AN ACUTE ALTERATION IN VASTUS LATERALIS MUSCLE LENGTH CAUSES A CHANGE IN MOTOR UNIT DISCHARGE RATE THAT IS NOT MEDIATED BY MUSCLE SPINDLE ACTIVATION.

Peter J. Adhihetty

Thesis submitted to the Faculty of Graduate Studies in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Graduate Programme in Kinesiology and Health Science
York University
Toronto, Ontario

September, 1999

Altering Vastus Lateralis Muscle Length Causes an Acute Adaptation in Motor Unit Discharge Rate that is not Mediated by Muscle Spindle Activation

by

Peter J. Adhihetty

a thesis submitted to the Faculty of Graduate Studies of York University in partial fulfillment of the requirements for the degree of

Master of Science

Abstract

To assess how changes in muscle contractile properties influence motor unit firing rates, we changed the length of quadriceps femoris by locking the knee joint at different angles prior to making isometric contractions (n=10). We also perturbed muscle spindles with high speed vibration (265 Hz) of the patellar tendon. When the muscle was shortened compared to its length at 90 degrees, twitch amplitude and ±dF/dt increased more than four-fold and MVC was 60% greater (all $p<0.001$). Average motor unit firing rates, obtained with tungsten microelectrodes from more than 400 single unit recordings were nearly 60% greater ($p<.05$) at any absolute submaximal force when the muscle was longest (e.g. decreased MVC and ±dF/dt). Lengthened vastus lateralis EMG was significantly higher than the short length during 50% MVC ($p<.05$) implying greater descending drive. Increases in lengthened vastus lateralis EMG may be compensatory for muscle deviating largely from optimal length with less force producing capacity and thus requiring increased activation. Biceps femoris EMG was also increased ($p.<.05$) while vastus lateralis was longest suggesting that the increased vastus lateralis EMG may be partially attributable to increased antagonistic activity. In contrast, average motor unit firing rates were lower ($p<.01$) than control when the tendon was vibrated during a 30% MVC contraction. Our data suggest that alterations in rate coding that occur at different muscle lengths are not mediated by muscle spindle activity.

KEY WORDS: average motor unit firing rate, MVC, ±dF/dt, antagonistic activity, optimal length, rate coding, descending drive, EMG

Acknowledgements

Firstly, I must thank Dr. Cafarelli, for his patience in putting up with my idiosyncracies and eccentric behaviour while enforcing just the right amount of discipline and tutelage to efficiently achieve my research goals. His encouragement and confidence in my academic abilities reassured my desire to continue the road of academia to the PhD level. More importantly, his reasoning, unique sense of humor, and ability to put every dilemma in perspective has implicitly taught me how to live and enjoy life. Although, I will undoubtedly forget some neuromuscular physiology in the future, his unspoken life-lessons cannot be forgotten and will always be used to conquer obstacles presented in my life.

Thank you Joanne Blake who directed a very enraged student towards Dr. Cafarelli's office two and a half years ago when it seemed that my application was lost and I would not be admitted to graduate school. I thank Dr. Cafarelli again, for calming me down, listening to my predicament and then offering me a position on the same day!!

Thanks Ilia and Albert for solving the technical problems in the lab and also saving my proposal presentation. Thank you, Dave Cox, for the computer assistance you have provided from the start and even while in England. Attending conferences was only made possible by Dr. Melo, Dr. Hood and Dr. Katzmarszyk providing accommodations and transportation. Thanks big sis, Merlyn, for providing airfare to ACSM.

Carley Benton reduced data for endless hours without complaint and provided support every step of the way. A medal for bravery should go to Brandon for being my first subject with intramuscular needles. Thanks Jennifer for some last minute plots and references.

My first-year lab mates, Jayne and Angela, without your help I would still be standing in awe at all the equipment and wires. My second-year lab mate, Carrie Plaskett's words, "SHUT UP, Peter!" will always stay in my mind. Carrie's zest and excitement made the second year pass quickly and her help with data collection was invaluable. More importantly, I know I have a friend for life. Love Ya Carrot!! My best friend in the program, Joe "RatMan" Gordon, was always there to provide sound advice in troubled times, especially on the freeway in Washington. Thanks Roxy for making me laugh when times were tough.

Lastly, I owe the most thanks to my parents who have supported my research goals, provided enormous amounts of food and shelter over the past two years. All of the prepared lunches and late night talks were much appreciated Mommy. My Dad's strength and perseverance with cancer over the past two years has made me appreciate the little things in life and put all obstacles into perspective. Although, I probably don't say it as much as I should, I love you both and truly appreciate everything you have both provided and sacrificed on my behalf.

Table of Contents

List of Terms and Abbreviations

% Activation - the percent of the total motor unit pool driven voluntarily as measured using the twitch interpolation technique

AMUFR - average motor unit firing rate

CNS - Central Nervous System- consists of the spinal cord and brain.

+ dF/dt_{max} - maximal instantaneous slope of the upward limb of an evoked twitch measured as the peak of the differentiated force channel.

-dF/dt_{max} - maximal instantaneous slope of the downward limb of an evoked twitch measured as the valley of the differentiated force channel.

$EMG_{max}+_{50\% MVC}$ -Electromyogram/Electromyography. A Graphical representation of electrical activity of muscle using either surface or indwelling electrodes. Electrical current changes that are measured actually represent differences in charge associated with the opening and closing of ion channels occurring at the level of the muscle cells. Subscript Max represents the electrical activity associated with a maximal contraction and 50% MVC represent the electrical activity during 50% force.

MVC - Maximal Voluntary Contraction. The largest amount of force produced voluntarily.

M-wave - mass action potential representing the simultaneous depolarization of all motor units elicited by a supramaximal electrical stimulus to the motor nerve.

RMS - Root Mean Square. A mathematical unit used to quantify the electrical signal obtained from surface electrodes.

½ RT - Half Relaxation Time. Amount of time taken to decrease from the peak force value of an evoked twitch to half that value.

TPT - Time to Peak Tension. Amount of time taken between the onset of force production of an evoked twitch response and the peak value.

Tw Amp - The peak force value in a twitch response evoked with a supramaximal stimulus.

List of Figures and Tables

Allocation of Work

All sections of this thesis were analyzed, produced and written by myself and editorial changes were completed by Dr. Cafarelli. A majority of the data collection for this study was assisted by Carrie Plaskett and data reduction from tape by Carley Benton. Additionally, some data reduction and analysis was performed by Brandon Meyers and Jennifer Nguyen.

Chapter I- Overview and Purposes

General Overview and Purposes

A major focus of our laboratory is the nervous system's ability to control muscle force and its capacity to adapt to external stressors and perturbations. All day-to-day movements involve muscle contraction and are dependent on descending drive originating in the motor cortex and terminating on the appropriate muscle via the spinal cord and motor nerves - the neuromuscular pathway. Maintaining the fidelity of this motor signal is of utmost importance. Failure to do this is clearly demonstrated by the disease multiple sclerosis. Multiple sclerosis is characterized by the loss of a fatty substance, myelin, encompassing the nerve and interferes with transmission of the signal down the neuromuscular pathway. As a result, the signal transmitted to the muscle is sporadic and diminished, making even the most basic movements jerky and difficult to achieve. In this disease, the neuromuscular system is incapable of adapting but in other circumstances it has been shown to be a highly adaptive and dynamic system.

The ability of the neuromuscular system to adapt to resistance overload has received considerable investigation in the last 30 years. Strength training a muscle increases the maximal voluntary force production and the rate of force development of the evoked twitch. Since contractile properties of muscle become faster with training, the obvious question would be: does the nervous system alter its rate of motor unit discharge to accommodate the faster contractile properties. Overall electrical activity of muscle or individual motor unit discharge rate measured with surface or indwelling electrodes provides information indicative of nervous system performance. Previous results indicate that electrical activity of muscle is

not augmented to sustain the increased contractile properties (Rich and Cafarelli: In Press) but one study has shown increases (Van Cutsem et al. 1998).

Immobilization and fatigue both decrease the contractile properties of muscle and nervous system output is modulated, resulting in a decrease in the motor unit firing rate (Bigland-Ritchie et al. 1983, Duchateau and Hainaut 1990). Thus, altering contractile rate, either acutely with fatigue or chronically with immobilization, triggers a corresponding adjustment in the output of the nervous system.

Changing muscle length alters the contractile properties of muscle (Rack and Westbury 1969). Contractile rate increases when a muscle is shortened and motor unit firing rates would be anticipated to increase based on the results of fatigue and immobilization experiments. The ability to acutely modify contractile properties provides a unique and time-efficient experimental model to monitor any adaptive responses of the nervous system. Two studies have used this approach and changed the length of tibialis anterior, however, their findings are inconclusive (Bigland Ritchie et al. 1992, Vander-Linden et al.1991).

Purposes

1. To change muscle length while carefully monitoring the contractile rate and measure the corresponding average motor unit discharge rate during submaximal and maximal contractions.

2. To determine if spindle activation plays a role in any adaptive response of changing muscle length. During submaximal contractions, muscle spindles were activated by

applying high speed vibration to the patellar tendon and motor unit firing rates were measured.

Chapter II- Review of Literature

Review Of Literature

Contraction of Skeletal Muscle

Contraction of skeletal muscle occurs via the cross-bridging of the intracellular force generators, actin and myosin (Huxley and Simmons 1971). Activation of cross-bridges is dependent upon neural activity originating in the motor cortex which travels down the motor pathway (descending drive) to the alpha motor neuron pool and eventually depolarizes the muscle membrane. The motor neuron pool in the spinal cord consists of cell bodies of alpha motor nerves innervating a specific muscle group or synergistic muscle group. Motor neuron excitability is dependent on the excitatory and inhibitory inputs and the size of the cell body (Eccles 1966, Hennemann et al. 1965). Provided sufficient excitatory input, depolarization occurs in an all-or-none fashion and an ensuing action potential passes down the motor nerve to the neuromuscular junction. Action potentials reaching the nerve terminal open voltage-sensitive Ca^{2+} channels inducing calcium inflow, triggering release of the neurotransmitter acetylcholine into the fissure between nerve and muscle, the synaptic cleft (Ashley and Ridgway 1970). Acetylcholine binds to ligand-dependent receptors on the muscle membrane causing Na^{+} inflow and K^{+} outflow resulting in a depolarization, termed the end plate potential (EPP). This depolarization triggers the opening of voltage gated Na^{+} channels found adjacent to the acetylcholine receptors resulting in a muscle action potential. The wave of depolarization passes along the sarcolemma, down the T-tubules triggering voltage sensitive membrane proteins called dihydropyridine channels (DHP). DHP channels are mechanically and/or chemically coupled to opposing ryanodine receptors found in the terminal cisternae of

the sarcoplasmic reticulum (Nosek et al. 1990, Rios and Pizarro1991, Wagenknecht et al. 1989). Voltage activation causes a conformational change in the DHP channels opening the coupled ryanodine receptors and allowing Ca^{+} outflow from the sarcoplasmic reticulum (Rios and Pizarro 1991, Wagenknecht et al. 1989). Calcium ions diffuse down a concentration gradient to the contractile apparatus inside the muscle cell and are bound by a large globular protein, troponin. The troponin complex consists of three subunits (T,I,C) and is attached to a thin molecule, tropomyosin filament, lying on the surface of the actin molecule. In the absence of calcium, the Troponin I subunit and tropomyosin filament, block the myosin binding site and prevent interaction between myosin and actin. Specifically, troponin C binds four Ca^{2+} ions causing a conformational shift in the troponin complex, pulling the tropomyosin molecule away from the actin and revealing the myosin binding sites. The myosin molecule attaches and rotates within the actin binding site pulling the two molecules together shortening the muscle fiber. Under any set of conditions, force modulation is controlled by two distinct strategies of the nervous system: recruitment of motor units and alteration of firing rate.

Motor Unit Recruitment

The neuromuscular system is able to activate a variable number of motor units by altering the intensity of the descending drive to the alpha motor neuron pool in the spinal cord and by changing the level of excitability of the motor neuron pool. Alpha motor neuron cell bodies summate excitatory and inhibitory inputs in the form of differential ionic conductances to determine whether a motor unit is recruited (Eccles 1966, Hennemann et al. 1965). All motor units in a motor unit pool are thought to be subjected to the same excitatory and

inhibitory inputs from either central or peripheral sources which led to the concept of 'common drive' (De Luca et al. 1982). Small cell bodies have lower thresholds of excitability primarily due to the smaller cell surface area and thus are more susceptible to depolarization than large ones (Henneman et al. 1974, Milner-Brown et al. 1973). A motor neuron pool receiving the same descending drive will cause small cell bodies with low thresholds to be recruited prior to the larger cell bodies with higher thresholds (De Luca et al. 1982, Hennemann et al. 1965, Milner-Brown et al., 1973). Increasing the descending drive to the motor neuron pool results in an orderly recruitment from small, low threshold motor units to large, high threshold motor units. This is referred to as the size principle of motor unit recruitment (Hennemann et al. 1965). Motor neuron pools for different muscles vary in cell body size and organization (Monster and Chan 1977). Motor neuron pool excitability of small distal muscles may be arranged so that recruitment of the entire motor neuron pool occurs during low descending drive and for large muscles, recruitment occurs throughout the entire range of descending drive (De Luca et al. 1982, Kukulka and Clamann 1981, Milner-Brown et al. 1973). The differential organization of the motor neuron pool excitabilities may depend on the functional requirements of the muscle. Small muscles require precise gradation of force which may be attained by recruiting all of the motor units at low force levels and presumably relying on a more force-sensitive rate coding strategy to modulate moderate and high force levels. Larger muscles are used to generate powerful contractions and depend primarily on recruitment to modulate force production (DeLuca et al. 1982, Kukulka and Clamann 1981, Milner-Brown et al. 1973). Recruitment was found to regulate forces up to 88% MVC in the biceps brachii, 50% MVC in adductor pollicis, 40%

in first dorsal interosseous and 80% in deltoid (DeLuca et al. 1982, Kukulka and Clamann 1981).

Various feedback mechanisms and eccentric contraction studies have shown that larger motor units can be recruited prior to small units which contradicts the size principle and suggests a certain degree of flexibility in the recruitment order (Andrew 1985, Garnett and Stevens 1981, Grimby and Hannerz 1968, 1974, Kato et al. 1985, Tax et al. 1990). Prolonged depolarization of motor neurons, "plateau potentials", caused by a short barrage of excitatory input has been shown to occur long after excitatory input has been withdrawn (Crone et al. 1988, Eken and Kiehn 1989, Llinas 1988, Hartline et al. 1988, Hounsgaard et al. 1988, Schwindt and Crill 1980). Excitability of motor neurons may not simply be a linear summation of excitatory and inhibitory inputs as previously noted but rather each neuron can be thought of as a complex, dynamic and modifiable integrator of synaptic inputs, and recruitment order may be variable under certain conditions (Andrew 1985, Garnett and Stevens 1981, Grimby and Hannerz 1968, 1974, Kaczmarek 1986, Kato et al. 1985, Llinas 1988, Tax et al. 1990).

Rate Coding

Alpha motor neurons which have already been recruited based on a threshold excitability can augment force production by increasing their discharge frequency. Increasing the descending drive to a neuron already discharging does not affect the size of the depolarization but rather accelerates the ionic conductances and increases the firing rate (DeLuca et al. 1982, Kukulka and Clamann 1981, 1977, Milner-Brown et al. 1973, Monster and Chan 1977). Individual motor unit firing rates increase rapidly at recruitment and

maximal force levels compared to the region of intermediate forces resulting in a sigmoidal relationship with force (Stein and Parmiggiani 1979, Erim et al.1996).

Motor units recruited at a higher threshold would intuitively be expected to fire at higher firing rates than lower threshold units and this has been supported in the literature (Mori 1973). However, high threshold motor units have been found to fire at lower discharge frequencies than low threshold motor units for forces up to 50%. This is known as the onion skin phenomenon (De Luca et al. 1982, Monster and Chan 1977, Person and Kudina 1972). The central nervous system may be attempting to minimize fatigue of the high threshold motor units by employing a low firing rate at low force levels because higher threshold units are more susceptible to fatigue (Hatze and Buys 1977).

Some motor units are known to discharge twice at high frequencies at the onset of contraction. These are termed 'doublets' (Zajac and Young 1980). Double discharges cause an immediate rise or "jump" in force production decreasing the time to fused tetanus and are followed by a lower steady firing rate. This is referred to as the catch property of muscle (Burke et al. 1970).

Motor unit firing rates at recruitment are generally faster than the derecruitment firing rates prior to any potential fatigue of the muscle and this is termed the "hysteresis effect" (Clamann 1970, Milner-Brown et al. 1973, Person and Kudina 1972). Faster motor unit firing rates at recruitment may be partially attributable to the catch-like property of muscle despite being at much lower frequencies than doublets.

Rate Coding and Contractile Properties

Contractile properties of muscle can be attained by shocking the muscle with a brief

supramaximal electrical stimulus. The mechanical response known as a twitch represents the simultaneous depolarization of all motor units. A succession of stimuli causes twitches to summate with force increasing progressively with each additional stimuli and eventually reaching a plateau force level, tetanic fusion. Electrically stimulating whole muscle with one supramaximal stimulus or numerous stimuli is unphysiological because it causes synchronous depolarization of all motor units and consequently requires high stimulation frequencies for tetanic fusion. Alternatively, voluntary contractions activate motor units in an asynchronous discharge pattern requiring lower firing rates for tetanic fusion. The contractile duration or rate of force development of the twitch appears to be the most important factor in dictating the external stimulation frequency necessary to cause tetanic fusion. Motor units and their associated muscle fibers can be generally classified according to contractile rate as either slow twitch or fast twitch. Rack and Westbury (1969) showed a higher external stimulation frequency was necessary to cause complete tetanic fusion in cat soleus muscle at a shortened length with fast contractile rate whereas a lower stimulation rate required for a longer length with slower contractile rate. These results were duplicated using human tibialis anterior and abductor digiti minimi (Gandevia and McKenzie 1988, Marsh et al. 1981).

Each individual motor unit contributes a small amount of force when activated during a voluntary contraction. Contractile properties of this 'motor unit twitch' dictate the optimal firing frequency for that particular motor unit. Motor units innervating the human biceps brachii, which is composed of an equal number of fast and slow twitch fibers, showed a three times higher mean firing rate than the primarily slow twitch fibres of the soleus (Bellemare et al. 1983). Quadriceps femoris is a mixed muscle with approximately equal proportions of fast

and slow twitch fibers similar to biceps brachii and has a range of firing rates between approximately 5 - 25 Hz (Lexell and Downham 1991). Young subjects have higher firing rates compared to old subjects who generally have fewer fast twitch fibers (Kamen et al. 1995). The proportion of fast to slow twitch fibers of a particular muscle determines the contractile characteristics and dictates the motor unit firing rates necessary for tetanic fusion.

In a chronic adaptation model, Duchateau and Hainaut (1990) found that after 6-8 weeks of immobilization, the contractile properties of adductor pollicis and first dorsal interosseous slowed and there was a corresponding decrease in the maximal motor unit firing rate. In an acute adaptation model, Bigland-Ritchie and colleagues (1983) found that contractile properties slowed with fatigue and the average motor unit firing rate decreased concurrently. The slowing of the motor unit firing rate during fatigue has been attributed to group III and IV neurons sensitive to changes in the metabolic state of the muscle (Bigland-Ritchie et al. 1986, Kniffki et al. 1978, Kumazawa & Mizumura 1977). Contractile properties have been shown to increase with resistance training (Alway et al. 1989) and corresponding motor unit firing rates have both increased (van Cutsem et al. 1998) and remained constant (Rich and Cafarelli, In Press).

Altering muscle length changes the rate of force production of the twitch, which dictates the external stimulation frequency needed for complete tetanic fusion in both in vivo and isolated animal muscle (Gandevia and McKenzie 1988, Marsh et al. 1981, Rack and Westbury 1969). The literature regarding the relationship between the change in muscle length and the motor unit firing rate during voluntary contractions is limited and contradictory. Vander Linden and colleagues (1991) found that the motor unit discharge rate

was altered with changes in the length of tibialis anterior but did not monitor the contractile rate. Bigland-Ritchie and colleagues (1992) found no change in the motor unit firing rate despite differences in the contractile properties.

Activation

To measure the ability of the nervous system to maximally activate muscle during a maximal voluntary contraction, Merton (1954) developed the twitch interpolation technique. A supramaximal electrical stimulus is delivered to the nerve supply of the pertinent muscle during a maximal voluntary effort. The absence of any twitch response evoked by the stimulus implies that all motor units are recruited and firing at or above the tetanic fusion rate. Activation level can be quantified by comparing any increment in force evoked by the interpolated stimulus during the maximal effort compared to the amplitude of a control potentiated twitch delivered at rest, immediately following the effort. Twitches following a maximal voluntary effort or prolonged tetanic stimulation, potentiate and become larger than twitches in a rested muscle. Phosphorylation of myosin light chains caused by contractile activity is the proposed mechanism for potentiation (Lowey et al. 1993, Moore and Stull 1984). Some studies have utilized a 'train' of repetitive stimuli superimposed on a maximal voluntary effort regarding it as a more sensitive measure of activation but this is not clearly established (Belanger and McComas 1981, Doherty et al. 1993, Kent-Braun and Ng 1999).

Direct electrical nerve stimulation recruits motor units in reverse to voluntary recruitment. This is because large axons are more susceptible to depolarization (Hennemann et al. 1974, Gorman and Mortimer 1983). However, electrical stimulation directly over the

muscle belly or motor point may provide a closer resemblance to the voluntary recruitment order of smallest to largest. Larger motor neurons have higher rates of electrical transmission down the axon and this can be quantified as an increase in conduction velocity compared to small motor neurons. Knaflitz and colleagues (1990) showed that progressively increasing the stimulating intensity caused an increase in the conduction velocity implying that successively larger motor units were being recruited. This may be due to the proximity of the neuron branches to the point of stimulation (Knaflitz et al. 1990). If a supramaximal stimulus is applied, all motor units are recruited regardless of the type of stimulation. Small interpolated twitch force during maximal efforts indicates a high degree of voluntary drive to the muscle. Using this technique, it has been shown that well motivated subjects are able to maximally activate many muscles including the quadriceps, tibialis anterior, biceps brachii and abductor minimi (Belanger and McComas 1981, Bigland-Ritchie et al. 1986, Gandevia and McKenzie 1988). However, it is more difficult to maximally activate the soleus and diaphragm (Allen et al. 1993, Belanger and McComas 1981, 1985).

Length-Tension Curve and Optimal Length

The classic length-tension relationship is based upon the amount of overlap of myosin and actin. Each myosin filament is surrounded by a hexagonal lattice of actin filaments which together comprise a sarcomere. Actin and myosin molecules are stacked together and aligned in series with one another to form a tube-like structure called the myofibril (Huxley and Niedergerke 1954). Actin molecules are lined up in series with one another and opposing actin filaments are separated by regular spaced intervals known as H-zones. Force

production occurs as a result of the sliding action or pulling of the actin filaments together, decreasing the H-zone and caused by independent cross-bridges. Two globular head and neck regions of the myosin molecule form the cross-bridge between actin and myosin and each head is comprised of three large protein complexes. The largest component contains the binding domain attaching to actin and a pocket for binding and hydrolizing ATP (Vibert and Cohen 1988). Release of calcium from the surrounding sarcoplasmic reticulum, as result of a muscle action potential, causes the inhibiting tropomyosin molecule to be shifted and allows the myosin head to interact with the actin binding site. Hydrolysis of ATP causes a conformational change in the large binding component of the myosin head to weaken and reattach further up the actin molecule resulting in the sliding of actin filaments together known as the power stroke (Rayment et al. 1993).

Cross-bridge overlap can easily be manipulated by stretching the muscle fiber. By stretching the muscle from an initial shortened position and measuring the maximal tension development with supramaximal electrical stimuli at increasing degrees of stretch, an inverted U-shaped length-tension curve can be constructed (Gordon et al. 1966). Force production at shortened muscle lengths is compromised due to an increasing lateral distance between the myosin and actin filaments and overlapping of the actin filaments may interfere with the cross-bridge mechanism (Gordon et al. 1966). Force production declines in lengthened muscle fibers because actin and myosin molecules are physically pulled apart from one another resulting in less overlap. The greatest force production occurs with the muscle at an intermediate length with the maximum number of cross bridges between actin and myosin filaments.

The length producing the maximal amount of tension is termed the optimal length (Gordon et al. 1966). Traditionally, optimal length of a muscle is its resting length in the anatomical position (Zierler 1974). Although resting length may be able to produce the largest tension if isolated and externally stimulated, functional movement and force production in vivo is dependent on muscle-joint systems. Thus, when determining optimal length of a muscle in vivo, maximal voluntary contractions are made at all functional angles for the joint and the angle at which maximal force is produced is the optimal muscle length (Clarke et al. 1950, Haffajee et al. 1972). The most widely accepted notation for describing the knee position is using flexion angles based on 0 degrees of flexion occurring with the knee joint completely opened. Isometric angle-torque curves of the quadriceps muscle group show the optimal angle for maximal torque production is approximately 60-70 degrees of flexion (Narici et al. 1996).

Each head of the quadriceps muscle may have slightly differing degrees of stretch as the knee is moved through its range of motion. This may result in different angle-torque relationships for each of the four muscles. The angle-torque data presented by Narici and colleagues (1996) represent the summation of torque produced by all four muscles of the quadriceps. It can only be inferred that all heads have the same torque-angle relationship.

Pennation

The fibres of most mammalian muscles are organized in a slanting arrangement, or pennation that is not in alignment with the overall axis of pull of the muscle. Changes in muscle length may produce significant changes in the angle of pennation which may affect the amount of torque produced at a given joint (Muhl 1982, Wottiez et al. 1984). For

example, both the angle and the torque produced around the elbow joint interact to produce significant non-linear increases in the pennation of the brachialis (Herbert and Gandevia 1995). These changes in pennation were 40-46% larger than the changes found in studies using the quadriceps muscle group. This is probably due to the smaller resting angle of pennation of quadriceps, compared to brachialis (Henriksson-Larsen et al.1992, Rutherford and Jones 1992). Recently, Fukunaga and colleagues (1997) used ultrasonography to observe a 1 degree increase in the angle of pennation of vastus lateralis when manipulating the knee joint angle from 90 to 65 degrees of flexion. The force applied to the tendon decreases by a factor of $\cos\theta$ (where θ is the angle of pennation) resulting in no measurable decrement in force at 65 degrees of flexion compared to 90 degrees (Fukunaga et al. 1997). Therefore, changing the angle of flexion of the knee results in a minimal change in the pennation angle of vastus lateralis muscle and has no effect on force production .

Biomechanics

The patellar ligament, patella and quadriceps tendon act together as a lever for the knee joint. The force producing capability of the knee joint is directly proportional to the length of the moment arm of the patellar ligament. The length of the patellar ligament moment arm increases as the angle of flexion is changed from 90 to 60 degrees and the longer moment arm results in a progressive biomechanical advantage as the joint angle is altered from 90 to 60 degrees of flexion (Yamaguchi and Zajac 1989). The moment arm length of the patella ligament is approximately 5cm at 60 degrees of flexion and 4.5 cm at 90 degrees of flexion (Herzog and Read 1993, Visser et al. 1990). The resultant biomechanical force increase at 60 degrees of flexion can be calculated by multiplying the force produced

at 90 degrees by a ratio of 5: 4.5. The change in moment arm length accounts for approximately 15% of the increase in force of the quadriceps at 60 degrees of flexion compared to 100 degrees of flexion. Thus, an increase in force at 60 degrees of flexion may be partially attributable to the mechanical advantage (15%) but the majority of the increase in force production (85%) can be ascribed to the change in muscle length.

Vibration

Vibration of muscle at 100Hz -200Hz stimulates muscle spindles and to a much lesser extent, golgi tendon organs, pacinian corpuscles and free nerve endings (Bianconi and van der Meulen 1963, Burke et al. 1976). Spindle discharge rates have been shown to have a one-to-one relationship with the vibration frequency (Vallbo 1970, 1974). Muscle spindles are part of the peripheral feedback mechanism that communicates via IA and IIA afferent neurons communicating monosynaptically and polysynaptically with the alpha motor neuron pool of the homonymous muscle. Spindles are responsible for detecting changes in muscle length and eliciting compensatory contraction to resume a set length. Mechanical vibration applied to a tendon or muscle belly provides sufficient excitatory input to the alpha motor neuron pool to recruit motor units and elicit a reflex muscle contraction named the tonic vibration response (TVR) (Eklund and Hagbarth 1966). The force production of the TVR is usually a small percentage of the maximal force producing capacity of the muscle. Rothmuller and Cafarelli (1995) vibrated the patellar tendon and found an average TVR of 3% maximal voluntary force of the knee extensors.

Motor unit recruitment thresholds induced by vibration are lower than the thresholds observed during voluntary contractions of the same force (Romaiguere et al. 1993).

Additionally, a facilitory after-effect of vibration causes lower motor unit recruitment thresholds during subsequent voluntary ramp contractions (Romaiguere et al. 1993). It was suggested that this response may be due to a post-synaptic potentiation or reflex sensitization of the muscle spindles.

Fatigue during repeated maximal voluntary contractions causes a slowing of the muscle contractile properties and causes a corresponding decrease in the maximal motor unit firing rate which has been attributed to afferent feedback (Bigland-Ritchie et al. 1986). Vibration of fatigued muscle initially provides sufficient excitatory input to temporarily restore maximal motor unit firing rates but when prolonged, vibration accentuates the normal decline in motor unit firing rates (Bongiovanni and Hagbarth 1990). These results imply vibration may initially compensate for reduced Ia afferent excitatory input due to fatigue of intrafusal fibres but extended vibration may reduce the synaptic efficacy of the Ia afferent loop by pre-synaptic inhibition and/or depleting available transmitters (Bongiovanni et al. 1990, Eccles 1966). Deafferentation of a non-fatigued muscle reduces the maximal motor unit discharge rate showing afferent input facilitates maximal motor unit discharge rates (Gandevia et al. 1990, Macefield et al. 1993). This result supports the reflex Ia origin of the decline in motor unit firing rates occurring during prolonged maximal voluntary contractions.

A brief burst of excitatory input induced by vibration has been shown to cause prolonged depolarization of a motor neuron called a plateau potential (Llinas 1988, Hartline et al. 1988). The neuron continues to fire independent of any excitatory input and may be an attempt by the nervous system to decrease descending drive to the motor neuron pool and minimize constant synaptic input (Gorassini et al. 1998). The physiological mechanism of

plateau potentials may be the reduction of K^+ conductance and/or by increasing inward Ca^{2+} currents to the neuronal cell body (Schwindt and Crill 1980).

References for the Review of Literature

Allen G.M., D.K. McKenzie, S.C. Gandevia and S. Bass. Reduced voluntary drive to breathe in asthmatic subjects. *Respir. Physiol.* (1):29-40, 1993.

Alway S.E., J.D. MacDougal and D.G. Sale. Contractile adaptations in the human triceps surae after isometric exercise. *Journal of Applied Physiology* 66 (6) : 2725-2732, 1989.

Andrew P.D. Motor unit activity under low tensions as muscle changes length. *Am. J. Phys. Med.* 64(5):235-254, 1985.

Ashley C.C. and E.B. Ridgway. On the relationships between membrane potential, calcium transient and tension in single barnacle muscle fibres. *J. Physiol. (Lond).* 209(1):105-30, 1970.

Belanger A.Y. and A.J. McComas. Extent of motor unit activation during effort. *J. Appl. Physiol.* 51: 1131-1135, 1981.

Belanger A.Y. and A.J. McComas. A comparison of contractile properties in human arm and leg muscles. *Eur. J. Appl. Physiol.* 54(3):326-30, 1985.

Bellemare F., J.J. Woods, R. Johansson and B. Bigland-Ritchie. Motor-unit discharge rates in maximal voluntary contractions of three human muscles. *J. Neurophysiol.* 50(6): 1380-92, 1983.

Bianconi R., and J.P. van der Meulen. The response to vibration of the end organs of mammalian muscle spindles. *J. Neurophysiol.* 26:177-190, 1963.

Bigland-Ritchie B., F.H. Furbush, S.C. Gandevia and C.K. Thomas. Voluntary discharge frequencies of human motoneurons at different muscle lengths. *Muscle Nerve* 15(2):130-7, 1992.

Bigland-Ritchie B., N.J. Dawson, R.S. Johansson and O.C.J. Lippold. Reflex origin for the slowing of motoneurone firing rates in fatigue of human voluntary contractions. *J. Physiol.* 379: 451-459, 1986.

Bigland-Ritchie B., R. Johansson, O.C.J. Lippold, S.Smith and J.J. Woods. Changes in motoneurone firing rates during sustained maximal voluntary contractions. *J. Physiol.* 340: 335-346, 1983.

Bongiovanni L.G. and K.E. Hagbarth. Tonic vibration reflexes elicited during fatigue from maximal voluntary contractions in man. *J. Physiol. (Lond.)*. 423:1-14, 1990.

Bongiovanni L.G., K.E. Hagbarth and L. Stjernberg. Prolonged muscle vibration reducing motor output in maximal voluntary contractions in man. *J. Physiol. (Lond.)* 423:15-26, 1990.

Burke R.E., P. Rudomin and F.E. Zajac. Catch property in single mammalian motor units. *Science* 168(927): 122-4, 1970.

Burke D., K.E. Hagbarth, L. Lofstedt and B.G. Wallin. The responses of human muscle spindle endings to vibration during isometric contractions. *J. Physiol.* 261: 695-711, 1976.

Clamann H.P. Activity of single motor units during isometric tension. *Neurology* 20(3): 254-260, 1970.

Clarke H.H., E.C. Elkins, G.M. Martin and K.G. Wakim Relationship between body position and the application of muscle power to movements of the joints. *Arch. Phys. Med.* 31: 81-89, 1950.

Crone C., H. Hultborn, O. Kiehn, L. Mazieres and H. Wigstrom. Maintained changes in motoneuronal excitability by short-lasting synaptic inputs in the decerebrate cat. *J. Physiol. (Lond.)* 405:321-43, 1988.

De Luca C.J., R.S. LeFever, M.P. McCue and A.P. Xenakis. Control scheme governing concurrently active human motor units during voluntary contractions. *J. Physiol. (Lond.)* 329: 129-42, 1982.

De Luca C.J., R.S. LeFever, M.P. McCue and A.P. Xenakis. Behaviour of human motor units in different muscles during linearly varying contractions. *J. Physiol. (Lond.)* 329: 113-28, 1982.

Doherty T.J., A.A. Vandervoort, A.W. Taylor and W.F. Brown. Effects of motor unit losses on strength in older men and women. *J. Appl. Physiol.* 74(2):868-74, 1993.

Duchateau J. and K. Hainaut. Effects of immobilization on contractile properties, recruitment and firing rates of human motor units. *J. Physiol.* 422: 555-65, 1990.

Eccles J.C. The ionic mechanisms of excitatory and inhibitory synaptic action. *Ann. N. Y. Acad. Sci.* 137(2):473-94,1966.

Eken T. and O. Kiehn. Bistable firing properties of soleus motor units in unrestrained rats. *Acta. Physiol. Scand.* 136(3): 383-94, 1989.

Eklund G. and K.E. Hagbarth. Normal variability of tonic vibration reflexes in man. *Exp. Neurol.* (1):80-92, 1966.

Erim Z., C.J. De Luca, K. Mineo and T. Aoki. Rank-ordered regulation of motor units. *Muscle Nerve* 19(5): 563-73, 1996.

Fukunaga T., I. Yoshiho, I. Masamitsu, Y. Kawakami and S. Fukashiro. Determination of fascicle length and pennation in a contracting human muscle in vivo. *J. Appl. Physiol.* 82 (1): 354-358, 1997.

Gandevia S.C. and D.K. McKenzie Activation of human muscles at short muscle lengths during maximal static efforts. *J.Physiol.* 407: 599-613, 1988.

Gandevia S.C., G. Macefield, D. Burke and D.K. McKenzie. Voluntary activation of human motor axons in the absence of muscle afferent feedback. The control of the deafferented hand. *Brain* 113 (Pt 5):1563-81, 1990.

Garnett R. and J.A. Stephens. Changes in the recruitment threshold of motor units produced by cutaneous stimulation in man. *J. Physiol. (Lond.)* 311:463-73, 1981.

Gorassini M.A., D.J. Bennett and J.F. Yang. Self-sustained firing of human motor units. *Neurosci. Lett.* 247(1):13-6, 1998.

Gordon A.M., A.F. Huxley and F.J. Julian. The variation in isometric tension with sarcomere length in vertebrate muscle fibres. *J. Physiol. (Lond.)* 184(1): 170-92, 1966.

Gorman P.H. and J.T. Mortimer. The effect of stimulus parameters on the recruitment characteristics of direct nerve stimulation. *IEEE Trans Biomed Eng.* 30(7): 407-14, 1983.

Grimby L. and J. Hannerz. Differences in recruitment order and discharge pattern of motor units in the early and late flexion reflex components in man. *Acta Physiol. Scand.* 90(3):555-64, 1974.

Grimby L. and J. Hannerz. Recruitment order of motor units on voluntary contraction: changes induced by proprioceptive afferent activity. *J. Neurol. Neurosurg. Psychiatry* 31(6):565-73, 1968.

Haffajee D., U. Moritz and G. Svantesson. Isometric knee extension strength as a function of joint angle, muscle length and motor unit activity. *Acta Orthop. Scand.* 43(2):138-47. 1972.

Hartline D.K., D.F. Russell, J.A. Raper and K. Graubard. Special cellular and synaptic mechanisms in motor pattern generation. *Comp. Biochem. Physiol. C.* 91(1):115-31, 1988.

Hatze H. and J.D. Buys. Energy-optimal controls in the mammalian neuromuscular system. *Biol. Cybern.* 27(1): 9-20, 1977.

Henneman E., G. Somjen and D.O. Carpenter. Functional significance of cell size in spinal motoneurons. *J Neurophysiol* 28: 560-580, 1965.

Henneman E., H.P. Clamann, J.D. Gillies and R.D. Skinner. Rank order of motoneurons within a pool: law of combination. *J. Neurophysiol.* 37(6): 1338-49, 1974.

Henriksson-Larsen K., M.L. Wretling, R. Lorentzon and L. Oberg. Do muscle fibre size and fibre angulation correlate in pennated human muscles? *Eur. J. Appl. Physiol.* 64: 68-72, 1992.

Herbert R.D. and S.C. Gandevia. Changes in pennation with joint angle and muscle torque: in vivo measurements in human brachialis muscle. *J. Physiol.* 484: 523-532, 1995.

Herzog W. and L.J. Read. Lines of action and moment arms of the major force-carrying structures crossing the human knee joint. *Journal of Anatomy* 182: 213-230, 1993.

Hounsgaard J., H. Hultborn, B. Jespersen and O. Kiehn. Bistability of alpha-motoneurones in the decerebrate cat and in the acute spinal cat after intravenous 5-hydroxytryptophan. *J. Physiol. (Lond.)* 405:345-67, 1988.

Huxley A.F. and R. Niedergerke. Structural changes in muscle during contraction. Interference microscopy of living muscle fibers. *J. Physiol.* 144, 426-441, 1954.

Huxley A.F. and R.M. Simmons. Mechanical properties of the cross-bridges of frog striated muscle. *J. Physiol. (Lond.)* 218(1): 59-60, 1971.

Kaczmarek L.K. Phorbol esters, protein phosphorylation and the regulation of neuronal ion channels. *J. Exp. Biol.* 124: 375-92, 1986.

Kamen G., S.V. Sison, C.C. Du and C. Patten. Motor unit discharge behavior in older adults during maximal-effort contractions. *J. Appl. Physiol.* 79(6): 1908-13, 1995.

Kato M., S. Murakami and K.Yasuda. Behavior of single motor units of human tibialis anterior muscle during voluntary shortening contraction under constant load torque. *Exp. Neurol.* 90(1): 238-253, 1985.

Kent-Braun J.A. and A.V. Ng. Specific strength and voluntary muscle activation in young and elderly women and men. *J. Appl. Physiol.*87(1):22-9, 1999.

Knaflitz M., R. Merletti and C.J. De Luca. Inference of motor unit recruitment order in voluntary and electrically elicited contractions. *J. Appl. Physiol.* 68(4): 1657-67, 1990.

Kniffki K.D., S. Mense and R.F. Schmidt. Responses of group IV afferent units from skeletal muscle to stretch, contraction, and chemical stimulation. *Exp. Brain Res.* 31: 511-522, 1978.

Kukulka C.G. and H.P. Clamann. Comparison of the recruitment and discharge properties of motor units in human brachial biceps and adductor pollicis during isometric contractions. *Brain Res.* 219(1): 45-55, 1981.

Kumazawa T. and K. Mizumura. Thin-fibre receptors responding to mechanical, chemical and thermal stimulation in the skeletal muscle of the dog. *J. Physiol.* 273: 179-194, 1977.

Lexell J. and D.Y. Downham. The occurrence of fibre-type grouping in healthy human muscle: a quantitative study of cross-sections of whole vastus lateralis from men between 15 and 83 years. *Acta Neuropathol. (Berl.)* 81(4):377-81, 1991.

Llinas R.R. The intrinsic electrophysiological properties of mammalian neurons: insights into central nervous system function. *Science* 242(4886):1654-64, 1988.

Lowey S., G.S. Waller and K.M. Trybus. Skeletal muscle myosin light chains are essential for physiological speeds of shortening. *Nature* 365(6445):454-6, 1993.

Macefield V.G., S.C. Gandevia, B. Bigland-Ritchie, R.B. Gorman and D. Burke. The firing rates of human motoneurones voluntarily activated in the absence of muscle afferent feedback. *J. Physiol. (Lond.)* 471:429-43, 1993.

Marsh E., D. Sale, A.J. McComas and J. Quinlan. Influence of joint position on ankle dorsiflexion in humans. *J. Appl. Physiol.* 51 (1): 160-167, 1981.

Merton P.A. Voluntary strength and fatigue. *J. Physiol.* 123: 553-564, 1954.

Milner-Brown H.S., R.B. Stein and R.Yemm. Changes in firing rate of human motor units during linearly changing voluntary contractions. *J. Physiol. (Lond.)* 230(2): 371-390, 1973.

Milner-Brown H.S., R.B. Stein and R. Yemm. The orderly recruitment of human motor units during voluntary isometric contractions. *J. Physiol. (Lond.)* 230(2): 359-370, 1973.

Monster A.W. and H. Chan. Isometric force production by motor units of extensor digitorum communis muscle in man. *J. Neurophysiol.* 40(6): 1432-43, 1977.

Moore R.L. and J.T. Stull. Myosin light chain phosphorylation in fast and slow skeletal muscles in situ. *Am. J. Physiol.* 247(5 Pt 1):C462-71, 1984.

Mori S. Discharge patterns of soleus motor units with associated changes in force exerted by foot during quiet stance in man. *J. Neurophysiol.* 36(3):458-71,1973.

Muhl Z.F. Active length-tension relation and the effect of muscle pennation on fibre lengthening. *Journal of Morphology* 173: 285-292, 1982.

Narici M.V., H. Hoppeler, B. Kayser, L. Landon, H. Claassen, C. Gavardi, M. Conti and P. Cerretelli. Human quadriceps cross-sectional area, torque and neural activation during six months strength training. *Acta Physiol. Scand.* 157: 175-186, 1996.

Nosek T.M., P.D. Clein and R.E. Godt. Inositol trisphosphate has no direct effect on the contractile apparatus of skinned cardiac muscles. *Pflugers Arch.* 417(4):370-4, 1990.

Person R.S. and L.P. Kudina. Discharge frequency and discharge pattern of human motor units during voluntary contraction of muscle. *Electroencephalog. Clin. Neurophysiol.* 32(5):. 471-483, 1972.

Rack P.M. and D.R. Westbury. The effects of length and stimulus rate on tension in the isometric cat soleus muscle. *J. Physiol. (Lond.)* 204(2): 443-460, 1969.

Rayment I., H.M. Holden, M. Whittaker, C.B. Yohn, M. Lorenz, K.C. Holmes and R.A. Milligan. Structure of the actin-myosin complex and its implications for muscle contraction. *Science* 261(5117): 58-65, 1993.

Rich and Cafarelli. Motor unit firing rates following training. *Med. Sci. Sports. Exer.* In Press.

Rios E. and G. Pizarro. Voltage sensor of excitation-contraction coupling in skeletal muscle. *Physiol. Rev.* 71(3):849-908, 1991.

Romaiguere P., J.P. Vedel and S. Pagni. Effects of tonic vibration reflex on motor unit recruitment in human wrist extensor muscles. *Brain Res.* 602(1):32-40, 1993.

Rothmuller C. and Cafarelli E. Effect of vibration on antagonist muscle coactivation during progressive fatigue in humans. *J. Physiol. (Lond.)* 485:857-64, 1995.

Rutherford O.M. and D.A. Jones. Measurement of fibre pennation using ultrasound in the human quadriceps in vivo. *Eur. J. Appl. Physiol.* 65: 433-437,1992.

Schwindt P.C. and W.E. Crill. Properties of persistent inward current in normal and TEA-injected motoneurons. *J. Neurophysiol.* 43(6): 1700-24, 1980.

Stein R.B. and F. Parmiggianni. Optimal motor patterns for activating mammalian muscle. *Brain Res.* 175(2): 372-376, 1979.

Tax A.A., J.J. Denier van der Gon, C.C. Gielen and M. Kleyne. Differences in central control of m. biceps brachii in movement tasks and force tasks. *Exp. Brain Res.* 79(1): 138-142, 1990.

Vallbo A.B. Discharge patterns in human muscle spindle afferents during isometric voluntary contractions. *Acta Physiol. Scand.* 80(4):552-66, 1970.

Vallbo A.B. Human muscle spindle discharge during isometric voluntary contractions. Amplitude relations between spindle frequency and torque. *Acta Physiol. Scand.* 90(2):319-36, 1974.

Van Cutsem M, J Duchateau and K. Hainaut. Changes in single motor unit behaviour contribute to the increase in contraction speed after dynamic training in humans. *J. Physiol. (Lond.)* 513(1): 295-305, 1998.

Vander Linden D.W., C.G. Kukulka and G.L. Soderberg. The effect of muscle length on motor unit discharge characteristics in human tibialis anterior muscle. *Exp. Brain. Res.* 84(1):210-8, 1991.

Vibert P. and C. Cohen. Domains, motions and regulation in the myosin head. *J. Muscle Res. Cell. Motil.* 9(4): 296-305, 1988.

Visser J.J., J.E. Hoogkamer, M.F. Bobbert and P.A. Huijing. Length and moment arm of human leg muscles as a function of knee and hip-joint angles. *Eur. J. Appl. Physiol.* 61: 453-460, 1990.

Wagenknecht T., R. Grassucci, J. Frank, A. Saito, M. Inui and S. Fleischer. Three-dimensional architecture of the calcium channel/foot structure of sarcoplasmic reticulum. *Nature* 338(6211):167-70, 1989.

Wottiez R.D., P.A. Huijing, H.B.K. Boom and R.H. Rozendal. A three-dimensional muscle model: a quantified relation between form and function of skeletal muscles. *Journal of Morphology* 182: 95-113, 1984.

Yamaguchi G.T. and F.E. Zajac. A planar model of the knee joint to characterize the knee extensor mechanism. *J. Biomechanics*, Vol.22, No.1, 1-10, 1989.

Zajac F.E. and J.L. Young. Properties of stimulus trains producing maximum tension-time area per pulse from single motor units in medial gastrocnemius muscle of the cat. *J. Neurophysiol.* 43(5):1206-20, 1980.

Zierler K.L. Mechanism of muscle contraction and its energetics. In: *Medical Physiology*, edited by V.B. Mountcastle. St.Louis, MO: Mosby, 1974, vol.1, p. 77-120.

Chapter III- Manuscript

An acute alteration in vastus lateralis muscle length causes a change in motor unit discharge rate that is not mediated by muscle spindle activation.

Peter Adhihetty and E.Cafarelli

Kinesiology and Health Science
Faculty of Pure and Applied Science
York University
Toronto, ON

Correspondence for: E. Cafarelli, PhD
346 Bethune College
York University
4700 Keele Street
Toronto, ON
M3J 1P3
(416) 736-5727 (Off)
(416) 736-5892 (Fax)
ecaf@yorku.ca

To assess how changes in muscle contractile properties influence motor unit firing rates, we changed the length of quadriceps femoris by locking the knee joint at different angles prior to making isometric contractions (n=10). We also perturbed muscle spindles with high speed vibration (265 Hz) of the patellar tendon. When the muscle was shortened compared to its length at 90 degrees, twitch amplitude and ±dF/dt increased more than four-fold and MVC was 60% greater (all $p<0.001$). Average motor unit firing rates, obtained with tungsten microelectrodes from more than 400 single unit recordings were nearly 60% greater ($p<.05$) at any absolute submaximal force when the muscle was longest (e.g. decreased MVC and ±dF/dt). Lengthened vastus lateralis EMG was significantly higher than the short length during 50% MVC ($p<.05$) implying greater descending drive. Increases in lengthened vastus lateralis EMG may be compensatory for muscle deviating largely from optimal length with less force producing capacity and thus requiring increased activation. Biceps femoris EMG was also increased ($p.<.05$) while vastus lateralis was longest suggesting that the increased vastus lateralis EMG may be partially attributable to increased antagonistic activity. In contrast, average motor unit firing rates were lower ($p<.01$) than control when the tendon was vibrated during a 30% MVC contraction. Our data suggest that alterations in rate coding that occur at different muscle lengths are not mediated by muscle spindle activity.

KEY WORDS: average motor unit firing rate, MVC, ±dF/dt, antagonistic activity, optimal length, rate coding, descending drive, EMG

Introduction

A brief, supramaximal electrical stimulus administered via percutaneous or direct nerve stimulation evokes a synchronous depolarization of all motor units and results in a twitch. By applying electrical impulses in trains at the appropriate frequencies, twitches will summate and reach tetanic fusion. Stimulation rates needed to attain tetanic fusion are dependent on the duration and contractile rate of the twitch response. Altering muscle length changes the contractile rate by manipulating the degree of actin and myosin overlap. Rack and Westbury (32) were the first to demonstrate that a higher stimulation rate was necessary to induce complete tetanic fusion in shortened muscle with fast contractile properties. This has been replicated in human tibialis anterior and abductor digiti minimi muscles (17, 27).

Based on these stimulation studies, it may be hypothesized that voluntary contractions would also require higher motor unit firing rates to tetanically fuse shortened muscle. Contractile properties change not only with muscle length but can also be altered by chronic external conditions such as immobilization (13) and training (2) or acute conditions such as fatigue (7). Motor unit firing rates adjust to accommodate changes in contractile rate occurring with immobilization, fatigue and training (13, 7, 35). This suggests motor unit discharge rates may also adapt to accommodate acute changes in contractile properties occurring with alterations in muscle length, thus providing a unique model to monitor adaptive responses of the neuromuscular system.

Only two reports in the literature consider the relationship between changes in muscle length and motor unit firing rate during voluntary contractions. Vander Linden et al. (36) found that motor unit firing rates increased when the length of tibialis anterior was shortened

but these authors did not measure the contractile rate of the muscle. In contrast, Bigland-Ritchie et al. (5) found no change in the motor unit firing rates at different lengths of tibialis anterior despite significant changes in the contractile properties.

The present study employed vastus lateralis and manipulated the knee joint resulting in slightly larger overall changes in muscle length compared to previous studies (16). We monitored changes in contractile properties associated with long and short muscle while measuring the corresponding average motor unit discharge rate during submaximal and maximal contractions. We also attempted to determine the origin of any adaptive response of the motor unit firing rate to changes in muscle length by observing the effect of high speed vibration. Vibration of a muscle tendon principally activates muscle spindle primary endings (4, 10). Neural compensations for changes in contractile properties may be mediated by excitatory input of spindles to the alpha motor neuron pool via Ia afferent feedback which alters muscle output (8, 18, 33). Vibration of the patellar tendon was introduced to determine the potential role of muscle spindles and any neuromuscular adaptations occurring with changes in muscle length.

Methods

Subjects

We used ten paid volunteers (4 males and 6 females) aged 24.1 ± 1.7 yrs (mean ● SD), who were regularly active, free of injury to the right knee and not currently engaged in any strength training. An explanation of all procedures of the experiment was given prior to signing the informed consent document and the experiment was approved by the York University Human Participants Review Committee.

Force Measurement

Isometric force generated by the right knee extensors was measured in a modified version of the dynamometer described by Psek and Cafarelli (31)(Appendix D). The modification is a sliding rod attached to the force transducer enabling the knee joint to be opened from 60 to 100 degrees of flexion while maintaining a right angle with the force transducer. A seatbelt secured subjects in the dynamometer and prevented hip extension. A padded cast aluminum cuff was clamped around the ankle 2 cm above the lateral malleolus, and was attached to a strain gauge to measure the isometric force of knee extension.

Electrical Stimulation

Supramaximal stimuli were applied to the femoral nerve through an anodal stimulating electrode (12.5x7cm) placed in the inguinal crease and a cathodal electrode (12.5 x 7cm) located midway between the superior aspect of the greater trochanter and inferior border of the iliac crest. The stimulator (Digitimer, Model DS7A, Hertfordshire, England) delivered a 200 μs square wave pulse of constant voltage (270V) and the current was adjusted to

increase the intensity. Maximal twitch response was attained by increasing the stimulus intensity by approximately 20mA increments until the evoked twitch response no longer increased. The stimulus was then increased by an additional 10% to ensure depolarization of all the motor axons in the femoral nerve.

Surface Electromyography

Bipolar silver-silver chloride recording electrodes (EQ Inc, Plymouth Meeting,PA) with an interelectrode distance of 2 cm, were placed over two heads of quadriceps femoris and fastened to the skin with a double-sided adhesive strip. A water soaked ground electrode was wrapped around the upper thigh. The skin under the recording electrodes had been shaved, cleaned with a 70% alcohol solution, and rubbed gently with an abrasive pad to decrease impedance. Electrode placement for each muscle was determined by palpation during a low level contraction. The vastus lateralis electrode was placed approximately 10cm proximal to the superior border of the patella over the lateral segment of the thigh. For vastus medialis it was placed approximately 5cm proximal to the superior border of the patella on the medial segment of the thigh and the biceps femoris electrode was placed midway between the ischial tuberosity and the popliteal fossa to measure antagonistic muscle activity.

Intramuscular Electromyography

Single motor unit action potentials were recorded with tungsten microelectrodes (Howarth Instruments, Cornwall, UK). The microelectrode was insulated down to the bared tip recording surface of approximately 10 micrometres. All needles were sterilized by

autoclaving at 200°C for 20 min prior to any experimental procedures. A sterile 25 gauge hypodermic needle was used to puncture the skin and fascia to permit smooth insertion without damaging the recording tip. The microelectrodes were inserted into the mid-belly of vastus lateralis and during a contraction were advanced at a very slow rate (approximately .5mm/sec) to obtain recordings from as many motor units as possible. A reference electrode was inserted into the subcutaneous fat approximately 1-2 cm proximal to the patella.

Maximal Voluntary Contractions

Subjects were instructed and then verbally encouraged to produce the most powerful and quickest voluntary contractions with the right knee extensors. The degree of voluntary activation to the muscle was assessed using the twitch interpolation technique and expressed as a percentage of the complete activation of the motor neuron pool (1). A supramaximal shock was administered to the femoral nerve during a maximal voluntary effort and if no additional force was evoked, all motor units were assumed recruited. Activation was assessed by calculating the ratio of the superimposed evoked force to the force of a maximally evoked and potentiated twitch [1-(superimposed twitch/potentiated twitch)] x 100.

Vibration

The vibrator was a modified engraving tool (Dremel Moto-Flex, Model 332-01. Racine, Wisconsin) and the head portion was secured over the patellar tendon with straps. A series of tendon taps were used to locate the optimal placement for the vibrator. A rubber platform was secured by a tensor bandage directly under the distal end of the patellar tendon

to provide support and two sorbathane pads were placed behind the knee to prevent transfer of vibration to the antagonist hamstring muscle group. A tensor bandage was applied in a figure-eight pattern around the vibrator and then secured with two non-extensible velcro straps applied tightly in a crossing pattern around the knee joint.

Signal Acquisition and Processing

Force

The force signal was digitized at 1000Hz and smoothed by taking an average of every 25 points using the Spike II for Windows program (version 2.24, Cambridge Electronic Design). All force values were converted from volts to Newtons using a regression equation determined from a volts-weight relationship obtained with known weights. The dynamometer was calibrated before and after the experiment.

Contractile Properties

The evoked twitch was characterized by the peak twitch amplitude (TW_{amp}), time to peak tension (TPT), ½ relaxation time (1/2RT) and the ± dF/dt. The TPT and ½ RT are frequently used to assess contractile properties (5,34) but we have found them to be less accurate measures than the ± dF/dt for variable twitch amplitudes (Figure 1). Figure 1 shows two twitches from the same muscle and same subject at the two different resting lengths. Although the two twitches have different amplitudes, TPTand ½ RT are the same. The obvious difference in the contraction and relaxation rates is only reflected by the derivation of the force profile.

Surface Electromyography

The surface EMG signal was pre-amplified at the electrode and passed through a variable gain, second-stage amplifier (York University, frequency response; flat from 5-1000 Hz) before being stored on tape for later analysis (VCR model 500D, PCM model 4000 A, Vetter, Rebersberg, Pennsylvania). The signal was A/D converted at 5000Hz and quantified by calculating the root mean square of a 500 msec sample preceding the interpolated twitch.

Intramuscular Electromyography

The intramuscular signal was pre-amplified at the recording site then passed through a variable gain second stage amplifier and bandpass filtered between 1 kHz and 50 kHz and then stored on FM cassette. The intramuscular signals were digitized from tape at 12,500 Hz. Action potentials were initially categorized by overall amplitude differences, using a window discriminator, followed by a process of spike template matching based on the shape of the spikes. Selected spikes were considered from the same motor unit if there were a minimum of four spikes with the same shape and the coefficient of variation of the interspike interval was below 20%. Only recordings meeting these criteria were considered suitable for calculating average motor unit firing rate (AMUFR).

Protocol

Prior to starting the experiment, we determined the angles of flexion producing the greatest differences in contractile rate of the muscle ($+dF/dt_{max}$ and $-dF/dt_{max}$). An angle torque curve using MVC and supramaximal twitches was constructed with all subjects

starting at 100 degrees of flexion and progressing to 60 degrees of flexion in 10 degree increments. Zero degrees of flexion was defined as the leg being fully extended. This range of flexion angles has been shown to significantly change muscle length (16) and consequently contractile properties. Three maximal twitches were produced at each angle. The supramaximal stimulus was verified each time the angle of flexion was changed by further increasing the stimulus intensity to account for any shifting of the stimulating pads or electrode gel caused by manipulation of the leg. A minimum of two maximal voluntary contractions were performed at each angle of flexion and had to be within 10% of one another before proceeding to the next position. A supramaximal stimulus was administered at the peak of each MVC and was immediately followed by a supramaximal stimulus producing a potentiated twitch response to determine the degree of voluntary activation. Contractions were separated by at least 2 minutes of rest.

Motor Unit Firing Rates at Short And Long Muscle Lengths

The angles of flexion which produced the largest differences in contractile rate were referred to as either the SHORT or LONG muscle length and used for experimentation on a second day. Half the subjects started this portion of the experiment in the SHORT and half in the LONG position to counterbalance the study and control for order effects. Subjects were asked to produce one maximal contraction which had to be within 10 % of the MVC performed on the first day for the protocol to continue with three maximal twitches. The intramuscular and reference electrode were inserted after the initial MVC and three twitches. Each subject produced five alternating 50% contractions and MVC contractions with the

intramuscular needle inserted to obtain individual motor unit recordings. Target forces of 50% and 100% MVC were displayed with horizontal cursors on a computer monitor placed in front of the subjects so they could match the required force. The 50 % contractions were held constant for 15-20 seconds and the 100% contractions for 5-10 seconds while the intramuscular needle was slowly advanced. A minimum of 2 minutes rest occurred between every contraction.

Motor Unit Firing Rates during Vibration

This part of the experiment was performed with the knee flexed to 90 degrees. Five 30% contractions with and without vibration were completed in random order and were separated by a minimum of 1 minute rest. The target force was indicated with a horizontal cursor on a computer monitor in front of the subject. During the vibrated contractions, the vibrator was turned on prior to the subjects voluntarily contracting to the 30% target in order to measure the amplitude of the evoked vibration response. Contractions were held constant for 15-25 seconds while the intramuscular needle was slowly advanced into the muscle belly.

The order of the muscle length manipulation protocol and vibration protocol were equally divided so that half of the subjects started with the muscle length manipulation and half with the vibration to counterbalance the study and control for order effects.

Statistical Analysis

The dependent variables (MVC, Tw amp, ½ relaxation, TPT, $+df/dt_{max}$, $-df/dt_{max}$, and M-wave amplitude) were analyzed using a one-way repeated measures ANOVA and post

hoc comparisons were made using the Tukey test. The dependent variable (AMUFR) was analyzed using a 2 x 2 ANOVA with muscle length (LONG and SHORT), and intensity (50 and 100%MVC) as the independent variables. The post-hoc comparisons were made using the Tukey test. The vibration results were analyzed using a one-way repeated measures ANOVA with the average motor unit firing rate as the dependent variable and vibration and control as the independent variables. All statistical analyses were performed using the STATISTICA program (Statistica for Windows, version 5.1, Statsoft, Tulsa, OK).

Results

Maximal Voluntary and Twitch Contractions

MVC amplitude increased as muscle length shortened. Figure 2A shows a plateau (±10 Newtons) in force between 60 and 80 degrees of flexion and much less force was produced at 90 and 100 degrees. The MVC values for the most extreme short and long muscle lengths were significantly different ($p<.05$). Data from the twitch interpolation technique indicated that voluntary activation did not change from shortest to longest muscle lengths (94.07% ±1.30 and 95.81% ±1.80, respectively). Twitch amplitude (Figure 2B) and $\pm dF/dt_{max}$ (Figure 2C + 2D) increased progressively as the muscle was shortened. Only the data obtained where the muscle was at its slowest and fastest were used for analysis. For the sake of brevity, increases and decreases are expressed as a change from long to short muscle lengths. Twitch amplitude increased 4.5 fold and the $+dF/dt_{max}$ and $-dF/dt_{max}$ increased 4.4 fold and 4.6 fold, (all $p<.001$ respectively). During maximal contractions, EMG of vastus lateralis was not different between SHORT and LONG muscle lengths (Figure 3) but the EMG was significantly higher for long muscle during relative 50% MVC ($p<.05$)(Table 1) Biceps femoris EMG was increased in long muscle at both 50% and 100% MVC relative force levels ($p<.05$). The time to peak tension, ½ relaxation time and M-wave amplitude did not change with muscle length (Table 1). Figure 4 shows mechanical and electrical characteristics at the two extreme muscle lengths for one subject and the pooled data for these variables are shown in Table 1.

Motor Unit Firing Rates

A total of 746 spike trains were recorded with an average of 19 trains per subject per

condition. Figure 5 shows a 1 sec intramuscular recording containing spike trains from 4 different motor units obtained during a brief 30% MVC contraction. This illustrates the spike identification, sorting and counting process. To the right of figure individual waveforms are overlayed on an expanded time-base.

None of the subjects in this sample were able to produce control MVC force at the longest length while the needle was inserted and maximal efforts averaged only 80% MVC. Consequently, AMUFR's obtained from contractions of 100% (short), 80% (long) and 50% MVC (both) are plotted against absolute force in Figure 6. This shows that at any absolute force level the AMUFR is approximately 60% higher in LONG muscle where the contractile properties are the slowest. Average motor unit firing rates were expected to be higher for shortened muscle with fast contractile rate, but the AMUFR in LONG, slower muscle was also significantly higher when comparing relative 50% force levels ($p < .05$, Table 1). This was opposite to our expectations. Despite a 20% decrease in relative force production in the LONG muscle during maximal efforts, the AMUFR was the same as in the short muscle.

Vibration

When vibration was applied to the patellar tendon at rest, the resulting evoked force averaged 6.16% ● 1.45 SE MVC. Recordings from this tonic vibration response (TVR) for one subject is shown in Figure 7. A total of 416 spike trains were recorded from 10 subjects during these submaximal contractions and each averaged 21 trains per condition. Surface EMG of biceps femoris and vastus lateralis were unaltered by vibration of the patellar tendon (Table 2). AMUFR of vastus lateralis during vibration was significantly lower than the control contractions (9.54 ± .54Hz vs.10.50 ● .66Hz, respectively $p<.05$) The results imply Ia

afferent input during constant level contractions exhibits an inhibitory effect at the level of the spinal cord causing a decrease in the AMUFR.

Table 1 : Summary of Electrical and Mechanical Properties of Vastus Lateralis at Long and Short Lengths

	Muscle Length	
Electrical Properties	**Long**	**Short**
EMG_{max} vastus lateralis (V)	0.180 ±.028	0.147 ±.028
$EMG_{50\% MVC}$ vastus lateralis (V)	0.076 ±.016	0.034 ±.005*
EMG_{max} biceps femoris (V)	0.121 ±.022	0.091 ±.012*
$EMG_{50\% MVC}$ biceps femoris (V)	0.066 ±.008	0.035 ±.003*
M-wave amplitude (V)	3.67 ±.59	3.54 ±.55
Percent Activation (%)	95.81 ±1.80	94.07 ±1.30
MVC AMUFR (Hz)	16.37 ±.82	15.58 ±1.40
50% AMUFR (Hz)	12.26 ±.57	10.15 ±.57*
Mechanical Properties	**Long**	**Short**
MVC (N)	423.05 ±45.61	694.55 ±88.52*
Twitch Amplitude (N)	58.25 ±6.69	258.18 ±30.01*
1/2 Relaxation Time (s)	0.085 ±.006	0.085 ±.004
Time to Peak Tension (s)	0.119 ±.005	0.120 ±.004
+dF/dt (N/s)	856.94 ±82.79	3597.39 ±465.25*
-dF/dt (N/s)	591.09 ± 44.02	2354.37 ±269.80*

* significant difference between short and long muscle ($p<.05$)

Table 2 : Summary of Electrical Properties of Vastus Lateralis at 30% MVC During Vibration and Control Contractions

Electrical Properties	Contraction Condition	
	Vibration	Control
EMG vastus lateralis (V)	0.045 ±.005	0.048 ±.007
EMG biceps femoris (V)	0.044 ±.004	0.042 ±.005
AMUFR (Hz)	9.54 ±.54	10.50 ±.65*

*significant difference between vibration and control ($p < .05$)

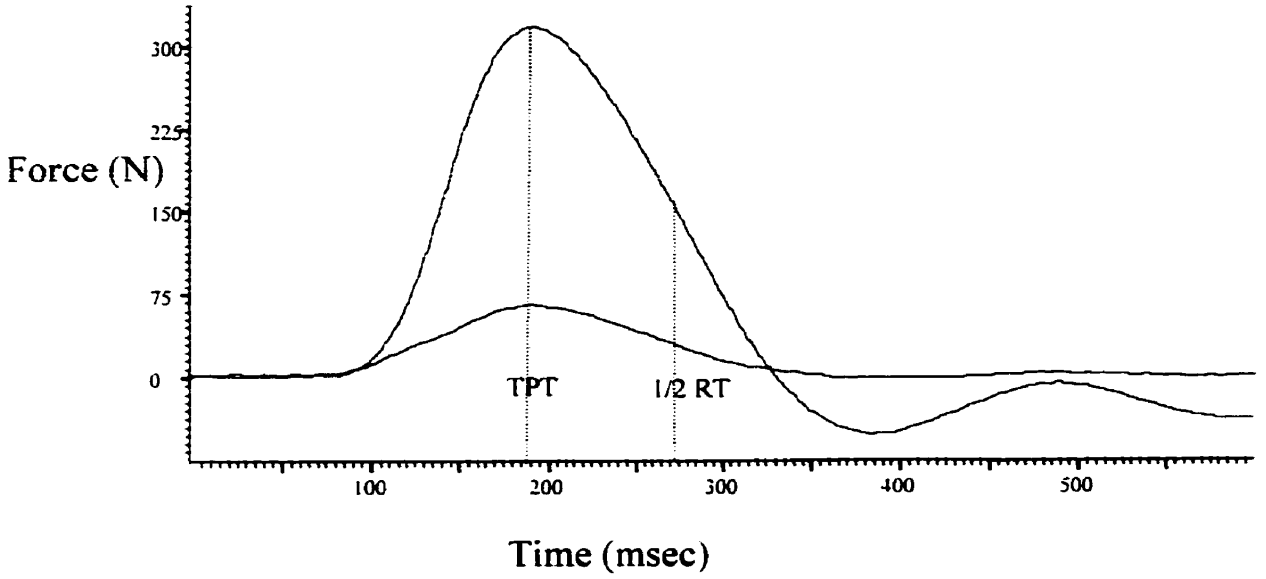


Figure 1: Knee extensor force tracing showing the time to peak tension and 1/2 relaxation time of a LONG and SHORT muscle twitch. This force tracing from one subject, shows the long (low amplitude) and short muscle (high amplitude) having the same TPT and 1/2 relaxation time indicating no change in the contractile rate. The maximal instantaneous slope of the twitches (±dF/dt) is more indicative of contractile rate when associated with variable twitch amplitudes.

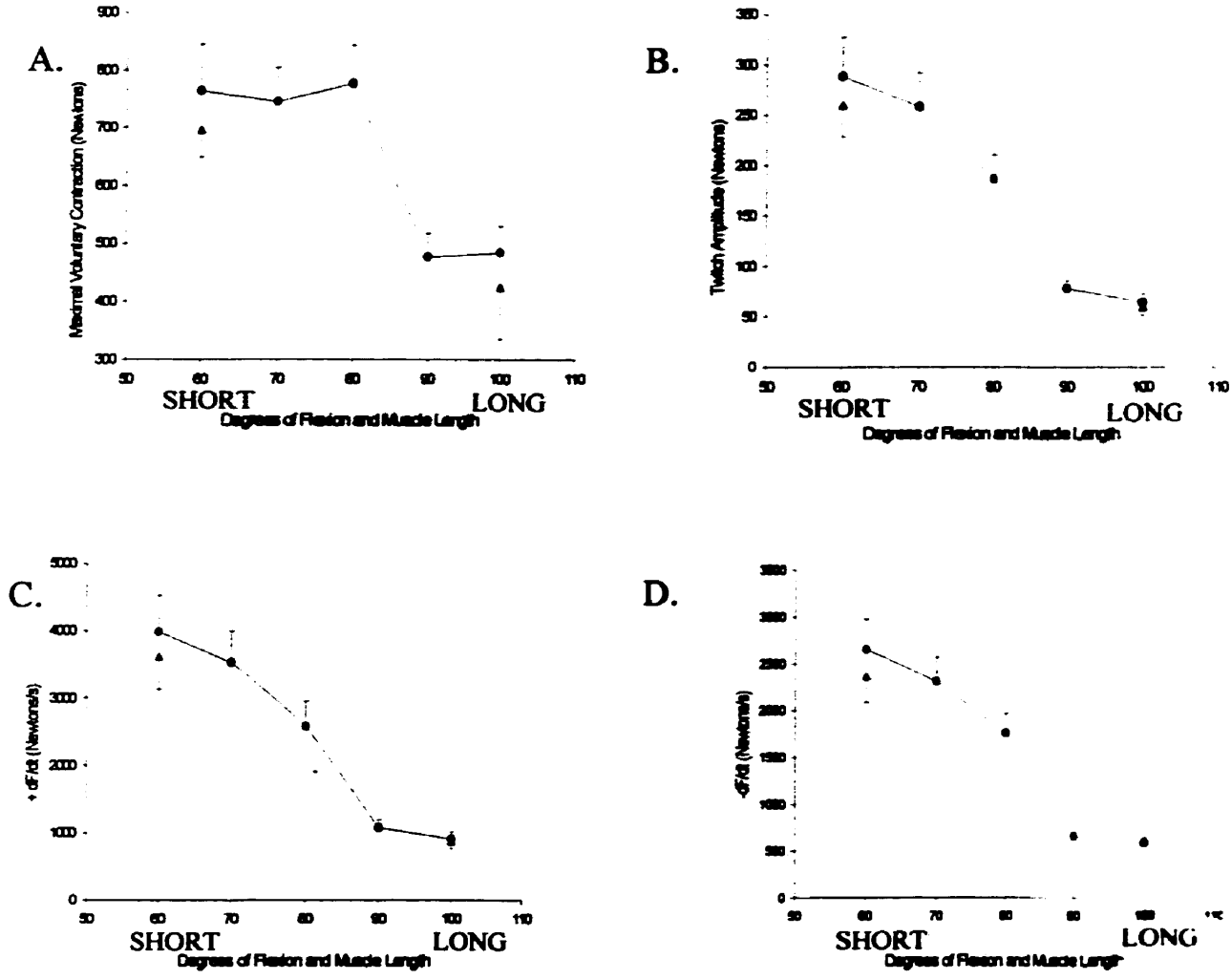


Figure 2: Contractile properties at different muscle lengths. The circles (●) represent the data from the full range of angles on the selection day and the triangles (▲) represent the data from the selected muscle lengths displaying the largest differences in contractile speed on a separate day. A. Maximal voluntary contractions increased from the LONG to SHORT muscle. B. Twitch amplitude shows the same progressive increase from 100 to 60 degrees of flexion and from LONG to SHORT muscle. C+D. There was a progressive increase in the +dF/dt as the angle of flexion was decreased from 100 to 60 degrees of flexion and the same increase occurred from LONG to SHORT muscle indicating an increase in the contractile rate.

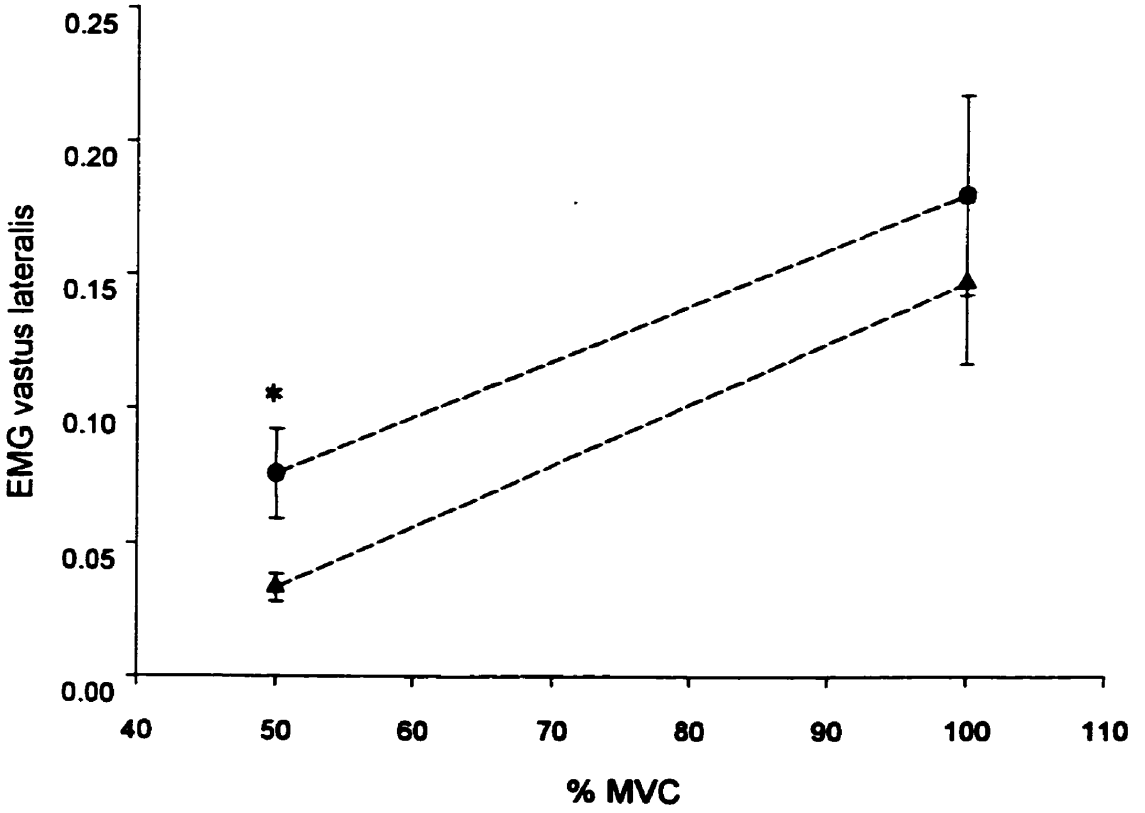


Figure 3: The RMS of vastus lateralis at short (▲) and long (●) muscle during 50 and 100% MVC. The electrical activity of vastus lateralis is not affected by length during maximal efforts but is significantly increased at long muscle at 50% MVC. Dotted lines are meant to indicate the well known linear relation between vastus lateralis EMG and relative force (Milner-Brown et al. 1973).

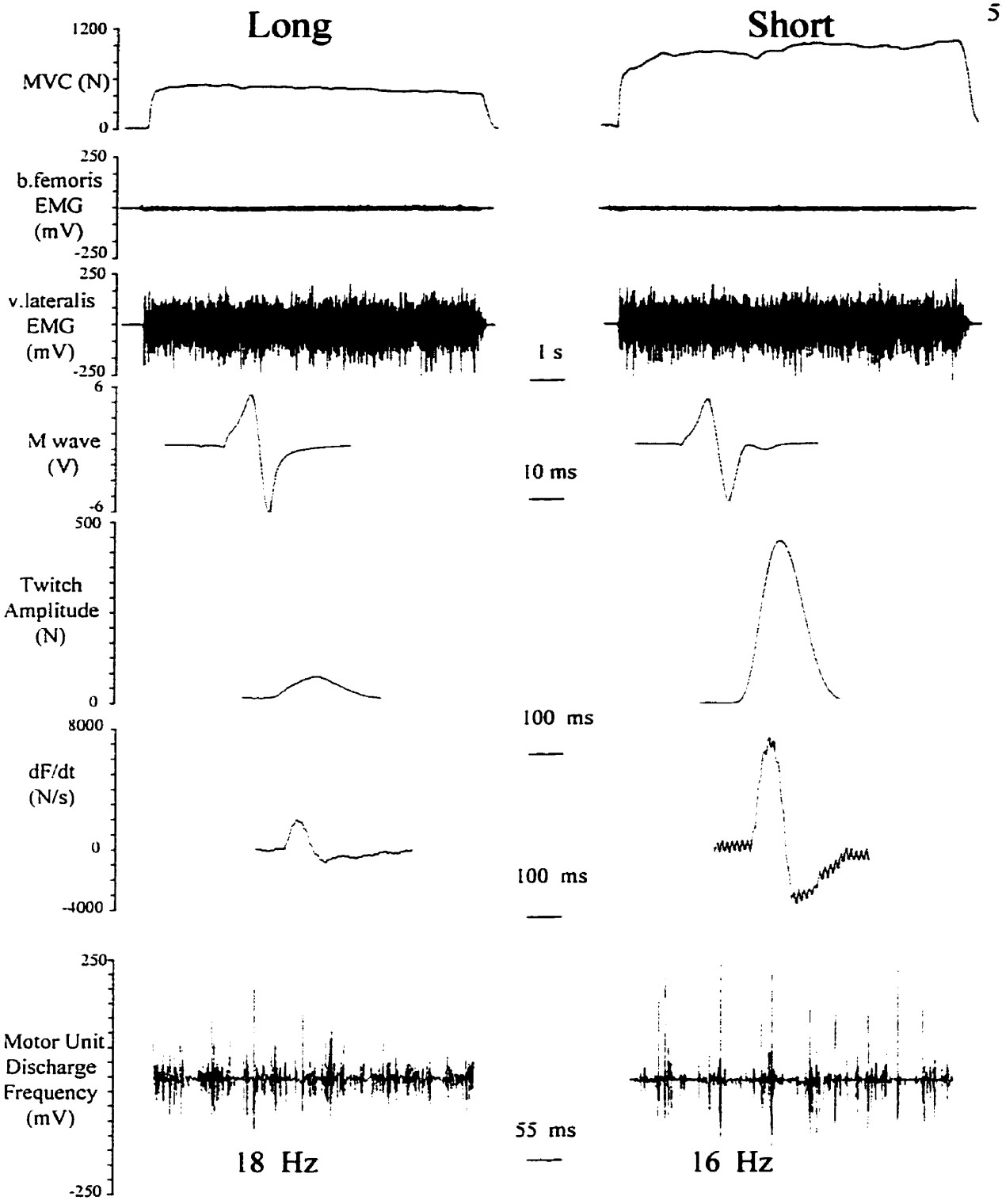


Figure 4: Mechanical and Electrical Characteristics at Short and Long Muscle Length. This figure illustrates the electrical activity and mechanical response associated with a maximal voluntary contraction and a supramaximal electrical stimulus. MVC, Tw Amp, and contractile rate all increased significantly in short muscle. Mass action potentials showed no difference with length. Vastus lateralis EMG showed no difference during maximal contractions. Biceps femoris EMG activity increased significantly for long muscle but is not discernable in this figure due to the scaling.

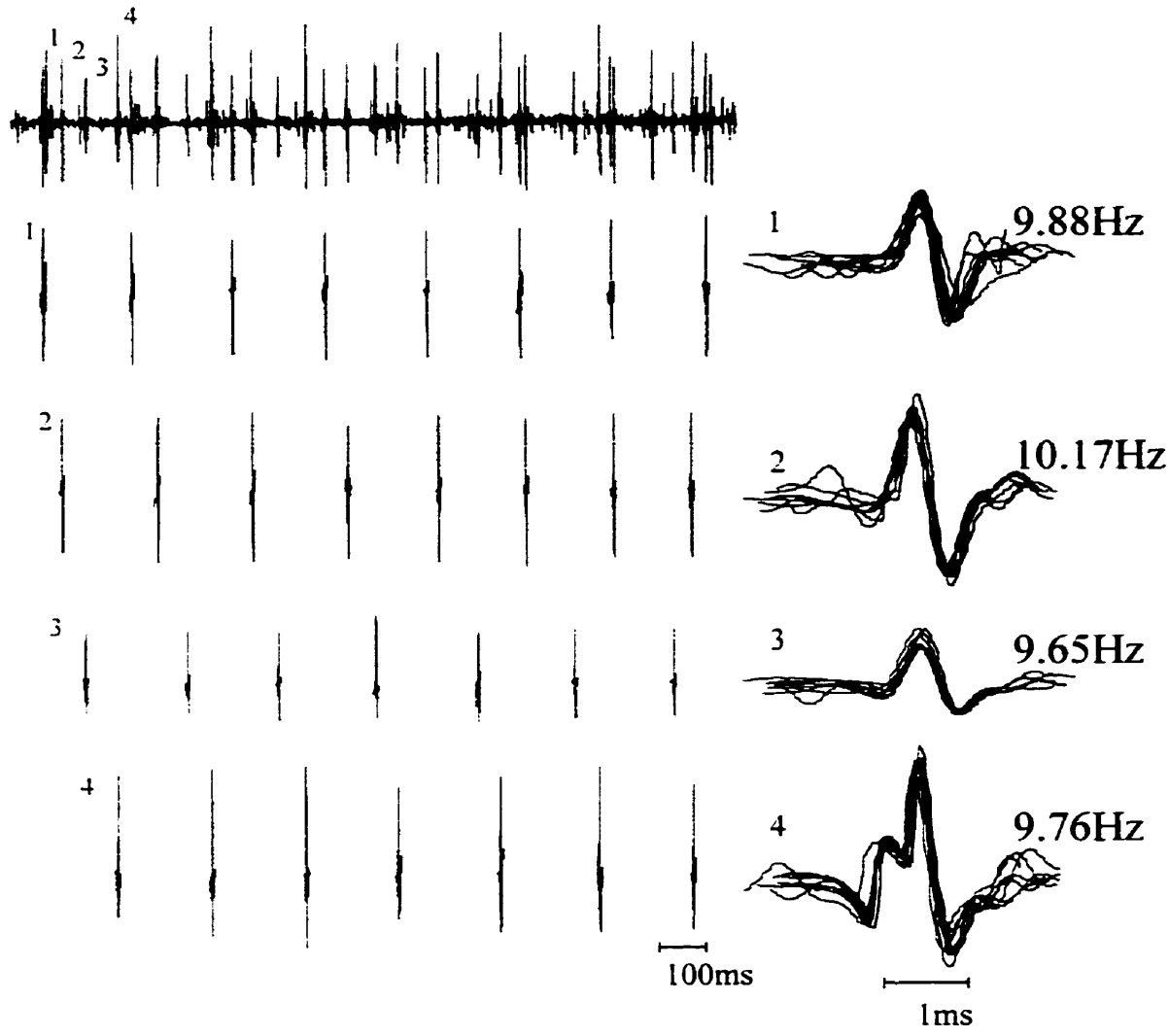


Figure 5: Individual Motor Units And Spike Sorting. An example of an intramuscular recording held at 30% MVC. Two horizontal cursors were positioned as a window around spikes with a desired minimal amplitude and then displayed on a new channel. At least, four separate motor unit action potentials are discernable in this record. In this case, action potentials maintained the same firing order as shown in the uppermost tracing for a 1 sec interval. Spikes having similar shape and amplitude were manually overlaid and only spikes with an interspike interval coefficient of variation under 20% were considered as being from the same motor unit.

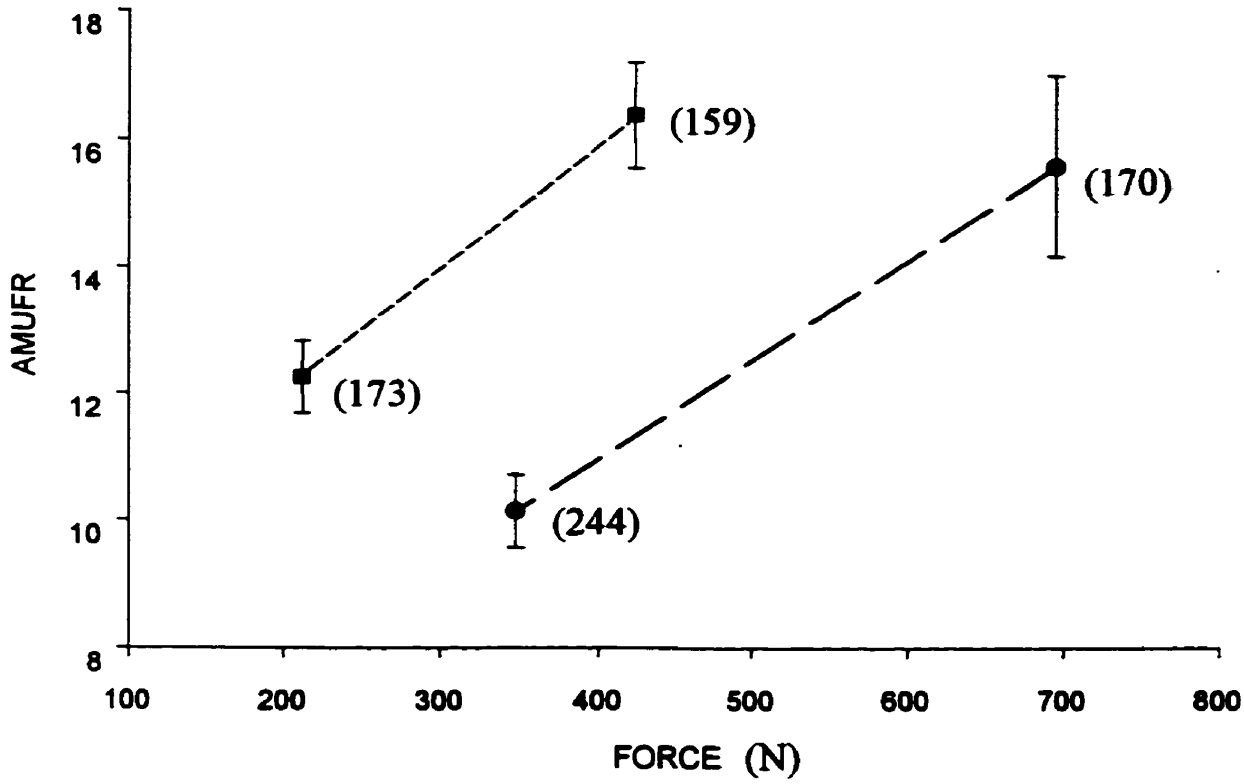


Figure 6: Absolute force and AMUFR at different muscle lengths. The average motor unit firing rate for any absolute force is approximately 60% higher in the long muscle (■-small dashed line) compared to the short (●-large dashed line). The number of spike trains contained in each data are shown in parenthesis. Dotted lines are meant to indicate the well known relation between motor unit firing rate and absolute force (Rich and Cafarelli: In Press).

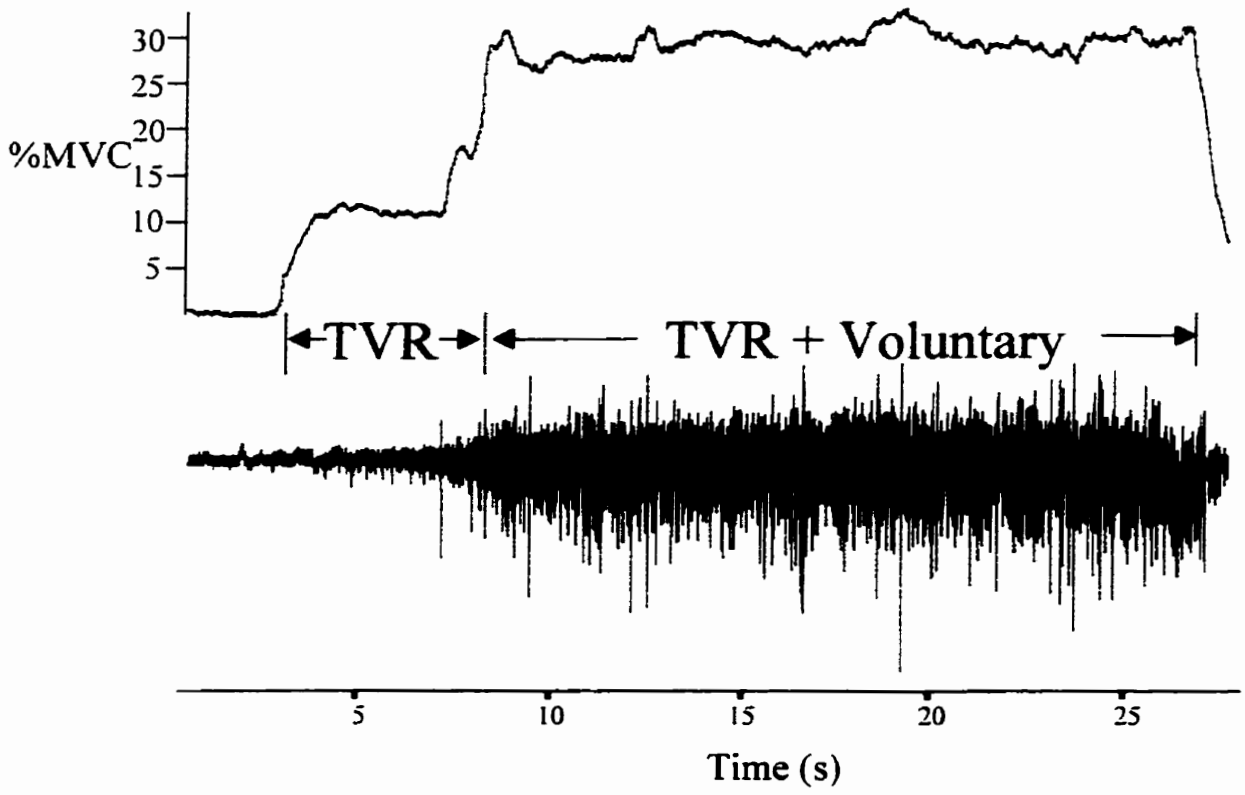


Figure 7 : Tonic Vibration Response (TVR) : The upper trace shows the force of the tonic vibration response (TVR) followed by a voluntary contraction to 30% MVC. The average force of the TVR was 6.16% ±1.45 of MVC. The lower tracing shows the corresponding surface electromyogram from vastus lateralis.

Discussion

Decreasing contractile rate of force development with fatigue and immobilization may dictate a corresponding reduction in the motor unit firing rate during voluntary isometric contractions (6,13). Similarly, contractile rate can be increased by shortening muscle length thus, requiring higher external stimulation frequencies to achieve tetanic fusion (17,27,32). This suggests that motor unit firing rates should be increased to accommodate the fast contractile properties of shortened muscle. Two studies have used this approach and changed the length of tibialis anterior, however, their findings are inconclusive (5,36). Based on external stimulation studies and firing rate adjustments observed in previous studies, we anticipated an increased motor unit firing rate during voluntary contractions of shortened muscle with fast contractile rate at any absolute force level. However, despite large increases in contractile properties, the average motor unit firing rates were significantly lower in SHORT muscle.

Most contractile properties were dramatically increased in shortened muscle and can be attributed to the position on the length tension curve for the knee extensors (29). The classic length-tension relationship is based on the amount of overlap between actin and myosin filaments. When deviating from optimal muscle length, force production is compromised due to less actin and myosin crossbridge formation (20, 23). This occurs because there is an overlap of the actin filaments which prevents access to binding sites and interferes with cross bridge formation (20, 23). The performance of shortened and lengthened muscle is described by opposite limbs of the inverted U-shaped length-tension curve; in both cases there is a decreased ability to generate force (20, 23).

In the previous studies, shortened tibialis anterior showed an increase in contractile rate, but also a decrease in twitch amplitude and maximal voluntary contractile force (5, 27, 36). In these experiments, tibialis anterior was shortened so that its limited performance was described by the left portion of the length-tension curve. In contrast, we shortened vastus lateralis muscle toward optimal length and also lengthened it away from optimal length shifting its performance rightward along the length-tension curve. Thus, shortened vastus lateralis in the present study and the shortened tibialis anterior of Bigland-Ritchie et al. (5) and Vander-Linden et al. (36) are operating on different parts of the length-tension curve. In the present study, lengthened muscle with low-tension producing ability and slow contractile rate had a higher firing rate than faster, shortened muscle with high force development. Vander Linden et al., (36), unlike the present observations, found reduced force production at a shortened muscle length and higher motor unit firing rates. However, these authors did not monitor contractile properties. In contrast, Bigland-Ritchie et al.,(5) found changes in contractile rate and no corresponding change in the motor unit firing rate, but had only a very slight reduction in MVC and twitch tension. These limited results imply that motor unit firing rates may be dictated by muscle length in relation to optimal length rather than to changes in contractile rate.

There were no changes in evoked M-wave, indicating that junctional and sarcolemmal transmission was unaffected by muscle length, but there was significantly higher EMG activity associated with LONG muscle during relative 50% MVC. At any absolute force level and during submaximal contractions, the motor unit firing rate at the LONG length was significantly higher than the SHORT length. Voluntary central drive or electrical activation

arriving at muscle deviating from optimal length terminate on muscle fibers with a reduced ability to generate force. Junctional transmission is maintained in LONG muscle but less force is produced due to less optimal overlap of actin and myosin.

Another reason for the increase in electrical activity of lengthened vastus lateralis may have been to overcome the increased antagonistic biceps femoris activity found during both maximal and submaximal contractions of lengthened vastus lateralis.

We predicted that motor unit firing rates would be higher during vibration due to the additional excitatory input to the alpha motor neuron pool from the Ia afferents. On the contrary, there was a small but significant decrease in firing rate during vibration. The decrease in firing rate was not a result of coactivating the hamstring muscle group because activity of biceps femoris was negligible in both conditions. Vibration induced recruitment thresholds are lower than voluntary contractions of the same force (33). This suggests larger motor units were recruited earlier during vibration. Although, large muscles, such as vastus lateralis, depend on recruitment throughout the entire range of forces, vibration may have elicited a modification in its normal recruitment and rate coding strategy of vastus lateralis (12,25).

The order of motor unit recruitment can be altered by various feedback mechanisms as well as eccentric contraction paradigms, which is contrary to the size principle of motor unit recruitment (3, 21, 22, 24, 34). During voluntary contractions, high threshold motor units fire at lower discharge frequencies than low threshold motor units for forces up to 50% (11, 28, 30). When whole muscle is vibrated during contraction, high threshold motor units may have been recruited at low levels of force and discharge at lower rates than low threshold

units. This may account for the lower discharge rates found during vibration.

Brief bursts of vibration can cause prolonged depolarization of motor neurons despite a withdrawal of the excitatory input (15, 19). Although we saw no evidence of these plateau potentials, they indicate motor unit excitability is not always a linear summation of excitatory and inhibitory inputs. This also implies recruitment order may be variable under the influence of vibration. Fatigue during repeated maximal voluntary contractions causes a decrease in the maximal motor unit firing rate and has been ascribed to inhibitory afferent feedback (6, 7). Vibration of fatigued muscle initially restores the maximal firing rates but prolonged vibration (>10sec) accentuates the normal decline of discharge rates (8). Vibration may initially compensate for reduced Ia afferent input due to fatigue of intrafusal fibers but continued vibration may attenuate the synaptic efficacy of the Ia afferent loop by pre-synaptic inhibition and/or depleting available transmitters (9, 14). Furthermore, deafferentation of non-fatigued muscle reduces maximal motor unit firing rate confirming the necessity of afferent input in achieving maximal discharge rates (18, 26). Finally, the prolonged inhibitory effect of vibration on motor unit discharge rate cannot be discounted in the present study since we applied vibration longer than in previous studies.

We have shown that altering the length of vastus lateralis changes the contractile rate when measured using the dF/dt but not when using TPT and ½ RT. Average motor unit firing rates decreased with shortened muscle and high contractile rate. This is opposite to previous studies using tibialis anterior which found either an increase or no change but not a decrease (5, 36). The disparity between our study and the previous ones using tibialis anterior can be resolved by considering the direction of deviation from optimal muscle length

rather than the contractile rate as the variable dictating the motor unit firing rate. Vibration elicited a decrease in the motor unit firing rate during submaximal contractions which may be due to alteration of the recruitment/rate coding strategy or decreased efficacy of the Ia afferent loop by presynaptic inhibition or depleting available transmitter (9, 14). Activating muscle spindles signaled muscle lengthening but rather than increasing the firing rate as in LONG muscle, the firing rate declined. Thus, muscle spindles can be excluded as the mediating mechanism for altering the motor unit firing rate with changes in muscle length.

References

1. Allen, G.M., S.C. Gandevia and D.K McKenzie. Reliability of measurements of muscle and strength and voluntary activation using twitch interpolation. *Muscle Nerve* 18: 593-600, 1995.

2. Alway, S.E., J.D. MacDougal and D.G. Sale. Contractile adaptations in the human triceps surae after isometric exercise. *J.Appl.Physiol.* 66 (6) : 2725-2732, 1989.

3. Andrew, P.D. Motor unit activity under low tensions as muscle changes length. *Am. J. Phys. Med.* 64(5):235-254, 1985.

4. Bianconi, R., and J.P. van der Meulen. The response to vibration of the end organs of mammalian muscle spindles. *J. Neurophysiol.* 26:177-190, 1963.

5. Bigland-Ritchie, B., F.H. Furbush, S.C. Gandevia and C.K. Thomas. Voluntary discharge frequencies of human motoneurons at different muscle lengths. *Muscle Nerve* 15(2):130-7, 1992.

6. Bigland-Ritchie, B., N.J. Dawson, R.S. Johansson and O.C.J. Lippold. Reflex origin for the slowing of motoneurone firing rates in fatigue of human voluntary contractions. *J. Physiol.* 379: 451-459, 1986.

7. Bigland-Ritchie, B., R. Johansson, O.C.J. Lippold, S.Smith and J.J. Woods. Changes in motoneurone firing rates during sustained maximal voluntary contractions. *J. Physiol.* 340: 335-346, 1983.

8. Bongiovanni, L.G., and K.E. Hagbarth. Tonic vibration reflexes elicited during fatigue from maximal voluntary contractions in man. *J. Physiol. (Lond.)*. 423:1-14, 1990.

9. Bongiovanni, L.G., K.E. Hagbarth and L. Stjernberg. Prolonged muscle vibration reducing motor output in maximal voluntary contractions in man. *J. Physiol. (Lond.)* 423:15-26, 1990.

10. Burke, D., K.E. Hagbarth, L. Lofstedt and B.G. Wallin. The responses of human muscle spindle endings to vibration during isometric contractions. *J. Physiol.* 261: 695-711. 1976.

11. De Luca, C.J., R.S. LeFever, M.P. McCue and A.P. Xenakis. Control scheme governing concurrently active human motor units during voluntary contractions. *J. Physiol. (Lond.)* 329: 129-42, 1982.

12. De Luca, C.J., R.S. LeFever, M.P. McCue and A.P. Xenakis. Behaviour of human motor units in different muscles during linearly varying contractions. *J. Physiol. (Lond.)* 329: 113-28, 1982.

13. Duchateau, J., and K. Hainaut. Effects of immobilization on contractile properties, recruitment and firing rates of human motor units. *J. Physiol.* 422: 555-65, 1990.

14. Eccles, J.C. The ionic mechanisms of excitatory and inhibitory synaptic action. *Ann. N. Y. Acad. Sci.* 137(2):473-94, 1966.

15. Eken, T., and O. Kiehn. Bistable firing properties of soleus motor units in unrestrained rats. *Acta. Physiol. Scand.* 136(3): 383-94, 1989.

16. Fukunaga, T., I. Yoshiho, I. Masamitsu, Y. Kawakami and S. Fukashiro. Determination of fascicle length and pennation in a contracting human muscle in vivo. *J. Appl. Physiol.* 82 (1): 354-358, 1997.

17. Gandevia, S.C., and D.K. McKenzie Activation of human muscles at short muscle lengths during maximal static efforts. *J.Physiol.* 407: 599-613, 1988.

18. Gandevia, S.C., G. Macefield, D. Burke and D.K. McKenzie. Voluntary activation of human motor axons in the absence of muscle afferent feedback. The control of the deafferented hand. *Brain* 113 (Pt 5):1563-81, 1990.

19. Gorassini, M.A., D.J. Bennett and J.F. Yang. Self-sustained firing of human motor units. *Neurosci. Lett.* 247(1):13-6, 1998.

20. Gordon, A.M., A.F. Huxley and F.J. Julian. The variation in isometric tension with sarcomere length in vertebrate muscle fibres. *J. Physiol. (Lond.)* 184(1): 170-92, 1966.

21. Grimby, L., and J. Hannerz. Recruitment order of motor units on voluntary contraction: changes induced by proprioceptive afferent activity. *J. Neurol. Neurosurg. Psychiatry* 31(6):565-73, 1968.

22. Henneman, E., H.P. Clamann, J.D. Gillies and R.D. Skinner. Rank order of motoneurons within a pool: law of combination. *J. Neurophysiol.* 37(6): 1338-49, 1974.

23. Huxley, A.F., and R.M. Simmons. Mechanical properties of the cross-bridges of frog striated muscle. *J. Physiol. (Lond.)* 218(1): 59-60, 1971.

24. Kato, M., S. Murakami and K.Yasuda. Behavior of single motor units of human tibialis anterior muscle during voluntary shortening contraction under constant load torque. *Exp. Neurol.* 90(1): 238-253, 1985.

25. Kukulka, C.G., and H.P. Clamann. Comparison of the recruitment and discharge properties of motor units in human brachial biceps and adductor pollicis during isometric contractions. *Brain Res.* 219(1): 45-55, 1981.

26. Macefield, V.G., S.C. Gandevia, B. Bigland-Ritchie, R.B. Gorman and D. Burke. The firing rates of human motoneurones voluntarily activated in the absence of muscle afferent feedback. *J. Physiol. (Lond.)* 471:429-43, 1993.

27. Marsh, E., D. Sale, A.J. McComas and J. Quinlan. Influence of joint position on ankle dorsiflexion in humans. *J. Appl. Physiol.* 51 (1): 160-167, 1981.

28. Monster, A.W., and H. Chan. Isometric force production by motor units of extensor digitorum communis muscle in man. *J. Neurophysiol.* 40(6): 1432-43, 1977.

29. Narici, M.V., H. Hoppeler, B. Kayser, L. Landon, H. Claassen, C. Gavardi, M. Conti and P. Cerretelli. Human quadriceps cross-sectional area, torque and neural activation during six months strength training. *Acta Physiol. Scand.* 157: 175-186, 1996.

30. Person, R.S., and L.P. Kudina. Discharge frequency and discharge pattern of human motor units during voluntary contraction of muscle. *Electroencephalog. Clin. Neurophysiol* 32(5): 471-483, 1972.

31. Psek, J.A., and E. Cafarelli. Behaviour of coactive muscles during fatigue. *J Appl Physiol.* 74(1):170-175, 1993.

32. Rack, P.M., and D.R. Westbury. The effects of length and stimulus rate on tension in the isometric cat soleus muscle. *J. Physiol. (Lond.)* 204(2): 443-460, 1969.

33. Romaiguere, P., J.P. Vedel and S. Pagni. Effects of tonic vibration reflex on motor unit recruitment in human wrist extensor muscles. *Brain Res.* 602(1):32-40, 1993.

34. Tax, A.A., J.J. Denier van der Gon, C.C. Gielen and M. Kleyne. Differences in central control of m. biceps brachii in movement tasks and force tasks. *Exp. Brain Res.* 79(1): 138-142, 1990.

35. Van Cutsem, M., J Duchateau and K. Hainaut. Changes in single motor unit behaviour contribute to the increase in contraction speed after dynamic training in humans. *J. Physiol. (Lond.)* 513(1): 295-305, 1998.

36. Vander Linden, D.W., C.G. Kukulka and G.L. Soderberg. The effect of muscle length on motor unit discharge characteristics in human tibialis anterior muscle. *Exp. Brain. Res.* 84(1):210-8, 1991.

Chapter IV- Summary, Conclusions and Recommendations

Summary

1. Shortening vastus lateralis length dramatically increases MVC, twitch amplitude and contractile properties. Shortened vastus lateralis in this study represented optimal length whereas previous studies using shortened tibialis anterior fell on the left portion of the length tension curve, substantially deviating from optimal length. Motor unit firing rates may be dictated by the position on the length tension curve rather than the contractile rate when altering muscle length and can be considered a novel hypothesis resulting from this study.

2. Vastus lateralis EMG and AMUFR were significantly higher with LONG muscle during submaximal contractions. This may represent an attempt by the CNS to compensate for decreased actin/myosin overlap and force production. Higher levels of EMG recorded from vastus lateralis in the LONG position may have been partially attributable to a significantly greater biceps femoris coactivity.

3. Vibration of the patellar tendon caused a decrease in the motor unit firing rate during submaximal contractions. Normally, vibration stimulates the Ia afferent endings in spindles. This suggests that the Ia afferent component of muscle spindles can thus be excluded as the mechanism for altering the AMUFR during muscle lengthening. It is possible that the IIa spindle afferents play a role in adjusting firing rates to muscle length.

Conclusion

Contractile rate does not alter motor unit firing rate when muscle length is changed. Higher vastus lateralis EMG and motor unit firing rates are associated with lengthened, slow muscle and may be an attempt by the CNS to compensate for poor actin/myosin overlap. Thus, muscle length in relation to optimal length may dictate corresponding motor unit firing rates. Spindle activation has an opposite effect on the motor unit firing rate than muscle lengthening and can be discounted in playing a role in altering the AMUFR with muscle lengthening. It is possible that the IIa spindle afferents are involved in adjusting the motor unit firing rate to muscle length.

Recommendations

The following recommendations would facilitate better understanding of the motor unit firing rate accommodations to changes in muscle length and the effect of vibration on the motor unit firing rate.

1. Increases in vastus lateralis AMUFR and EMG were found in lengthened muscle deviating (right shift) from optimal length and explained as compensatory increases in descending drive for the low tension producing capacity. Shortened tibialis anterior also has a reduced tension capacity and deviates from optimal length on the opposite side of the length tension curve. It is anticipated that tibialis anterior EMG would be increased for SHORT muscle

compensating for reduced tension ability but EMG was not measured in previous studies. Measuring tibialis anterior EMG in conjunction with the AMUFR during submaximal contractions would confirm if there is a corresponding increase in descending drive similar to vastus lateralis when deviating from optimal length. This would support the hypothesis that the system is attempting to compensate for reduced tension producing capacity.

2. Vastus lateralis EMG and AMUFR were higher in the LONG muscle at 50% MVC. Varying level submaximal contractions should be performed to determine if vastus lateralis EMG and AMUFR are higher for LONG at all relative force levels. This would provide support for increased descending drive for LONG muscle. Vastus lateralis EMG activity was higher in the LONG muscle during the submaximal contractions and it would have been useful to have interpolated supramaximal shocks to determine the voluntary activation to provide further evidence for increased descending drive. Supramaximal shocks should be utilized at various submaximal intensities for both LONG and SHORT muscle to determine the voluntary activation.

3. Vibration of the patellar tendon decreased the average motor unit firing rate during submaximal contractions. It was hypothesized that larger, higher threshold motor units were recruited with vibration. It would be valuable to vibrate the patellar tendon and attain single motor units from the TVR response alone and record the recruitment threshold (% MVC) for that unit. Tracking the same motor unit during a voluntary ramp contraction and recording the recruitment threshold would confirm that vibration changes the recruitment threshold of

individual units in vastus lateralis.

Chapter V- Appendices

APPENDIX A: AGE OF SUBJECTS AND PROTOCOL ORDER

APPENDIX A: Age of Subjects and Protocol Order

		Days					
Subject	**Age**	**Day 1**	**Day 2**		**Day 3**		
AR-1	24	Angle-MVC-Twitch	short	long	Vibration/Control		
BR-2	22	Angle-MVC-Twitch	long	short	Vibration/Control		
CA-3	23	Angle-MVC-Twitch	Vibration/Control		long	short	
PE-4	28	Angle-MVC-Twitch	short	long	Vibration/Control		
SA-5	24	Angle-MVC-Twitch	Vibration/Control		long	short	
PA-6	26	Angle-MVC-Twitch	Vibration/Control		short	long	
EL-7	23	Angle-MVC-Twitch	Vibration/Control		long	short	
CA-8	23	Angle-MVC-Twitch	Vibration/Control		long	short	
IS-9	24	Angle-MVC-Twitch	short	long	Vibration/Control		
RO-10	24	Angle-MVC-Twitch	short	long	Vibration/Control		
Mean	24.1						
SD	1.7						

Angle MVC-Twitch- 2 MVC's and 3 twitches obtained from 60 to 100 degrees of flexion in 10 degree increments

Short and Long Muscle Lengths- (order for that day reads from left to right) - 5 MVC's and five 50% MVC at each length

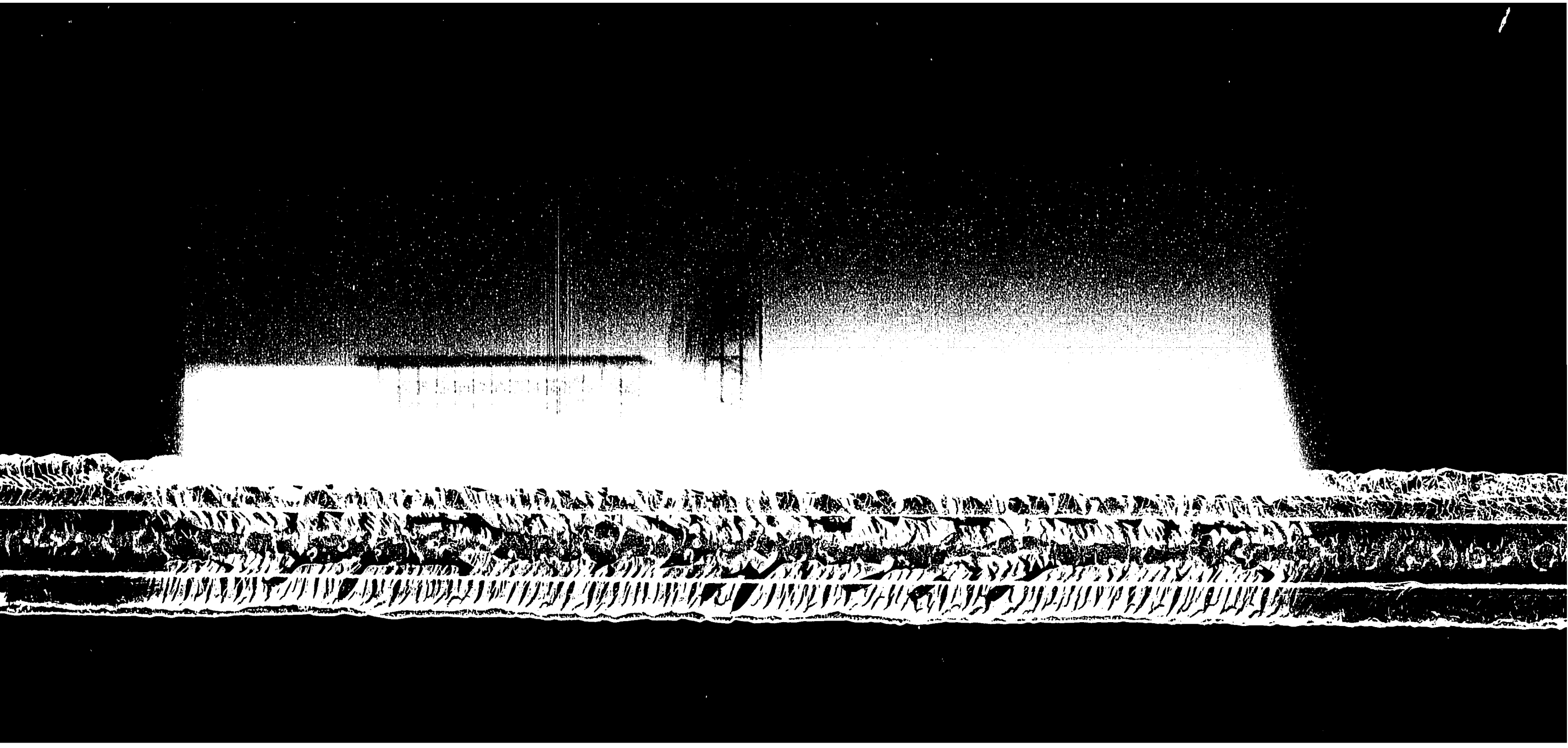
Vibration/Control- 5 control and 5 vibration contractions assigned randomly using cards

APPENDIX B: DATA TABLES AND STATISTICAL ANALYSIS

PART I

TWITCH CHARACTERISTICS AND MAXIMAL CONTRACTIONS FROM 60 TO 100 DEGREES OF FLEXION

The statistical analysis of data in the following tables was produced using Statistica. Data from Part One were analyzed using a one-way repeated measures analysis of variance (ANOVA) for each variable.



PART I: TWITCH AMPLITUDE

	Degrees of Flexion				
Subjects	60	70	80	90	100
AR-1	400.20	361.58	246.04	88.62	83.54
BR-2	296.12	214.40	100.58	72.09	56.75
CA-3	251.88	297.63	155.07	64.08	63.42
PE-4	256.30	228.10	178.48	105.25	88.90
SA-5	287.14	155.43	303.09	111.24	71.46
PA-6	186.20	174.00	119.51	36.93	31.70
EL-7	218.16	228.02	178.15	69.54	61.19
CB-8	169.93	150.45	79.12	39.43	29.80
IS-9	218.14	262.65	201.73	75.72	42.21
RO-10	592.64	500.93	297.83	108.66	112.66
MEAN	287.67	257.32	185.96	77.16	64.16
SE	39.72	34.02	24.56	8.43	8.29

Summary of All Effects

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	4*	103621*	36*	3400.15*	30.47542*	0.001*

PART I: +dF/dt

	Degrees of Flexion				
Subjects	60	70	80	90	100
AR-1	5030.03	4623.09	2659.10	1097.00	1043.92
BR-2	4064.48	3058.47	1314.38	990.84	786.10
CA-3	3470.48	3899.54	2320.39	861.93	887.21
PE-4	3728.30	3230.35	2092.90	1516.59	1127.34
SA-5	4074.59	2264.78	4616.14	1544.40	1150.09
PA-6	2216.13	2024.65	1427.50	482.78	470.14
EL-7	2628.77	2643.93	2120.71	824.02	722.91
CB-8	2742.51	2429.08	1453.40	679.94	573.78
IS-9	3601.92	4008.87	3490.70	1182.94	631.92
RO-10	8262.94	7074.93	4309.66	1594.95	1642.98
MEAN	3982.01	3525.77	2580.49	1077.54	903.64
SE	541.56	474.94	375.46	121.10	110.26

Summary of All Effects

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	4*	19474300*	36*	678401.6*	28.70617*	0.001*

PART I: -dF/dt

	Degrees of Flexion				
Subjects	60	70	80	90	100
AR-1	3374.42	2664.15	2115.65	674.89	631.92
BR-2	2333.03	2067.62	1018.65	576.31	568.72
CA-3	2537.77	2195.27	1399.06	626.86	485.31
PE-4	2310.28	2343.14	1817.39	813.91	712.80
SA-5	2340.61	1357.35	2400.01	821.49	462.56
PA-6	2633.19	2330.50	1643.61	447.40	353.87
EL-7	2262.25	2022.13	1557.04	561.14	583.89
CB-8	1329.55	1251.19	649.61	561.14	543.45
IS-9	2151.04	2666.68	1958.94	636.97	470.15
RO-10	5242.36	4211.08	3002.86	816.43	985.79
MEAN	2651.45	2310.91	1756.28	653.65	579.85
SE	328.52	259.31	213.20	40.48	55.03

Summary of All Effects

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	4*	8981530*	36*	234386.4*	38.31933*	0.001*

PART I: TPT

	Degrees of Flexion				
Subjects	60	70	80	90	100
AR-1	0.1477	0.1532	0.1554	0.1511	0.1447
BR-2	0.1256	0.1146	0.1192	0.1194	0.1246
CA-3	0.1318	0.1286	0.1300	0.1272	0.1214
PE-4	0.1246	0.1159	0.1282	0.1197	0.1276
SA-5	0.1218	0.1215	0.1150	0.1182	0.1082
PA-6	0.1347	0.1277	0.1240	0.1238	0.1306
EL-7	0.1377	0.1357	0.1461	0.1373	0.1313
CB-8	0.1053	0.1046	0.1043	0.0959	0.1001
IS-9	0.1098	0.1131	0.1086	0.1124	0.1151
RO-10	0.1132	0.1135	0.1237	0.1196	0.1363
MEAN	0.1252	0.1228	0.1254	0.1224	0.1240
SE	0.0042	0.0044	0.0050	0.0046	0.0042

Summary of All Effects

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	4	0.000018	36	0.000029	0.64127	0.636539

PART I: 1/2 RT

	Degrees of Flexion				
Subjects	60	70	80	90	100
AR-1	0.10	0.10	0.09	0.10	0.10
BR-2	0.09	0.08	0.07	0.09	0.08
CA-3	0.09	0.07	0.07	0.10	0.12
PE-4	0.08	0.10	0.08	0.08	0.13
SA-5	0.10	0.09	0.09	0.10	0.11
PA-6	0.06	0.06	0.06	0.09	0.09
EL-7	0.07	0.08	0.08	0.09	0.09
CB-8	0.09	0.09	0.08	0.06	0.05
IS-9	0.08	0.08	0.09	0.09	0.07
RO-10	0.08	0.08	0.07	0.10	0.08
MEAN	0.08	0.08	0.08	0.09	0.09
SE	0.00	0.00	0.00	0.00	0.01

Summary of All Effects

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	4	0.000354	36	0.00018	1.965768	0.120689

PART I: M WAVE AMPLITUDE

	Degrees of Flexion				
Subjects	60	70	80	90	100
AR-1	2.71	2.77	2.20	2.29	4.56
BR-2					
CA-3	1.84	2.61	2.10	2.15	1.97
PE-4					
SA-5	2.44	2.36	2.27	2.40	2.45
PA-6	1.52	1.46	1.32	1.07	1.05
EL-7	1.14	1.40	1.32	1.39	1.19
CB-8	1.13	1.63	2.02	2.56	2.14
IS-9	2.83	2.72	3.77	3.65	3.60
RO-10	4.62	4.37	4.25	4.39	4.70
MEAN	2.28	2.42	2.41	2.49	2.71
SE	0.41	0.34	0.38	0.39	0.50

Summary of All Effects

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	4	0.20122	28	0.206915	0.972478	0.438196

PART I: MVC

	Degrees of Flexion				
Subjects	60	70	80	90	100
AR-1	869.50	934.26	1231.74	590.07	568.31
BR-2	893.65	864.18	647.43	489.29	391.96
CA-3	531.57	641.34	609.37	290.16	304.96
PE-4	492.17	630.52	916.71	667.76	690.96
SA-5	711.59	615.78	757.36	564.70	476.54
PA-6	999.74	992.12	875.63	335.02	409.05
EL-7	740.40	560.61	700.93	416.04	426.20
CB-8	587.61	563.22	518.40	326.03	314.85
IS-9	521.51	601.59	607.13	488.45	516.55
RO-10	1293.24	1028.59	899.23	600.52	742.55
MEAN	764.10	745.22	776.39	476.80	484.19
SE	80.61	60.07	66.50	41.36	46.63

Summary of All Effects

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	4*	238867.6*	36*	19017.44*	12.56045*	0.001*

PART I: % ACTIVATION

	Degrees of Flexion				
Subjects	60	70	80	90	100
AR-1	93.57	95.88	93.13	99.92	99.64
BR-2	99.43	98.09	99.16	96.64	92.32
CA-3	90.84	89.49	96.93	90.69	96.14
PE-4	95.71	93.72	96.90	98.87	98.28
SA-5	89.94	83.94	87.14	85.78	80.86
PA-6	95.13	99.35	96.03	98.90	99.50
EL-7	97.46	94.85	98.91	97.91	96.23
CB-8	88.12	92.13	79.27	98.77	98.32
IS-9	88.39	95.01	89.34	96.36	99.21
RO-10	98.10	99.33	99.01	99.35	97.61
MEAN	93.67	94.18	93.58	96.32	95.81
SE	1.31	1.51	2.06	1.44	1.80

Summary of All Effects

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	4	16.10806	36	13.84147	1.163754	0.342969

PART I: VASTUS LATERALIS EMG

	Degrees of Flexion				
Subjects	60	70	80	90	100
AR-1	0.22	0.25	0.32	0.36	0.33
BR-2	0.59	0.76	0.74	0.72	0.64
CA-3	0.07	0.07	0.08	0.09	0.09
PE-4	0.19	0.22	0.28	0.29	0.34
SA-5	0.09	0.08	0.06	0.10	0.10
PA-6	0.03	0.03	0.03	0.04	0.04
EL-7	0.07	0.06	0.06	0.07	0.06
CB-8	0.12	0.16	0.14	0.12	0.14
IS-9	0.11	0.10	0.09	0.15	0.17
RO-10	0.17	0.17	0.17	0.22	0.23
MEAN	0.16	0.19	0.20	0.22	0.21
SE	0.05	0.07	0.07	0.06	0.06

Summary of All Effects

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	4*	0.004352*	36*	0.001224*	3.555757*	0.015218*

PART I: VASTUS MEDIALIS EMG

	Degrees of Flexion				
Subjects	60	70	80	90	100
AR-1	0.60	0.67	0.85	0.86	0.78
BR-2	0.43	0.42	0.47	0.40	0.24
CA-3	0.21	0.19	0.18	0.18	0.20
PE-4	0.16	0.21	0.25	0.30	0.27
SA-5	0.13	0.14	0.10	0.23	0.22
PA-6	0.11	0.14	0.12	0.15	0.17
EL-7	0.17	0.18	0.19	0.17	0.16
CB-8	0.32	0.34	0.36	0.28	0.28
IS-9	0.45	0.41	0.39	0.54	0.61
RO-10	0.33	0.51	0.48	0.38	0.49
MEAN	0.29	0.32	0.34	0.35	0.34
SE	0.05	0.06	0.07	0.07	0.07

Summary of All Effects

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	4	5.82E-03	36	0.004226	1.376817	0.26133

PART I: BICEPS FEMORIS EMG

	Degrees of Flexion				
Subjects	60	70	80	90	100
AR-1	0.12	0.04	0.17	0.19	0.20
BR-2	0.11	0.12	0.12	0.10	0.07
CA-3	0.10	0.11	0.10	0.10	0.11
PE-4	0.12	0.14	0.16	0.16	0.18
SA-5					
PA-6	0.05	0.06	0.06	0.09	0.12
EL-7	0.04	0.04	0.04	0.04	0.04
CB-8	0.06	0.08	0.08	0.08	0.09
IS-9	0.06	0.05	0.06	0.07	0.10
RO-10	0.05	0.04	0.05	0.05	0.05
MEAN	0.08	0.08	0.09	0.10	0.11
SE	0.01	0.01	0.02	0.02	0.02

Summary of All Effects

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	4	0.001618	32	0.000632	2.559109	0.057494

PART II

TWITCH CHARACTERISTICS, MAXIMAL AND SUBMAXIMAL CONTRACTIONS AND AMUFR FOR LONG AND SHORT MUSCLE

The statistical analysis of data in the following tables was produced using Statistica. Each measured variable from Part Two was analyzed using a one-way ANOVA for short and long muscle except for average motor unit firing rates. A 2 x 2 ANOVA was employed for the AMUFR taking into account 50% MVC and 100% MVC intensities along with long and short muscle length.

PART II: TWITCH AMPLITUDE

Subjects	Long	Short
AR-1	82.20	320.31
BR-2	46.05	258.60
CA-3	53.43	195.46
PE-4	84.60	264.62
SA-5	70.07	246.40
PA-6	36.89	181.18
EL-7	57.13	235.49
CB-8	30.03	120.93
IS-9	36.80	283.45
RO-10	85.31	475.33
MEAN	58.25	258.18
SE	6.69	30.01

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	1*	199853.6*	9*	3315.912*	60.27079*	0.001*

PART II: dF/dt

Subjects	Long	Short
AR-1	1102.06	4087.22
BR-2	745.66	3510.92
CA-3	821.49	2401.28
PE-4	1180.42	3700.49
SA-5	1175.36	3538.72
PA-6	513.75	2373.47
EL-7	793.69	3213.50
CB-8	533.34	1821.81
IS-9	616.75	4170.64
RO-10	1086.89	7155.81
MEAN	856.94	3597.39
SE	82.79	465.25

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	1*	37550200*	9*	906972.9*	41.40171*	0.001*

PART II: -Df/dt

Subjects	Long	Short
AR-1	662.25	2588.32
BR-2	467.62	2623.71
CA-3	530.81	1506.49
PE-4	674.89	2815.81
SA-5	695.11	1870.47
PA-6	549.77	1936.19
EL-7	545.98	2064.26
CB-8	369.04	1169.67
IS-9	545.97	2762.73
RO-10	869.52	4206.02
MEAN	591.09	2354.37
SE	44.02	269.80

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	1*	15545700*	9*	283267.1*	54.8799*	0.001*

PART II: TPT

Subjects	Long	Short
AR-1	0.14	0.14
BR-2	0.1262	0.1221
CA-3	0.1259	0.1232
PE-4	0.1263	0.1350
SA-5	0.1134	0.1103
PA-6	0.1160	0.1213
EL-7	0.1278	0.1201
CB-8	0.0911	0.0994
IS-9	0.1003	0.1198
RO-10	0.1203	0.1042
MEAN	0.1192	0.1200
SE	0.0048	0.0043

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	1	0.000004	9	0.00005	0.073824	0.791979

PART II: 1/2 RT

Subjects	Long	Short
AR-1	0.1068	0.1002
BR-2	0.0832	0.0725
CA-3	0.0818	0.1058
PE-4	0.0902	0.0835
SA-5	0.0968	0.0925
PA-6	0.0607	0.0718
EL-7	0.0778	0.0940
CB-8	0.1154	0.0838
IS-9	0.0582	0.0738
RO-10	0.0812	0.0755
MEAN	0.0852	0.0853
SE	0.0057	0.0039

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	1	0.000	9	0.000137	0.000623	0.980632

PART II : M WAVE AMPLITUDE

Subjects	Long	Short
AR-1	5.67	4.03
BR-2	5.00	5.79
CA-3	2.76	2.13
PE-4	5.84	5.50
SA-5	3.02	2.38
PA-6	1.85	1.97
EL-7	1.22	3.33
CB-8	1.77	1.39
IS-9	3.26	2.79
RO-10	6.29	6.14
MEAN	3.67	3.54
SE	0.59	0.55

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	1	0.076306	9	0.498255	0.153146	0.70465

PART II: MVC

Subjects	Long	Short
AR-1	492.74	936.27
BR-2	322.73	824.50
CA-3	273.44	367.09
PE-4	647.47	495.93
SA-5	341.35	574.37
PA-6	325.23	981.08
EL-7	443.53	525.50
CB-8	344.19	318.56
IS-9	349.69	767.93
RO-10	690.09	1154.36
MEAN	423.05	694.56
SE	45.61	88.52

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	1*	368596.5*	9*	34739.91*	10.61017*	.009881*

PART II: % ACTIVATION

Subjects	Long	Short
AR-1	99.64	93.57
BR-2	92.32	99.62
CA-3	96.14	95.71
PE-4	96.28	88.01
SA-5	80.86	89.94
PA-6	99.50	95.13
EL-7	96.23	97.46
CB-8	98.32	88.12
IS-9	99.21	95.01
RO-10	97.61	98.10
MEAN	95.81	94.07
SE	1.80	1.30

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	1	15.2	9	19.86279	0.765436	0.404375

PART II:VASTUS LATERALIS EMG_{MAX}

Subjects	Long	Short
AR-1	0.3124	0.3004
BR-2	0.2504	0.2766
CA-3	0.1376	0.0686
PE-4	0.3775	0.1513
SA-5	0.0798	0.0650
PA-6	0.0471	0.0649
EL-7	0.0761	0.0531
CB-8	0.1081	0.0892
IS-9	0.1088	0.1480
RO-10	0.3006	0.2531
MEAN	0.1798	0.1468
SE	0.0375	0.0305

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	1	0.005445	9	0.002853	1.908389	0.20047

PART II:VASTUS LATERALIS EMG_{MAX} NORMALIZED TO M WAVE

Subjects	Long	Short
AR-1	0.0551	0.0745
BR-2	0.0501	0.0478
CA-3	0.0498	0.0313
PE-4	0.0646	0.0275
SA-5	0.0285	0.0274
PA-6	0.0255	0.0330
EL-7	0.0624	0.0159
CB-8	0.0611	0.0643
IS-9	0.0334	0.0530
RO-10	0.0478	0.0413
MEAN	0.0476	0.0416
SE	0.0046	0.0058

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	1	0.000182	9	0.000244	0.744133	0.410737

PART II:VASTUS MEDIALIS EMG_{MAX}

Subjects	Long	Short
AR-1	0.4302	0.3611
BR-2	0.5178	0.5166
CA-3	0.1967	0.1216
PE-4	0.2431	0.1099
SA-5	0.2909	0.2144
PA-6	0.1577	0.1425
EL-7	0.1176	0.1338
CB-8	0.2075	0.1953
IS-9	0.4207	0.4288
RO-10	0.3091	0.3898
MEAN	0.2891	0.2614
SE	0.04	0.05

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	1	0.003851	9	0.001862	2.067533	0.184311

PART II: VASTUS LATERALIS EMG$_{50\%MVC}$

Subjects	Long	Short
AR-1	0.1055	0.0351
BR-2	0.0682	0.0549
CA-3	0.0388	0.0185
PE-4	0.1226	0.0221
SA-5	0.0310	0.0298
PA-6	0.0250	0.0273
EL-7	0.0414	0.0147
CB-8	0.0613	0.0524
IS-9	0.0536	0.0221
RO-10	0.1909	0.0588
MEAN	0.0758	0.0336
SE	0.0164	0.0051

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	1*	0.00893*	9	.000997*	8.961061	0.015115

PART II: VASTUS LATERALIS EMG$_{50\%MVC}$ NORMALIZED TO M WAVE

Subjects	Long	Short
AR-1	0.0186	0.0087
BR-2	0.0176	0.0095
CA-3	0.0140	0.0087
PE-4	0.0210	0.0040
SA-5	0.0103	0.0125
PA-6	0.0135	0.0139
EL-7	0.0340	0.0044
CB-8	0.0347	0.0377
IS-9	0.0164	0.0079
RO-10	0.0303	0.0096
MEAN	0.0211	0.0117
SE	0.0028	0.0030

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	1*	0.000438	9*	.000055*	7.900830*	.020349*

PART II: BICEPS FEMORIS EMG DURING QUADRICEPS MVC

Subjects	Long	Short
AR-1	0.1616	0.1372
BR-2	0.2477	0.1541
CA-3	0.1343	0.1215
PE-4	0.1755	0.0795
SA-5	0.0811	0.0024
PA-6	0.0830	0.0747
EL-7	0.0859	0.0678
CB-8	0.1044	0.0615
IS-9	0.0468	0.0714
RO-10	0.0464	0.0471
MEAN	0.1167	0.0817
SE	0.0201	0.0142

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1*	1*	0.006103*	9*	0.000865*	7.057216*	0.026194*

PART II: BICEPS FEMORIS EMG DURING QUADRICEPS 80%

Subjects	Long	Short
AR-1	0.0745	0.0433
BR-2	0.0818	0.0475
CA-3	0.0775	0.0372
PE-4	0.1095	0.0437
SA-5	0.0318	0.0025
PA-6	0.0551	0.0308
EL-7	0.0556	0.0199
CB-8	0.0864	0.0410
IS-9	0.0320	0.0327
RO-10	0.0454	0.0232
MEAN	0.0630	0.0322
SE	0.0076	0.0044

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	1*	0.004741*	9*	0.000138*	34.25788*	0.001*

AMUFR for Individual Subjects at 50% and 100% MVC

50%

Subjects	Long	Short
AR-1	14.81	11.92
BR-2	10.20	10.55
CA-3	10.31	8.34
PE-4	13.50	9.12
SA-5	9.91	8.87
PA-6	14.38	10.503
EL-7	12.17	10.44
CB-8	13.17	14.19
IS-9	12.97	8.70
RO-10	11.129	8.85
MEAN	12.26	10.15
SE	0.565	0.573

100%

Subjects	Long	Short
AR-1	21.44	24.72
BR-2	17.05	15.29
CA-3	12.85	11.71
PE-4	13.67	11.08
SA-5	13.76	9.14
PA-6	16.90	14.84
EL-7	15.98	16.19
CB-8	16.39	17.46
IS-9	18.95	18.92
RO-10	16.74	16.43
MEAN	16.37	15.58
SE	0.565	1.401

Summary of All Effects

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	1*	21.063*	9*	2.095811*	10.05005*	0.011363*
2	1*	227.8276*	9*	7.600345*	29.97596*	0.000393*
12	1	4.3015	9	1.968993	2.18464	0.173514

1- LENGTH
2- INTENSITY

PART III

AMUFR AND ELECTRICAL ACTIVITY DURING VIBRATION AND CONTROL CONTRACTIONS AT 30%MVC

The statistical analysis of data in the following tables was produced using Statistica. Each measured variable from Part Three was analyzed using a one-way ANOVA for vibrated and control conditions.

Tonic Vibration Response for Individual Subjects at 90 degrees of Flexion

Subjects	TVR value (N)	MVC value (N)	Percentage
AR-1			
BR-2	14.98	492.82	3.04
CA-3	32.08	290.24	11.05
PE-4	13.74	665.92	2.06
SA-5	62.33	566.53	11.00
PA-6			
EL-7	18.52	417.44	4.44
CB-8	26.65	327.99	8.12
IS-9	16.62	491.99	3.38
RO-10			
MEAN	26.42	464.71	6.16
SE	6.50	49.70	1.45

PART III: AMUFR AT 30% MVC

Subjects	Vibration	Control
AR-1	13.30	15.84
BR-2	9.31	11.11
CA-3	7.16	8.86
PE-4	9.72	9.13
SA-5	8.07	9.67
PA-6	10.21	10.42
EL-7	9.58	9.81
CB-8	9.97	11.07
IS-9	10.20	10.51
RO-10	7.85	8.60
MEAN	9.54	10.50
SE	0.54	0.65

Summary of all Effects

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	1*	4.672354*	9*	0.452803*	10.32*	0.01062*

PART III: VASTUS LATERALIS $EMG_{30\%MVC}$

Subjects	Vibration	Control
AR-1	0.0536	0.0556
BR-2	0.0740	0.0683
CA-3	0.0201	0.0192
PE-4	0.0292	0.0301
SA-5	0.0336	0.0453
PA-6	0.0507	0.0525
EL-7	0.0556	0.0527
CB-8	0.0277	0.0263
IS-9	0.0442	0.0403
RO-10	0.0640	0.0713
MEAN	0.0453	0.0482
SE	0.0055	0.0066

Summary of all Effects

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	1	0.000019	9	0.000042	0.448093	0.520043

PART III: BICEPS FEMORIS $EMG_{30\%MVC}$

Subjects	Vibration	Control
AR-1	0.0568	0.0569
BR-2	0.0556	0.0657
CA-3	0.0562	0.0330
PE-4	0.0496	0.0483
SA-5	0.0514	0.0588
PA-6	0.0370	0.0404
EL-7	0.0241	0.0218
CB-8	0.0270	0.0267
IS-9	0.0483	0.0413
RO-10	0.0299	0.0239
MEAN	0.0436	0.0417
SE	0.0041	0.0049

Summary of all Effects

Effect	df Effect	MS Effect	df Error	MS error	F	p-level
1	1	0.000042	9	0.000019	2.178393	0.174069

APPENDIX C: INFORMED CONSENT DOCUMENT

INFORMED CONSENT

Department of Kinesiology and Health Science, Faculty of Graduate Studies
York University (416) 736-2100 ext. 33859

The Effect of Different Muscle Lengths on the Motor Unit Discharge Rate in Human Vastus Lateralis Muscle

Our research team is interested in studying the effects of different muscle lengths on the neuromuscular system. The research team is headed by Dr. E. Cafarelli and the Human Participant's Review Committee has approved the study. There are no risks with these procedures with the exception of those below:

- Electrical shocks will be administered to a nerve at the top of the leg to produce a contraction in your thigh muscles. Although these shocks may feel unpleasant, no tissue damage will occur.
- A needle electrode will be inserted into a thigh muscle. Redness and slight bruising at the site of insertion may occur but will not cause permanent tissue damage. As with all invasive techniques there is a risk of infection but strict sterile procedures will be followed to ensure that there is minimal risk. This procedure has been performed in our laboratory for five years with no incidence of any infection.
- A vibrator will be placed on the patellar tendon just below the knee which may result in some discomfort to the tendon and a numbing sensation in the leg. The patellar tendon may be slightly sore the following day but again permanent tissue damage will not occur.

The total amount of participation time will be approximately 6-8 hours. Subject identity will be kept confidential in all future publications.

I have been informed about the nature and procedures of the study and understand them entirely. I know that I may withdraw at any time if I feel uncomfortable with any of the procedures.

_____ _____

Signature of Participant Signature of Witness

_____ _____

Date Name of Witness

APPENDIX D: EXPERIMENTAL SETUP

Experimental Setup