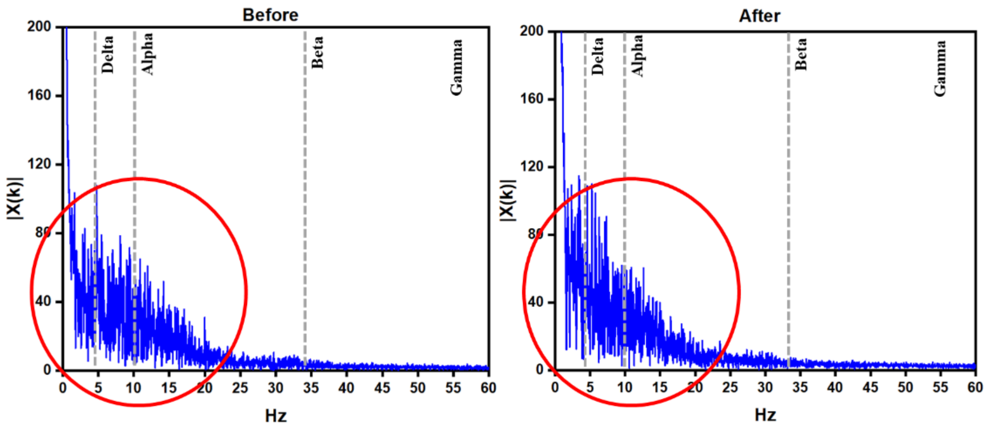
In particular, the neuromuscular strength training protocol increased average inter-pulse interval of motor units at all four-target torque: 35%MVT (p<0.002, ηp^2=0.464), 50%MVT (p<0.028, ηp^2=0.414), 75%MVT (p<0.008, ηp^2=0.452), and 90%MVT (p<0.019, ηp^2=0.364). also, there was n significant increase in discharge rate variability for 35% and 50%MVT.

Table 5.4 Changes in motor unit mean discharge rate variability for all conditions

Condition Groups Target torque	Control Group			Intervention Group		
	Before	After	P Value	Before	After	P Value
35%	95.8±7.0	110±11.6	< 0.708	112.6±8.5	100.8±7.1	**< 0.033***
50%	96.2±9.4	97.2±9.94	< 0.644	112±12.4	99.1±7.07	**< 0.026***
75%	76±4.78	84.8±10.0	< 0.361	76.7±4.44	76.96±6.24	< 0.134
90%	88.7±5.4	85.1±5.20	< 0.180	86.1±12.04	71.2±6.31	< 0.084

Data are presented as means ± SE; n=15 subjects for the both group. *Significantly higher torque values in intervention group (IG) than control group (CG).

There was no statistical difference for MU3 and MU4, which are relatively middle motor units whereas, in MU1, MU2, and MU5, the main effect by *Intervention* ($F_{[1,14]}$ = MU1:14.56, p<0.001; MU2:12.342, p<0.002; MU5:11.35, p<0.005). In particular, it showed a statistically large increase at 0-4 Hz (delta), 4-10 Hz (Alpha), and 10-35 Hz (Beta) after strength taring with the intervention group in 50%,75% and 90%MVT conditions. For the relative power in five motor units discharge, there was a significant main effect for *Intervention* ($F_{[3,42]}$ = 27.523, p<0.0001) and frequency band ($F_{[3,42]}$ = 66.471, p<0.0001). Particularly, post-hoc analysis indicated that the intervention group compared with control group exhibited greater relative power from 0- 4Hz (t = -1.96, p=0.001) (fig. 4). Specifically, intervention group participants exhibited increased power in all frequency bands (delta(0-4Hz):36%; alpha(4-10Hz):27%; beta(10-35Hz): 31%; gamma(35-60Hz): 25%).



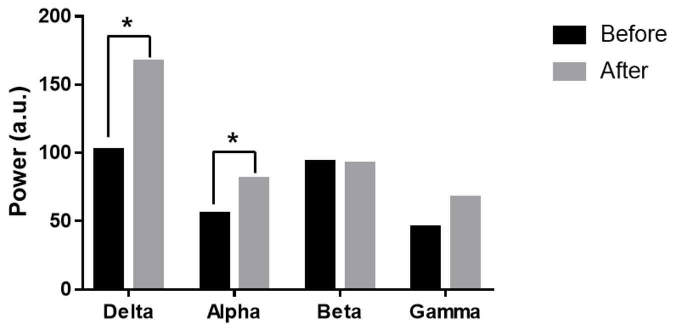


Figure 5.7. The power spectrum of the discharge rate was divided into the following four frequency bands: 0-4(delta), 4 -10(alpha), 10-35(beta), and 35-60(gamma)Hz. Power spectral density of the biceps brachii (BB) muscle motorneuron pool for before and after intervention group.

Correlation Between Mean Firing Rate (MFR) and Recruitment Thresholds

(RT). We analyzed the relationship between the mean firing rate (MFR) and motor unit recruitment thresholds (RF) observed during the MVT, 35%, 50%, 75%, and 90%MVT. The recruitment threshold of each motor unit was recorded as the torque level achieved, measured in percent MVT at the instance at which the first firing of the motor unit occurred.

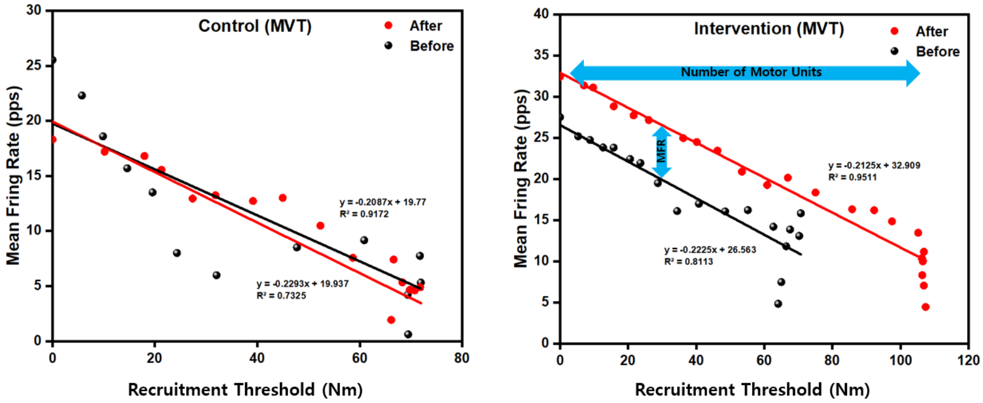
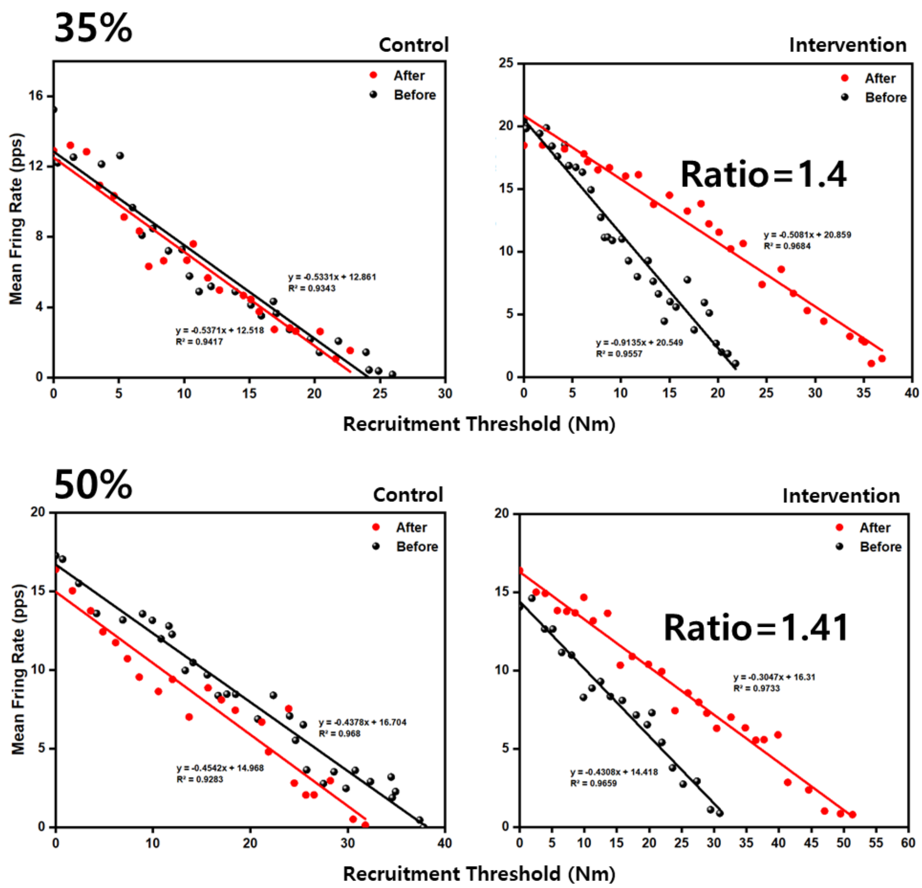


Figure 5.8. Linear regression between mean firing rate (MFR) and recruitment threshold (RT) for maximum voluntary torque (MVT) condition. Scatter plots of the recruitment thresholds for the same motor units in each participant in the control (left) and strength-training groups (intervention, right). The recruitment thresholds are shown before (black circle) and after (red circle) the intervention. Slope ratio (a) from the linear regression with before (black line) and after (red line).

Figure 5.8 shows an example of a linear regression of the relationship between the motor unit MFR and the RF for a representative subject of each group before and after. The MFR versus RF relationship is typically best fit with a linear model (Harmon, Kylie K., et al. 2019). In the current study, we analyzed relationships examined on an individual contraction basis. After the intervention group, linear slopes were decreased with increased y-intercepts, with a significant effect on neuromuscular strength training intervention (Figure 5.8). A three-way repeated-measures ANOVA supported these findings with factors *Intervention* (two levels: before and after) and *Groups* (two levels: intervention and control) and *Torque levels* (four levels: 35%, 50%,75%, and 90%), which showed that there was a significant main effect of *Intervention* ($F_{[1,14]}$ = 9,132, p<0.01,ηp²=0.737) and *Groups* ($F_{[1,14]}$ = 6.923, p < 0.03,ηp²=0.619) with significant factor interactions (interaction = *Intervention* × *Groups*; $F_{[1,14]}$ = 34.241 p<0.000, ηp²=0.948) reflected the fact that that the effect of group was intervention group only. Post-hoc pairwise comparison confirmed that the MVT, 50%, 75% and 90% MVT of intervention group. In particular, the intervention group was significantly increased motor units after strength training conditions confirmed by post-hoc pairwise comparisons (p<0.008).



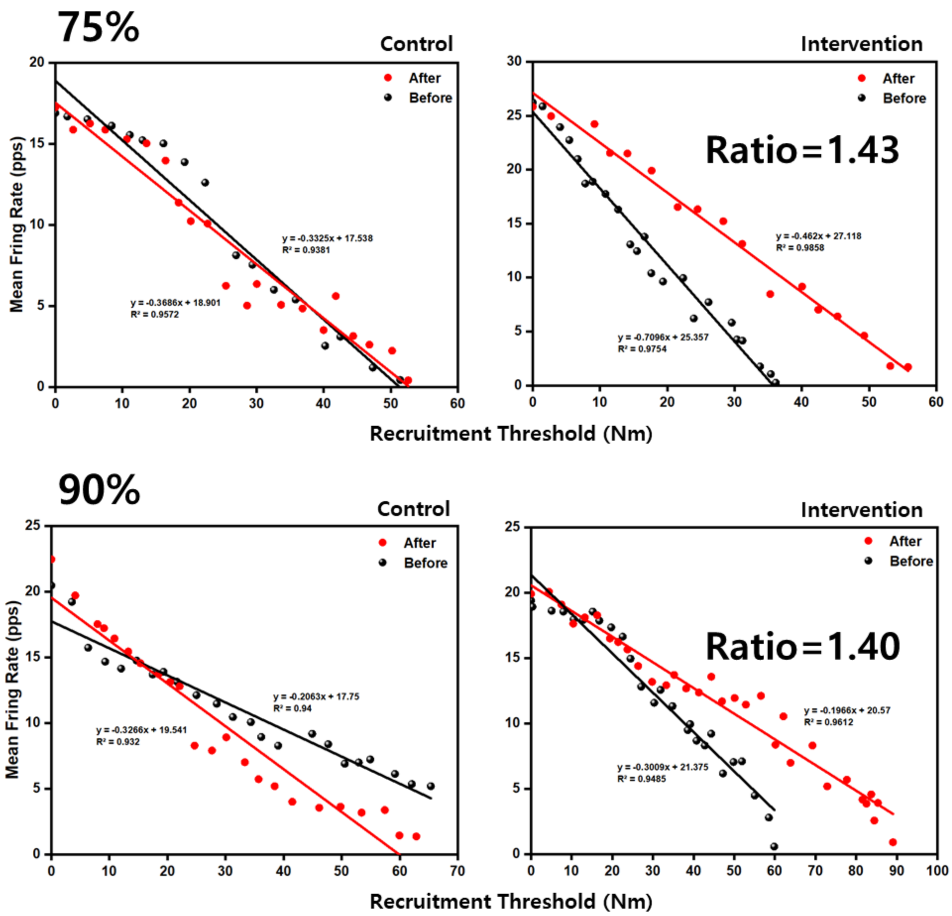


Figure 5.9. Linear regression between mean firing rate (MFR) and recruitment threshold (RT) for all submaximal trapezoidal contraction task conditions, specifically at torque levels of 35%, 50%, 75%, and 90% of maximum voluntary torque (MVT). Scatter plots of the recruitment thresholds for the same motor units in each participant in the control (left) and strength-training groups (intervention, right). The recruitment thresholds are shown before (black circle) and after (red circle) the intervention. Slope ratio (a) from the linear regression with before (black line) and after (red line).

5.4. Discussion

In this study, neuromuscular strength training was performed based on neural adaptation for 4 weeks to find out the long-term effect of the neuromuscular system according to maximize the activation of the motor unit. The main finding of the present study was that the maximal force for the isometric elbow flexion torques was increased significantly after the four weeks of neuromuscular strength training. In other words, neuromuscular strength training improved strength. It increased MU recruitment and firing rate and lowered MU variability at relatively low target force values, thereby more stably controlling joint torque. These results were further associated with significant increments of power spectral densities of the delta band (0-4 Hz). This suggests that the gains in muscle strength may be attributable to an increase in the net excitatory synaptic input or to adaptations in the regulation of muscle activation patterns at the level of motor units.

Consistent with previous research, our study demonstrated a substantial increase in MVT following the four-week intervention period (Car- roll et al., 2001; Folland & Williams, 2007; Balshaw et al., 2016; Škarabot et al., 2021). The elbow flexor muscle exhibited a significant increase. This substantial improvement in maximal torque output suggests that our neuromuscular strength training program effectively enhanced force generation capabilities. Furthermore, our results indicated that increased muscle strength led to statistically significant recruitment of more motor units during submaximal trapezoidal contraction tasks. Specifically, at target torques of 50%, 75%, and 90%MVT, the intervention group demonstrated greater recruitment of motor units compared to before the intervention. These findings suggest that neuromuscular strength training promotes enhanced motor unit recruitment and coordination, contributing to improved force generation at submaximal levels (Duchateau, Semmler & Enoka, 2006; Sale, 1988; Enoka,1997).

In line with the increased recruitment and activation of motor units, the intervention group also exhibited a statistically significant increase in mean discharge rate across all conditions. This finding indicates that the agonist muscle was activated more vigorously after training intervention, resulting in more frequent firing of motor units. The heightened mean discharge rate reflects improved neural drive and coordination of motor units, contributing to the observed enhancements in torque output (Patten, Kamen, & Rowland, 2001; Fimland et al. 2010). Additionally, our study assessed discharge rate variability to indicate motor unit firing pattern consistency. The intervention group demonstrated a statistically significant decrease in discharge rate variability at 35% and 50% of their maximal torque levels. This reduction suggests that neuromuscular strength training induced more regular and consistent firing patterns among motor units, further supporting the improved neuromuscular control and coordination observed in the intervention group (Tracy, Byrnes, & Enoka, 2004; Vila-Chã & Falla, 2016).

Examining the power values in the delta(0~4Hz) and alpha (4~10Hz) frequency ranges during the 50% submaximal task, we found a significant increase after the intervention. This finding suggests that neuromuscular strength training influenced the neural activity associated with muscle contraction, as indicated by changes in specific frequency ranges. Specifically, the delta (Deluca & Erim, 2002) frequency band is related to the common drive signal, and when the common drive signal becomes stronger, it can affect both the agonist muscle and the antagonist muscle, enabling coordinated movement between the two muscles.

Moreover, the linear regression analysis revealed important insights into motor unit recruitment thresholds and mean firing rates during the MVT task. While the control group showed no significant changes, the intervention group exhibited higher mean firing rates as torque levels increased, indicating motor units were recruited at higher thresholds after the intervention. (De Luca & Hostage, 2010; De Luca & Contessa, 2012; Martinez-Valdes et al., 2017) This finding suggests that neuromuscular strength training modified the activation control mechanism of motor units, enabling them to generate higher forces before being recruited. Nonetheless, the submaximal task, which required precise torque control at lower levels, demonstrated a different trend than the MVT task. No significant changes were observed in the control group, indicating stability in the control mechanisms for submaximal torque regulation. However, the intervention group exhibited significant changes before and after training. Analyzing the slope ratio, we observed a greater ratio after training, suggesting a flatter regression slope. This indicates that the activation control mechanism of motor units may have been altered or tuned, allowing for more precise and efficient torque regulation during submaximal tasks (Heckman & Enoka, 2012).

5.5. Conclusion

In conclusion, this study provides extensive evidence of the neuromuscular adaptations associated with a four-week neuromuscular strength training program. Neuromuscular strength training increased strength and functionally controlled MU recruitment and firing rate according to the target torque, lowered MU discharge variability even at the submaximal level, and controlled strength more stably and accurately. These results prove that the training intervention involves modulation of motor neuron output signals transmitted from the central nervous system to muscles and promotes the effective utilization of muscle fibers (Aagaard, P, 2003; Heckman & Enoka, 2004; Heckman & Enoka, 2012). Understanding these neuromuscular adaptations could be crucial for developing targeted training protocols for optimizing strength gains and performance outcomes in various populations and activities.

Chapter 6. General Conclusion

In this dissertation, the neuromuscular mechanism of voluntary muscle force production was explored, and based on this, various experimental research for improving the efficiency and performance of force production were studied.

This dissertation has concluded three experimental studies. Firstly, the length of the muscle changes according to the elbow joint angle, which may be evidence that the CNS detects changes in body posture and controls muscle contraction. Secondly, changes in neural adaptation that accompany various interventions varied. Changes in the neuromuscular system following warm-up given as a short-term enhanced central output to motor neurons and effectively activated large motor units like a fast-twitch muscle. Thirdly, relatively long-term neuromuscular strength training showed a greater increase in muscle strength compared to warm-up and a greater increase in the range of recruitment threshold. In addition, neuromuscular training increased strength and functionally adjusted MU recruitment and firing rates according to the target torque, lowered MU discharge variability at the submaximal level, and was more stably and accurately controlled. That proves that neuromuscular strength training is related to the modulation of motor neuron output signals transmitted from the CNS to muscles and promotes the effective utilization of muscle fibers. Finally, in vivo, experimental research was performed by linking the neuromuscular mechanism of human movement with actual performance ability, and it was revealed that specific intervention could improve voluntary force production ability by regulation of activation patterns on motor units, e.g., changes in the number or rate coding.

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국문 초록

인간의 자발적 움직임 및 힘 생성은 근신경계 시스템 (neuromuscular system)과 운동단위(motor unit, MU) 활성화 사이의 복잡한 상호 작용에 의해 발생합니다. 이러한 복잡한 근신경학적 메커니즘(neuromuscular mechanism) 내에서 작동하는 운동단위는 중추신경계와 운동 실행 사이의 주요 링크 역할을 합니다. 본 연구는 인간의 자발적 움직임에 대한 근신경학적 메커니즘을 근력의 코딩 소스인 운동단위 모집(MU recruitment)과 발화율(firing rate)을 정량화 함으로써 이를 기반으로 근육의 힘 생성 효율성과 근력 향상을 위한 다양한 방법을 연구하였습니다. 3가지 연구를 통해 나타난 결과들을 종합하면 다음과 같습니다. 첫째, 중추신경계는 신체 자세의 변화를 감지하고 그 변화에 따라 근육의 운동단위 모집과 발화율 코딩을 조절합니다. 둘째, 다양한 운동 또는 개입에 따라 수반되는 신경적응의 변화는 다양했습니다. 단기로 주어진 웜업운동에 따른 근신경계의 변화는 개별 운동단위 발화율을 높일 뿐만 아니라 높은 임계값의 운동단위를 활성화하여 모집 임계값(recruitment thresholds)의 범위를 증가시켰습니다. 마지막으로 상대적으로 장기간으로 실시한 근신경 근력 트레이닝 (neuromuscular strength training)은 웜업 연구에 비해 근력이 더 큰 폭으로 증가하였으며 모집 임계값의 범위 또한 더 크게 증가시켰습니다. 또한, 근신경 근력 트레이닝은 근력만 증가시켰을 뿐만 아니라 더 많은 운동단위의 모집과 발화율을 타겟 토크에 따라 기능적으로 조절하여 최대하 힘 수준 (submaximal torque level)에서 운동단위 변동성(MU discharge variability)을 낮춰 안정적이고 정확하게 힘을 조절하였습니다. 이는 트레이닝이 중추신경계에서 근육으로 전달되는 운동 뉴런 출력 신호의 변조와 연관이 있다는 증거를 제공하며 근섬유의 효과적인 활용을 촉진함을 시사합니다. 결론적으로 본 논문에서는 인간움직임의 근신경학적 메커니즘을 실제적 수행능력과 연결시켜 연구를 진행하였고 특정 운동 또는 훈련이 운동단위 조절을 개선하여 자발적 근력 생산 능력을 향상시킬 수 있음을 확인하였습니다. 또한, 중추신경계와 근육 수축 사이의 복잡한 상호 작용에 대한 이해를 크게 향상시켜 다양한 개입(intervention)이 운동단위 활성화 조절에 영향을 미치고 궁극적으로 자발적 근력 생산 능력에 영향을 미치는 방법에 대한 귀중한 통찰력을 제공합니다.

주요어: 근신경학적 메커니즘, 자발적 근력 생성, 운동단위 활성화, 신경적응, 근신경 근력 트레이닝, 근활성화

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