Task-dependent motor unit subpopulations in older adults.

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Task-Dependent Motor Unit Subpopulations in Older Adults

by

Brad Harwood

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Submitted to the Faculty of Graduate Studies
through Kinesiology
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ABSTRACT

Task-dependent motor unit (MU) activity has not been studied in old adults and its relationship to force steadiness is unknown. The purpose of this study was to determine whether task-dependent MU activity of the long and short head of the biceps brachii influences elbow flexion steadiness in young and old men for neutral, pronated and supinated wrist positions at 10% MVC. In the short head MU discharge rates in young and old men were greater during neutral and supinated, whereas in the long head neutral and pronated had higher discharge rates. Force steadiness was lower in old men, but irrespective of age the supinated position was steadiest followed by pronated and neutral. A relationship between steadiness and MU discharge behaviour was observed in the long but not short head of the biceps brachii. These data suggest task-dependent MU behaviour of the long head of the biceps brachii influences force steadiness.
DEDICATION

To all those who have helped me realize true happiness still exists following great disappointment.
ACKNOWLEDGEMENTS

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**TABLE OF CONTENTS**

ABSTRACT ............................................................................................................................. iii  
DEDICATION .......................................................................................................................... iv  
ACKNOWLEDGEMENTS ....................................................................................................... v  
LIST OF TABLES ................................................................................................................... ix  
LIST OF FIGURES .................................................................................................................. x  
GLOSSARY ............................................................................................................................. xi  

**CHAPTER**

I. REVIEW OF LITERATURE  
1.0 Functional Organization of Neuromuscular System ............... 1  
1.1 Production, Control, and Steadiness of Force ....................... 3  
1.2 Relative Contributions of Elbow Flexors ............................. 7  
1.3 Task-Dependent Subpopulations of Motor Neuron Pools ...... 8  
1.4 Age-Related Neuromuscular Adaptation ............................ 11  
1.5 Summary of Literature ......................................................... 14  
1.6 References ........................................................................... 15  

II. PURPOSE AND HYPOTHESES  
2.0 Purpose ........................................................................... 19  
2.1 Specific Objectives (So) ....................................................... 19  
2.2 Research ($H_i$) and Null ($H_0$) Hypotheses ...................... 19  

III. MANUSCRIPT  
3.0 Introduction .......................................................................... 21  
3.1 Methods ............................................................................. 23  
3.2 Experimental Protocol ....................................................... 24  
3.3 Physiological Assessment ................................................... 27  
3.4 Motor Unit Data Processing .............................................. 30  
3.5 Statistical Analysis ............................................................. 31  
3.6 Results ................................................................................. 33  
3.7 Discussion ........................................................................... 43  
3.8 Conclusion ........................................................................... 52  
3.9 References ........................................................................... 53

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IV. CONCLUSION AND RECOMMENDATIONS

4.0 Conclusion .......................................................................................57
4.1 Summary of Specific Objectives (So) ...........................................57
4.2 Summary of Research (H1) and Null (H0) Hypotheses ..........58
4.3 Limitations and Recommendations ...............................................59

APPENDICES

Consent Form...................................................................................................................64
University of Windsor Research Ethics Board Approval .........................67
Pictorial Representation of Wrist Positions..........................................................68

VITA AUCTORIS .................................................................................................................69
LIST OF TABLES

Table 1. Experimental protocol ................................................................. 27
Table 2. Subject characteristics ................................................................. 34
### LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Spinal connections of the αMN, γMN, and Ia afferents</td>
<td>3</td>
</tr>
<tr>
<td>2</td>
<td>Motor unit recruitment and discharge relationships to force</td>
<td>5</td>
</tr>
<tr>
<td>3</td>
<td>Initial mean firing rates observed during ramp muscle contraction</td>
<td>6</td>
</tr>
<tr>
<td>4</td>
<td>Flexors of the elbow</td>
<td>8</td>
</tr>
<tr>
<td>5</td>
<td>Motor unit activity during contractions of the biceps brachii</td>
<td>10</td>
</tr>
<tr>
<td>6</td>
<td>Graphical sequence editor output of tracking task and force output for a young man</td>
<td>26</td>
</tr>
<tr>
<td>7</td>
<td>Template matching algorithm and spike discrimination</td>
<td>33</td>
</tr>
<tr>
<td>8</td>
<td>Waveform discrimination output</td>
<td>33</td>
</tr>
<tr>
<td>9</td>
<td>Force steadiness in young and old men for neutral, pronated, and supinated positions during the first and second phase</td>
<td>35</td>
</tr>
<tr>
<td>10</td>
<td>Normalized surface EMG for the four muscles studied in young and old men for the neutral, pronated and supinated positions</td>
<td>37</td>
</tr>
<tr>
<td>11</td>
<td>Motor unit discharge rates of the short and long head of the biceps brachii in the neutral, pronated, and supinated positions for the first phase</td>
<td>39</td>
</tr>
<tr>
<td>12</td>
<td>Ratio of active to inactive motor units of the short and long head of the biceps brachii for three wrist positions</td>
<td>40</td>
</tr>
<tr>
<td>13</td>
<td>Motor unit discharge rates in three wrist positions</td>
<td>41</td>
</tr>
<tr>
<td>14</td>
<td>Motor unit discharge variability of the short and long head of the biceps brachii in three wrist positions</td>
<td>41</td>
</tr>
<tr>
<td>15</td>
<td>Relationship between motor unit discharge behaviour and force steadiness for the first phase and second phase</td>
<td>43</td>
</tr>
</tbody>
</table>

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GLOSSARY

Action potential – The electrochemical voltage transmitted along and between neurons in order to relay information.

Afferent – Term used to describe a neuron that travels from a sensory receptor to the spinal cord.

Anisometric – A force production that involves a change in joint position or limb movement. (See isotonic)

Coefficient of Variation – A statistical measure indicating the amount of variability of a sample population assessed by dividing each individual sample’s standard deviation from the mean of the sample population by the mean value of the sample population.

Efferent – Term used to describe a neuron that travels from the spinal cord to an effector (i.e. muscle)

Exorotation – The movement of the forearm in which the wrist is rotated laterally.

Force steadiness – The ability to maintain a constant force quantified by the coefficient of variation of force. An increase in the coefficient of variation of force equals a reduction in force steadiness.

Henneman's Size Principle – The substantiated theory that describes the process of orderly motor unit recruitment in which small motor units are recruited initially followed by larger motor units as force demands exceed those of small motor units.

Ia afferent – A neuron that transmits information regarding length and rate of length change from the spindle apparatus of the intrafusal fibre of skeletal muscles to the motor nucleus in the ventral spinal cord.

Ib afferent – A neuron that transmits information regarding tension from the Golgi tendon organ in the aponeurotic region of the musculotendinous junction to the motor nucleus in the ventral spinal cord.

II afferent – A neuron that transmits information regarding length change from the spindle apparatus of the intrafusal fibre of the skeletal muscles to the motor nucleus in the ventral spinal cord.

Isometric – A force production without a change in joint position.

Isotonic – A force production that involves a change in joint position or limb movement. (See anisometric)
Lateral corticospinal tract – Bundle of neurons originating in the primary cortical neurons in the brain that travel down the spinal cord to the motor nuclei in the contralateral ventral horn.

Motor unit – One motor neuron and all the muscle fibres innervated by that motor neuron.

Motor unit discharge rate – The frequency at which an action potential is released from the motor neuron.

Motor unit recruitment – A force grading mechanism by which additional motor units are activated in response to an increase in force demand.

Motor unit remodeling – The process by which orphaned muscle fibres, typically type II are reinnervated by type I motor units.

Node of Ranvier – Non-myelinated region of the axon of a neuron dense with ion channels for the regeneration of action potentials during saltatory conduction.

Neutral – The anatomical position of the wrist in which the palm is facing medial (Appendix C).

Primary motor cortical neurons – The collection of nerve cells located anterior to the central sulcus in the frontal lobe of the brain responsible for planning, organization, and initiation of voluntary movement.

Pronated – The anatomical position of the wrist in which the palm is facing posterior (Appendix C).

Resting membrane potential – The voltage (-70mV to -90mV) of an excitable cell observed at electrochemical equilibrium.

Saltatory conduction – The transmission of an action potential from one Node of Ranvier to another Node of Ranvier through the myelinated axon without disruption.

Sarcopenia – The age-related reduction in size of type II muscle fibres.

Supinated – The anatomical position of the wrist in which the palm is facing anterior (Appendix C).

Task-dependent subpopulations – A group of motor units within a motor neuron pool that respond similarly to a specific direction or type of force production or movement.
CHAPTER 1
REVIEW OF LITERATURE

1.0 Functional Organization of Neuromuscular System

Initiation of voluntary muscle contraction begins in the primary motor cortical area of the brain with the formation of a representation of the movement that specifies the kinematics and dynamics of the intended action (Kandel, Schwartz, & Jessel, 2000). From this area and other supraspinal sources, input converges on the cell body of the alpha motor neuron (αMN) via the lateral corticospinal tract in the ventral horn of the spinal cord to generate an electrochemical potential, that if it reaches threshold, transmits an action potential along the αMN, through the neuromuscular synapse, across the invaginated synaptic cleft, down a network of t-tubules, and to the muscle fibres (Kandel et al., 2000). In a few words, the signal to contract a muscle is transmitted from the brain, to the spinal cord, to the motor neuron, and finally to the muscle to contract. In this situation the αMN and muscle fibre constitute the motor unit. The formal definition of a MU is one αMN and all the muscle fibres innervated by that αMN, and this unit has been termed the ‘final unit of force production’ (Kandel et al., 2000). In this manner, only one αMN in an individual MU innervates a muscle fibre, but many muscle fibres in a MU are innervated by one αMN.

In addition to supraspinal input, other excitatory and inhibitory connections influence the probability of an excitatory threshold potential being reached at the cell body of the αMN in the ventral horn of the spinal cord. The gamma motor neuron (γMN) which is co-activated with the αMN is responsible for maintaining the sensitivity of the primary sensory afferents of the muscle; the muscle spindle. The muscle spindle
apparatus, which is imbedded parallel to the muscle fibres, is sensitive to changes in length and the rate of change in length of the muscle. Changes in the muscle spindle apparatus are transmitted to the αMN via the Ia and II afferent fibres (Figure 1), thereby influencing the resting membrane potential and in turn the probability of reaching threshold of an action potential. Another sensory organ, the golgi tendon organ, which is responsible for sensing changes in tension also conveys information to the αMN via the Ib afferent fibre. Input from the Ia and II afferents is excitatory to the αMN, while Ib afferent input may be excitatory or inhibitory (Figure 1). Together, the net synaptic input from these numerous sources must exceed the excitatory threshold potential of the αMN before an action potential, the electrochemical command to contract the muscle is achieved, and inevitably transmitted all or none down the axon (Kandel et al., 2000). The axon is surrounded by an insulating myelinated sheath that speeds conduction of the action potential along the axon (Kandel et al., 2000). However, non-myelinated regions dense with ion channels exist along the axon in order for the action potential to be regenerated and continue its propagation to the axon terminal for transmission to a subsequent neuron or muscle fibre. These non-myelinated regions are called Nodes of Ranvier (Kandel et al., 2000). Transmission of an action potential down an axon from one Node of Ranvier to the next without failure is a process termed saltatory conduction.

Motor units (MU) are grouped in the ventral horn of the spinal cord according to which muscles they innervate where the flexor muscles are dorsal to the extensor muscles in the lateral ventral horn. A motor neuron pool is the term used to describe the population of MU that innervate a muscle (McArdle, Katch, & Katch, 2007). Each motor neuron pool contains two types of MU, fast and slow. Fast MU contain more muscle
fibres (~100-500) and subsequently produce larger forces, but are more susceptible to fatigue (McArdle et al., 2007). Slow MU contain fewer muscle fibres (~10-100), produce less force, but are fatigue resistant (McArdle et al., 2007). The muscle fibres belonging to both types of MU in a motor neuron pool are arranged heterogeneously in the muscle (Kandel et al., 2000). However, muscle fibres belonging to a MU typically only occupy a small region within the muscle (ter haar Romeny, Denier van der Gon, & Gielen, 1984).

![Figure 1](image)

Figure 1. The spinal connections of the i) αMN, and ii) γMN projecting from the spinal cord to the muscle and iii) Ia afferent fibres projecting from muscle to spinal cord. The intrafusal fibre, which lies parallel to the extrafusal fibre is indicated (1). The dorsal horn of the spinal cord (2) is the region in which the afferent fibres and supraspinal input converges upon the motor nucleus (3) of the αMN (i).

1.1 Production, Control, and Steadiness of Force

Many force grading mechanisms of the neuromuscular system contribute to the production, control, and steadiness of voluntary movement. Motor unit recruitment and MU discharge rate are traditionally utilized to characterize the behaviour of a MU.
Motor unit recruitment is defined as the process by which MU are activated in response to a voluntary supraspinal input or sensory stimulation (McArdle et al., 2007). The activation of a MU is not random, rather it follows a pattern of orderly recruitment as described by Henneman's Size Principle (1957). Orderly recruitment states that slow MU are recruited initially during increasing force production and followed by fast MU as the force demands exceed the capabilities of the slow MU (Figure 2B). The relationship between MU recruitment and force production is curvilinear (Figure 2B). However, during recruitment of the slow MU at the beginning of force production, the rate of rise in force is less than that during recruitment of the faster MU at higher force levels (Figure 2B).

Motor unit discharge rate is defined as the frequency at which active MU elicit action potentials (McArdle et al., 2007). Modulation of MU discharge rate follows MU recruitment (Erim, Beg, Burke, & de Luca, 1999). Newly recruited MU initially discharge at a higher rate than earlier recruited MU. (Erim et al., 1999) (Figure 3). However, earlier recruited MU are able to sustain higher MU discharge rates for longer than newly recruited MU (Erim et al., 1999) (Figure 3). The relationship between MU discharge rate and force production is roughly linear (Figure 2A). The rate of increase in MU discharge initially rises following recruitment as force increases. As more MU are recruited at medium force levels, the rate of increase of MU discharge slows (Figure 2A). Following recruitment of all available MU at higher force levels, the rate of increase of MU discharge again continues to rise (Figure 2A).
Figure 2. MU recruitment and discharge relationships to force. A. Left Panel: A linear increase in force is associated with an increase in mean firing rate. However, the mean firing rate increases in three phases. The initial rise in mean firing rate increases at a faster rate than the second phase. The second phase rises at a slower rate due to the recruitment of additional MU. Once all the MU are recruited at high force levels, the mean firing rate increases at a rapid rate once again. A. Right Panel: The linear increase in force associated with the increase in mean firing rate presented in the left panel. B. Left Panel: The addition of two MU to create a rise in force. B. Right Panel: A curvilinear increase in force is associated with an increase in MU recruitment. The initial rise in force production due to recruitment occurs at a slower rate than the latter because slow MU are recruited first and due to the small number of muscle fibres they innervate, less force is produced. The rate of force production increases as faster MU are recruited and more muscle fibres contribute to the resulting force. (Adapted from Erim et al., 1999)
Figure 3. Initial mean firing rates observed during ramp muscle contraction. Recently recruited MU discharge at lower mean firing rates than previously recruited MU. (Adapted from Erim et al., 1999)

A number of studies have investigated MU activity and corresponding isometric force steadiness (Burnett, Laidlaw, & Enoka, 2000; Galganski, Fuglevand, & Enoka, 1993; Graves, Kornatz, & Enoka, 2000; Laidlaw, Bilodeau, & Enoka, 2000; and Tracy, Maluf, Stephenson, Hunter, & Enoka, 2005). Although dependent upon the muscle group studied and physical activity status of the subject, force steadiness generally increases with increasing target force (Enoka, Christou, Hunter, Kornatz, Semmler, Taylor, & Tracy, 2003). Most investigations of force steadiness have focused on knee extensors where fine control is typically not employed or on intrinsic hand muscles where fine motor control is essential (Enoka et al., 2003). However, execution of fine hand movements is dependent upon larger multi-directional arm muscles, such as the biceps brachii. The limited literature for this muscle suggests for an isometric contraction, the extent of force fluctuations is dependent upon the target force (Enoka et al., 2003). These
studies were isometric and conducted at optimal joint angles for force production which is atypical of functional daily movement.

1.2 Relative Contributions of Elbow Flexors

Con contractions about the elbow and wrist joint are dependent upon not only the direction of the movement (i.e. flexion, extension, wrist rotation) but also by the relative activation of the elbow flexors, extensors, pronators, and supinators (Figure 4). During isometric flexion in a neutral wrist position, the main contributors to force are the brachialis, brachioradialis, and biceps brachii (Buchanan, Rovai, & Rymer, 1989). However, application of flexion in combination with pronated or supinated provides different relative contributions from the elbow flexors. The relative activation of the brachialis and brachioradialis, as measured using surface EMG, is very similar and consistent through the movement range of supinated to pronated when combined with flexion (Buchanan et al., 1989). On the other hand, the biceps brachii demonstrates clear task-dependent recruitment and surface EMG activity (Buchanan et al., 1989; van Zuylen, Gielen, & Denier van der Gon, 1988). Surface EMG recording of the short head of the biceps brachii indicates that it is most active during flexion combined with supinated and least active during flexion combined with pronated (Buchanan et al., 1989). The long head of the biceps brachii is most active during flexion when combined with pronated and least active during flexion combined with supinated in recordings of surface EMG (Buchanan et al., 1989). As expected, the triceps brachii are relatively inactive during flexion (Buchanan et al., 1989). Although these surface EMG data are necessary to gain a global representation of muscle activity, they are somewhat limited (Merletti, Farina, Gazzoni, & Schieroni, 2002; and Merletti, Lo Conte, Cisari, & Actis,
In order to fully understand force production and control single MU activity must be considered.

Figure 4. Flexors of the elbow. The two heads of the biceps brachii, the long head and the short head (1), originate from two different locations. The long head of the biceps brachii originates from the supraglenoid tubercle of the scapula while the short head of the biceps brachii originates from the coracoid process of the scapula. Both heads insert at the radial tuberosity (2). The long head inserts medial to the insertion of the short head. The other two elbow flexors, the brachialis and brachioradialis lie beneath the superficial biceps brachii. The pronator teres opposes supinated during flexion (Buchanan et al., 1989). (Adapted from Behnke, 2001)

1.3 Task-Dependent Subpopulations of Motor Neuron Pools

Subpopulations of MU may become active within a motor neuron pool relative to the task performed (Denier van der Gon, Gielen, & ter haar Romeny, 1983; Denier van der Gon, ter haar Romeny, & van Zuylen, 1985; Jongen, Denier van der Gon, & Gielen, 1989; Tax, Denier van der Gon, & Erkelens, 1990a; Tax, Denier van der Gon, Gielen, & Kleyne, 1990b; ter haar Romeny, Denier van der Gon, & Gielen, 1982; ter haar Romeny Denier van der Gon, & Gielen, 1984; and van Zuylen et al., 1988). A task-dependent
subpopulation of the motor neuron pool is a group of MU that respond to activation parameters in a similar manner relative to the muscle's movement type or direction (Figure 5). For example, during walking, different subpopulations of MU become active depending on whether the individual is planting their foot or swinging their foot forward (Loeb, 1985). However, when activated, these task-dependent subpopulations are recruited according to Henneman's Size Principle (1957). The threshold for MU recruitment in the biceps brachii have been shown to differ depending upon whether elbow flexion is combined with supinated or combined with exorotation of the wrist. In particular, recruitment thresholds of the short head of the biceps brachii are lower when the wrist is in a supinated position (van Zuylen et al., 1988). Moreover, when the intended force is uni-directional, recruitment thresholds are higher than if the force is multi-directional (ter Haar Romeny et al., 1982). Given that muscle fibres of a MU usually occupy a small portion of the cross-sectional area of the muscle (ter Haar Romeny et al., 1984), the existence of task-dependent subpopulations of the motor neuron pool provides an additional means in which force may be produced only in the desired line of force production. In this way, task-dependent subpopulations of MU eliminate inappropriate movements, for instance supinated torques during elbow flexion (Buchanan et al., 1989). Inappropriate supinated torques may be attributed to the anatomical configuration of the biceps brachii. Both heads of the biceps brachii insert onto the radial tuberosity (Figure 4) and during contraction of the short head of the biceps brachii, more supinated is generated because its insertion is more medial than that of the long head of the biceps brachii (Buchanan et al., 1989). Thus, simultaneous activation of a pronator is required to eliminate the influence of the supinated force on the flexion task.
(Buchanan et al, 1989). In comparison, when the wrist is in a neutral position, MU recruitment thresholds of the short head of the biceps brachii occur later to prevent supinated force, whereas a wrist in the supinated position would require MU recruitment thresholds to occur earlier to generate both torques simultaneously. This MU recruitment position dependency is likely to influence force steadiness of multi-directional muscles, but has not been considered to date.

![Motor Unit Recording](image)

**Figure 5.** MU activity during shortening and lengthening contractions of the biceps brachii. An additional MU is recruited at onset of shortening contraction (right panel) suggesting the presence of a task-dependent MU behaviour. (Adapted from Tax, Denier van der Gon, Gielen, & van den Tempel, 1989)

The existing literature related to identification of subpopulations of MU has only focused on recruitment. Yet, modulation of discharge rate is an important component of force generation and control and has been studied in response to increases in force, and in isometric compared with isotonic contractions, not as a function of changes in task (Tax et al, 1989; Tax et al, 1990a). Understanding task-dependent discharge behaviour of MU subpopulations during changes in wrist position would elucidate additional information with respect to force development, control, and steadiness in healthy young adults and
most importantly changes in wrist position are more representative of functional movement than single planar isometric contractions.

1.4 Age-Related Neuromuscular Adaptation

Investigation of age-related alterations in the neuromuscular system has focused on a wide range of areas from sarcopenia, muscle weakening, MU remodeling, including age-related decrease in MU discharge rate, and alterations in fibre type proportions (Rice, Cunningham, Patterson, & Rechnitzer, 1989; Klein, Marsh, Petrella, & Rice, 2003; Deschenes, 2004; and Galea, 1996). Beginning at the contractile level, age-related muscle mass reductions, termed sarcopenia, have been observed in the biceps brachii, with a 27% increase in non-contractile tissue in the arm flexors with increasing age (Rice et al., 1989). More rapid muscle fibre size reduction and loss have also been reported in type II fibres of old adults compared with young adults in the thigh muscles (Lexell, 1995). Yet, recent studies in the elbow flexors reported no difference in fibre type composition (Klein et al., 2003; and Deschenes, 2004). These age-related adaptations in contractile tissue contribute to some of the loss of strength and power observed in older adults. Studies of the elbow flexors indicate that older adults (ages 60-88) are 33-49% weaker than young adults (Doherty, Vandervoort, Taylor, & Brown, 1993; and Jakobi, Connelly, Roos, Allman, & Rice, 1999), but this reduction in strength does not result from an inability to exert a maximal effort (Jakobi & Rice, 2002). When given sufficient practice and with utilization of the twitch interpolation technique, activation of the elbow flexors of young and old adult muscle averages 90-98% suggesting that it is not a lack of motivation or central drive that contributes to a decrease in force (Jakobi & Rice, 2002).
In addition to changes in muscle, neural adaptations also occupy an important role in age-related declines in strength and power. Reduction in the number of MU begins before the age of 30 and accelerates after 60 years of age (Galea, 1996; Rice, 2000). The functional effects of a reduction in MU number generally appear at approximately age 65, intensifying past the age of 80 (McNeil, Doherty, Stashuk, & Rice, 2006) and it is only into the 9th decade of life that these MU losses have a significant impact upon maximal contractile force (McNeil et al., 2006). Although declines in motor neuron number occur the orphaned fibres, typically type II, undergo re-innervation by type I motor neurons termed MU remodeling (Rice, 2000), thus MU number decreases but the size of the remaining MU increase. During MU remodeling, behaviour of re-innervated type II fibres begins to resemble that of the type I fibre (Rice, 2000).

MU remodeling may also play an important role in the loss of voluntary force control in older adults. An increase in the number of muscle fibres belonging to a remodeled slow MU increases the force production capability of each individual MU (Rice, 2000). The larger force per MU may contribute to the manifestation of variability in fine control as the ability to recruit smaller increments of force as observed in young adults is diminished in old adults due to the remodeling process. The variability may emerge as an inability to move smoothly between positions or as an inability to sustain a level of constant force. Other factors that may possibly contribute to a decrement in force production and control with age include: increased corticospinal excitability thresholds, increased electrical resistance of the cell membrane, and decreases in conduction velocity of the motor neuron (Rice, 2000). Both increased corticospinal excitability thresholds and electrical resistance of the cell membrane are studied in vivo in animals. In order to
consider conduction velocity, stimulation must be administered, and because it seemingly
disrupts recruitment order it is not feasible technically in its application to voluntary force
control and steadiness at the present time.

MU discharge behaviour in old adults has been studied extensively in the small
intrinsic muscles of the hand, specifically the first dorsal interosseus (FDI) (Barry,
Pascoe, Jesunathadas, & Enoka, 2007; Burnett et al., 2000; Erim et al., 1999; Galganski
et al., 1993; Laidlaw et al., 2000; Laidlaw, Hunter, & Enoka, 2002; Tracy et al., 2005).
In the FDI, with increasing age, reductions in MU discharge rate are observed and this is
accompanied by an increase in variability of MU discharge rate (Erim et al., 1999;
Laidlaw et al., 2000; and Tracy et al., 2005). Other studies have investigated muscles of
the thigh and leg (Christie & Kamen, 2006; Connelly, Rice, Roos, & Vandervoort, 1999;
Erim, DeLuca, Mineo, & Aoki, 1996; Kamen, Sullivan, Rubenstein, & Christie, 2006;
Knight & Kamen, 2005; and Tracy & Enoka, 2002), and the elbow flexors (Erim et al.,
1999; Laidlaw et al., 2000; and Tracy, Mehoudar, Ortega, and Enoka, 2002). The limited
literature pertaining to the elbow flexors in older adults suggests a reduction in mean
discharge rate across force levels (Erim et al., 1999; and Jakobi et al., 1999) and greater
MU discharge variability in older adults compared with young (Tracy et al., 2002). In
these studies acknowledgement of whether MU were recorded in the short or long head
was not made.

Many studies have demonstrated a decrease in force steadiness in old adults
compared to young adults (Burnett et al., 2000; Galganski et al., 1993; Graves et al.,
2000, Laidlaw et al., 2000; and Tracy et al., 2005) and greater MU discharge variability
has been implicated as a contributor to decreased force steadiness (Laidlaw et al., 2000;
and Tracy et al., 2005). The relationship between decreased force steadiness and MU discharge variability has been observed across a broad range of muscles and forces in young and old adults (Tracy et al., 2002; Tracy et al., 2005), but not in the elbow flexors (Enoka et al., 2003). A reduction in force steadiness in the biceps brachii of old adults compared with young adults is equivocal (Graves et al., 2000, Tracy & Enoka, 2002), but as force increases steadiness also increases in young adults (Semmler, Tucker, Allen, & Proske, 2007). Thus, another means of force control, possibly task-dependent MU discharge behaviour, may be influenced by the aging process and contribute to the reduction in force steadiness.

1.5 Summary of Literature

The principle of orderly recruitment and discharge rate continues to prevail as the primary mechanisms grading force production during muscle contraction. However, task-dependent subpopulations have been proposed and seem to depend on the type and direction of the force exerted. Task-dependent subpopulations of MU within a motor neuron pool have been identified in young adults primarily by a trend in recruitment thresholds across MU. However, the existence of subpopulations in older adults has never been studied and the discharge behaviour of task-dependent subpopulations has not been reported for isometric contractions in either young or old adults for more than one wrist orientation.
1.6 References


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Tracy, B.L., & Enoka, R.M. (2002). Older adults are less steady during submaximal isometric contractions with the knee extensor muscles. *J Appl Physiol, 92*(3), 1004-1012.


CHAPTER II
PURPOSE AND HYPOTHESES

2.0 Purpose

To determine whether age alters the existence or control strategy of task-
dependent motor neuron pools in the biceps brachii and whether force steadiness differs
between young and old adults. Specifically, MU activity in the long head and short head
of the biceps brachii was quantified in young adults during isometric elbow flexion in
three wrist positions (neutral, supinated and pronated) and compared with old adults (>80
years) to determine whether force steadiness is related to MU discharge rates or
variability.

2.1 Specific Objectives (So)

1. To record MU discharge rates of the long head and short head of the biceps
   brachii during three different wrist positions.

2. To assess task-dependent MU discharge rates in young and old adults.

3. To measure MU discharge rates across subpopulations of the motor neuron
   pool in young and old adults.

4. To determine MU discharge rate variability in young and old adults for the long
   and short head of the biceps brachii.

5. To evaluate force steadiness in three different positions in the same young and old
   adults.

2.2 Research ($H_1$) and Null ($H_0$) Hypotheses

Note: Numbers correspond to specific objectives.

2. $H_1$: Motor unit task-dependency will be evident based upon differential MU
discharge rates in three wrist positions during isometric elbow flexion in
young and old adults.

$H_0$: Task-dependency will not be observed because MU discharge rates will be
similar between the three wrist positions.
3. \( H_I \): A reduction in mean MU discharge rates will be observed in old adults compared with young adults across subpopulations of the motor neuron pool.

\( H_0 \): No difference in mean MU discharge rates will be observed between young and old adults across subpopulations of the motor neuron pool.

4. \( H_I \): Older adults will exhibit more variable MU discharge rates than young adults.

\( H_0 \): No difference in MU discharge rate variability will be observed between young and old adults.

5(i). \( H_I \): Old adults will demonstrate less force steadiness than young adults.

\( H_0 \): No difference in force steadiness will be observed between young and old adults.

5(ii). \( H_I \): The order from least steady to most steady wrist position during elbow flexion will be the same in young and old adults.

\( H_0 \): No difference in order of steadiness of wrist positions during elbow flexion will be observed between young and old adults.
CHAPTER III
MANUSCRIPT

3.0 Introduction

Motor unit (MU) recruitment occurs in an orderly fashion and is governed by the Size Principle (Henneman, 1957). This phenomenon is maintained in older adults in light of sarcopenia and age-related MU remodelling (Erim, Beg, Burke, & de Luca, 1999; and Rice, 2000). However in young adults, MU activation has also been reported to be task-dependent, whereby subpopulations of a motor neuron pool operate independent of other subpopulations (Jongen, Denier van der Gon, & Gielen, 1989; Tax, Denier van der Gon, Gielen, & van den Tempel, 1989; Tax, Denier van der Gon, & Erkelens, 1990a; Tax, Denier van der Gon, Gielen, & Kleyne, 1990b; ter haar Romeny, Denier van der Gon, & Gielen, 1982; ter haar Romeny, Denier van der Gon, & Gielen, 1984; and van Zuylen, Gielen, & Denier van der Gon, 1988) by demonstrating activation strategies that are specific to the type of contraction (isometric, isotonic) or direction (pronated, supinated) of force production. Prior studies indicate that MU recruitment thresholds in multidirectional muscles of young adults such as the biceps brachii are both direction- and type-dependent, but that orderly recruitment is maintained in task-dependent MU according to the Size Principle (Tax et al., 1990a; ter haar Romeny et al., 1982; and ter haar Romeny et al., 1984). Task-dependent MU discharge rates have also been reported for shortening, lengthening, and isometric contractions of the biceps brachii in a neutral wrist orientation in young men (Tax et al. 1989; and Tax et al., 1990a). Although MU discharge task-dependency is prevalent for contraction type, no study has determined whether task-dependent MU discharge rates are evident consequent to a position change.
in the wrist, which alters the anatomical configuration of each elbow flexor muscle and in turn the total force produced. The concept of task-dependent MU subpopulations affords the neuromuscular system with an additional means whereby force may be controlled. Investigation of MU discharge behaviour following position change is important because functional human movement often involves one or more changes in limb position during performance of a task, and the contribution of the short and long head of the biceps brachii to force production is dependent upon wrist orientation in each movement (Buchanan, Rovai, & Rymer, 1989).

Although an age-related decrease in MU discharge rates increase in MU variability has been demonstrated and it has been well established that the ability to maintain a steady force declines with increasing age, the concept of task-dependent changes in MU activity with respect to force steadiness is unknown (Barry, Pascoe, Jesunathudas, & Enoka, 2007; Burnett, Laidlaw, & Enoka, 2000; Connelly, Rice, Roos, & Vandervoort, 1999; Enoka, Christou, Hunter, Kornatz, Semmler, Taylor, & Tracy, 2003; Erim et al., 1999; Galganski, Fuglevand, & Enoka, 1993; Laidlaw, Bilodeau, & Enoka, 2000; Laidlaw, Hunter, & Enoka, 2002; Tracy & Enoka, 2002; and Tracy, Maluf, Stephenson, Hunter, & Enoka, 2005). It has been suggested that non-uniform activation of muscles does not influence force steadiness (Laidlaw et al, 2002; and Enoka et al., 2003). However, surface EMG was utilized to derive these relationships, and although this recording technique is valuable and extensively utilized to assess peripheral and central contributions to movement, it is not without limitations (Farina, Merletti, & Enoka, 2004) which include MU properties of recruitment and discharge rates which are well known to change with age. Thus, the contribution of muscle activation to force
steadiness may have been masked. Moreover, this concept of non-uniform activation has only been studied in the uni-directional force generating bipennate first dorsal interosseus and not a large multi-directional muscle such as the biceps brachii (Laidlaw et al. 2002). Because the recruitment and rate-coding strategies employed are dissimilar between these muscles (Seki & Narusawa, 1996) the contribution of MU activity to force steadiness is also likely to differ between these muscles. Moreover, considering that MU activity is task-dependent in young (Tax et al., 1990a) and that force output is related to the activation of different anatomical contractile compartments (Nichols, 1994) it is possible that the contributions of individual MU to force steadiness will be position dependent and vary between muscle heads. The purpose of the present study was to assess whether task-dependent MU discharge behaviour is evident in the biceps brachii in young and old adults based upon changing muscle orientation via alterations in wrist position. Secondly, the relation between MU discharge behaviour and force steadiness was evaluated in young and old adults through studying two separate heads (long and short) of the multi-directional biceps brachii during low force isometric contractions in three wrist positions.

3.1 Methods

Subjects

Force and muscle activity were recorded from the heads of the long (LBB) and short (SBB) biceps brachii in six young (22 ± 3yrs) and six old men (84 ± 3yrs) free of stroke, neuromuscular/orthopedic limitations and not participating in regular exercise training programs. As well, persons trained in fine motor co-ordination (musicians) were excluded from this study. Informed written consent (Appendix A) was obtained from all
subjects prior to participating and all procedures were approved according to the policies and guidelines of the Research Ethics Board at the University of Windsor and conformed to the declaration of Helsinki (Appendix B).

3.2 Experimental Protocol

Two laboratory visits were required. The first visit consisted of an orientation, physical activity assessment, and surface EMG recording of the task in seven conditions. Subject characteristics of age, height, weight, and dominant hand as well as the Yale Physical Activity Survey and Paffenbarger Questionnaire were administered by the same experimenter. The second visit consisted of intramuscular recording of the task in seven conditions.

Experimental Setup

In both visits, subjects were seated in a firm high-back chair and visual feedback for the task was provided by a 19 inch flat screen computer monitor (1280 x 1024 resolution) one metre in front of the subject and 15° below eye level. The subject’s non-dominant left elbow was positioned at 100° flexion, arm abducted 10°, and shoulder flexed forward 15°. The left hand grasped a wrist apparatus that consisted of a handle fastened to a bearing which enabled supinated and pronated of the wrist while maintaining a consistent elbow and wrist position. The underside of the wrist apparatus was attached to a linear calibrated force transducer (Transducer Techniques, Temecula, CA) which was connected to a horizontal platform to measure application of upward and downward forces. The wrist apparatus position was adjustable for individual arm length. The elbow was placed on a molded support that attached to a second adjustable force transducer to measure elbow depression (Transducer Techniques, Temecula, CA). The
right arm rested on the right leg across the lap. Knee angle was maintained at approximately 110° by foot rests at the appropriate height. Subjects were instructed to remain in an upright position with their back resting against the chair throughout each session and for every contraction.

**Experimental Procedures**

First Visit

Subjects performed three maximal voluntary contractions (MVC) of the biceps brachii and triceps brachii where force and EMG were measured, and three maximal voluntary exertions for the brachioradialis where only EMG was assessed. Each contraction was sustained for three seconds and separated by one minute rest. The biceps brachii MVC data was used to establish the target force for the tracking task. Subjects proceeded to practice the tracking task in seven conditions (Table 1). The task involved five distinct phases indicated by six cursors labelled 1 through 6, and three wrist orientations: a) neutral, b) supinated, and c) pronated. (Figure 6). A graphical sequence editor (Spike 2 version 6.03, Cambridge Electronics Design, Cambridge, England) was programmed to output a template of the task to be performed. Beginning at cursor 1, elbow flexion force was slowly increased in a ramp contraction lasting 7.5s ending at cursor 2 at 10% MVC. Between cursor 2 and cursor 3, 10% MVC was maintained for 7.5s. Between cursor 3 and cursor 4, position was either maintained or changed while elbow flexion force was maintained at 10% MVC for 5s. Following the transition phase, 10% MVC was held for 7.5s till they reached cursor 5. After reaching cursor 5, a descending ramp contraction lasting 7.5s was initiated until a zero force level at cursor 6 was evident. Verbal feedback and encouragement were provided for all tasks by the
same investigator. Following practice, surface electrode placement sites were prepared by gently abrading the skin with a coarse brush and swabbing the skin with 70% isopropyl alcohol pads (Webcol, Tyco Medical, Montreal, Quebec). Surface electrodes were placed on the long head (LBB) and short head (SBB) of the biceps brachii, the triceps brachii, and the brachioradialis with an inter-electrode distance of 2cm. Palpations and functional contractions were performed to ensure proper placement. Signal inspection was utilized for isolation of the desired muscle and presence of crosstalk. Following verification of an isolated signal from the desired muscles, surface EMG was recorded during the seven conditions (Table 1). To protect against fatigue, each trial was separated by 30 - 60s rest.

Figure 6. Graphical sequence editor output and representative force output for a young man (22 years old). The solid line represents the output of the graphical sequence editor which plateaus at 10% of the subject's MVC. The variable line depicts the corresponding elbow flexion force produced by the subject. Cursors one through six are represented by vertical dotted lines and labelled with the appropriate number.

Second Visit

Maximal voluntary contraction data from the first visit was used to program the output of the graphical sequence editor at 10% MVC for the second visit. The subject's skin was prepared by cleaning the surface area with 70% isopropyl alcohol pads.
Intramuscular electrodes were inserted into the two heads of the biceps brachii. Similar to the first visit, subjects performed the seven tracking tasks but intramuscular EMG was recorded from the LBB and SBB of the biceps brachii. Multiple trials of each were often required in order to record the same MU in all phases of the tracking task especially following a change in wrist position. In a situation where the MU became undetectable, the wrist position was returned to neutral and the presence of the tracked unit verified, or the intramuscular electrode manipulated until another stable MU was identified and the tasks continued (Table 1). The time allotted to each constant force phase of the task was 7.5s, and the order of contractions was randomized.

<table>
<thead>
<tr>
<th>Condition</th>
<th>1st Constant Force Phase (7.5s)</th>
<th>2nd Constant Force Phase (7.5s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>NN</td>
<td>N</td>
<td>N</td>
</tr>
<tr>
<td>SS</td>
<td>S</td>
<td>S</td>
</tr>
<tr>
<td>PP</td>
<td>P</td>
<td>P</td>
</tr>
<tr>
<td>NS</td>
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<td>NP</td>
<td>N</td>
<td>P</td>
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<tr>
<td>SN</td>
<td>S</td>
<td>N</td>
</tr>
<tr>
<td>PN</td>
<td>P</td>
<td>N</td>
</tr>
</tbody>
</table>

Conditions were identified by two letters where the first letter corresponded to the first phase between 17.5s and 25s (1st constant force phase) and the second letter identified the second phase between 30s and 37.5s; N, neutral; S, supinated; P, pronated. The transition period was 25s to 30s.

**3.3 Physiological Assessment**

**Force**

Elbow flexion and extension force were recorded using a MLP-150 linear calibrated force transducer (68kg) (Transducer Techniques, Temecula, CA) with a sensitivity of 32.6N/mV. The linearly calibrated transducer at the elbow (23kg) (Transducer Techniques, Temecula, CA) was not utilized in the analytical measurements, rather as a means to ensure that all forces recorded were not due to shoulder depression creating forearm leverage and thus false flexion force output. Force signals were
collected using a V72-25 resistive bridge strain gauge transducer coupler (Coulbourn, Allentown, Pennsylvania) and converted from an analog to digital format by a 16-bit 1401 plus A/D converter (CED, Cambridge, England) at a sampling rate of 100Hz. Average force, standard deviation of the force, and coefficient of variation were determined for the 17.5s-25s phase and the 30s-37.5s phase.

**Surface EMG**

Two pairs of 4mm Ag/AgCl surface electrodes were placed on the belly of the biceps brachii at the midpoint of the humerus. One pair was placed medially and the other laterally to measure activity of the LBB and the SBB of the biceps brachii, respectively. Two ground reference electrodes for the LBB and SBB were placed on the olecranon process of the ulna. One pair of 4mm Ag/AgCl surface electrodes was also placed above the musculo-spiral groove of the humerus over the triceps brachii, and another pair distal to the lateral epicondyle of the humerus over the brachioradialis. A ground reference electrode for each bipolar electrode configuration was placed on the acromion process of the scapula. All electrode pairs were separated by an interelectrode distance of 4cm. The surface EMG signal was amplified (x1000) with an isolated bioamplifier (Coulbourn Electronics, Allentown, Pennsylvania), band-pass filtered (13Hz-1kHz) (Coulbourn, Allentown, Pennsylvania), sampled at 1024Hz (1401 plus, CED, Cambridge, England), and converted from analog to digital format (CED, Cambridge, England). Surface EMG was expressed relative to the maximal EMG recorded for each muscle. EMG from all muscles was rectified and averaged (root mean square) over a window that corresponded to the force record for each 7.5s of the first and second phase of the tracking task and subsequently normalized to the maximum EMG to
enable comparison between subjects and muscles (Spike 2 version 6.03, CED, Cambridge, England).

**Intramuscular EMG**

Intramuscular tungsten microelectrodes (FHC, Bowdoin, Maine) were used to record MU activity. The tungsten microelectrodes were approximately 3.0-5.0 cm in length and had a diameter of approximately 125 µm. Two tungsten microelectrodes were inserted into the biceps brachii penetrating the fascia and subcutaneous tissue approximately 1.0-3.0 cm. One electrode was placed between the surface electrodes on the SBB and a second tungsten microelectrode was inserted into the LBB between the second pair of Ag/AgCl surface electrodes. The common reference electrode for the SBB was placed over the medial shaft of the humerus and for the LBB approximately 4 cm proximal to lateral epicondyle. A ground reference electrode for each bipolar electrode configuration was placed on the acromion process of the scapula. Following insertion, the tungsten microelectrode’s depth and orientation were altered to optimize the individual MU recordings and subsequently provide collection of different MU. Upon initiation of muscular contraction during the ramp phase of the task, individual MU were identified as they were recruited and microelectrode placement adjusted and stabilized. Intramuscular EMG data were pre-amplified at the site of recording (x10) with a custom made amplifier (Don Clarke, University of Windsor, Windsor, Ontario), then amplified (500-1000x) and filtered (20 Hz-10 kHz) (Coulbourn, Allentown, Pennsylvania). All intramuscular EMG data was converted from analog to digital format by a 16-bit A/D converter (1401 plus, CED, Cambridge, England) at a rate of 10 kHz.
3.4 Motor Unit Data Processing

After data acquisition, off-line analysis was conducted with a customized software package (Spike 2 version 6.0, CED, Cambridge, England). MU recordings were analyzed with a template matching algorithm (Spike 2 version 6.0 waveform discrimination, CED, Cambridge, England) where individual MU action potentials were identified by waveform shape, and firing behaviour by comparing and overlaying sequential action potentials with respect to temporal and spatial characteristics (Figure 7, 8). However, visual inspection of MU action potentials was the final determinant in deciding whether a MU action potential belonged within a train of potentials. Criterion for MU trains to be included within the group analysis of total MU was a continuous discharge of at least six consecutive MU action potentials with less than 30% variability of discharge rate (Fuglevand, Winter, & Patla, 1993). MU discharge times (s) were automatically recorded for each MU action potential and the MU discharge rate (Hz), inter-spike intervals (ISIs) and MU discharge variability (standard deviation of discharge rates) were calculated using customized software (Spike 2 version 6.03) based upon the absolute MU discharge times. An activity ratio was also calculated in order to determine whether the number of MU recruited and continuously discharging differed between the first and second phase, wrist positions or heads of the biceps brachii. An active MU was assigned the number ‘one’ and an inactive MU was assigned the number ‘zero’, and the ratio calculated (number of active units / total number of active and inactive units for each situation) and expressed in arbitrary units (au). An activity ratio of one indicates that the number of MU active are equal to the total number of MU recorded for that situation (phase, wrist position and head), thus the closer the activity ratio to one, the
greater the number of active MU recorded in a situation (L. Stitt, statistical consultation, July 12, 2007).

3.5 Statistical Analysis

The dependent measures analyzed included coefficient of variation of force (au) (standard deviation / mean force), average EMG (%MVE) ((average root mean square / average root mean square of MVC)*100), MU discharge rate (Hz), standard deviation (SD) of MU discharge rates and MU activity ratio (au). A four factor analysis of variance with a repeated measures design was used to compare the dependent variable of average surface EMG for the between-subject factor of age (young, old), and the within subject factors of wrist positions (neutral, supinated, pronated), muscles (SBB, LBB, brachioradialis, triceps brachii) and tracking period (first phase, second phase). Force steadiness (coefficient of variation) was evaluated with a 2 (age) x 3 (wrist position) x 2 (phase) repeated measures ANOVA. MU discharge rate and variability were assessed within the first phase with a three way repeated measures ANOVA (age x wrist position x head of the biceps brachii).

A preliminary analysis was done to assess the differences in MU activity between phases a four way repeated measures ANOVA (age x wrist position x phase x head of the biceps brachii) was conducted. This four way interaction was not significant (p=0.61) because of parallel response to changes in wrist position for the young and old men, thus age was made a covariate for subsequent analyses (L. Stitt, statistical consultation, July 12, 2007) of task-dependent MU behaviour. The succeeding analysis of covariance involved a three factor ANCOVA (wrist position x head of biceps brachii x phase) with repeated measures on phase to assess the dependent variables of MU activity.
(active/inactive rate, discharge rates, discharge variability). Linear regressions were performed on the coefficient of variation of force and MU discharge rate, as well as the coefficient of variation of force and MU discharge rate variability for each of the three wrist positions (neutral, pronated and supinated) in the SBB and the LBB to examine whether an increase in MU discharge behaviour was associated with a change in force steadiness. All statistical procedures were performed using SPSS version 15.0 and Microsoft Excel XP Version. An alpha level of 0.05 was employed for all statistical comparisons and Tukey Post Hoc Tests and T-tests were performed to post hoc test possible combinations of dependent variables based on the interaction examined. Because there are expected differences between muscles, due to the agonist-antagonist, and synergist contributions to force production, Post Hoc Analyses were not performed on muscle. Data in the text and tables are presented as values ± standard deviation of the mean (SD), whereas Figures are reported as values ± standard error of the mean (SEM).
Figure 7. Template matching algorithm and spike discrimination. The triangles in the upper window indicate the selected acceptable width of a MU action potential. Two horizontal bars (not shown) are utilized to establish the positive and negative threshold that the action potential must exceed to meet the criteria of a ‘counted’ action potential. The lower window displays the motor unit action potential template for three separate MU observed in this recording. The recorded MU action potentials from the data overlay in the respective template.

Figure 8. Waveform discrimination output. The top trace represents the output of template matching algorithm. Each box represents a different motor unit (1, 2, 3). The corresponding original data recording can be seen in the bottom trace.

3.6 Results

Subject Characteristics
The six young men (21.8±2.7 years) were significantly taller (p=0.02) than the six old men (83.5±2.9 years) but similar in body mass (p=0.25) and all men were right hand dominant. Young and old men participated in comparable levels of activity for all subsections (routines, vigorous, leisurely, moving, standing, sitting, and stairs) of the Yale Physical Activity Survey (p=0.49) (Table 2). However, young men (9891.8±3695.1au) had significantly greater scores than old men (2948.7±1254.7au) on the Paffenbarger Physical Activity Questionnaire (p=0.002). Apart from the expected differences in maximal elbow flexion force between the young men (228.5±58.0N) and old men (121.1±59.7N) (p=0.005), the relative forces exerted for the tracking task were similar between young (9.66±0.36%MVC) and old men (9.30±0.30%MVC) (p=0.08), and the force produced by the young and old men did not change between the first phase and second phase of the tracking task (p=0.9).

Table 2. Subject characteristics of young and old men.

<table>
<thead>
<tr>
<th></th>
<th>Young (n=6)</th>
<th>Old (n=6)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (years)</td>
<td>22 ± 2.7*</td>
<td>84 ± 2.9</td>
</tr>
<tr>
<td>Height (cm)</td>
<td>182.9 ± 8.8*</td>
<td>171.0 ± 5.9</td>
</tr>
<tr>
<td>Body Mass (kg)</td>
<td>79.6 ± 6.6</td>
<td>74.2 ± 8.4</td>
</tr>
<tr>
<td>MVC (N)</td>
<td>228.5 ± 58.0*</td>
<td>129.6 ± 40.9</td>
</tr>
<tr>
<td>Routines (au)</td>
<td>12046 ± 7782.9</td>
<td>6796 ± 4159.9</td>
</tr>
<tr>
<td>Vigorous (au)</td>
<td>39 ± 15.2</td>
<td>35 ± 24.1</td>
</tr>
<tr>
<td>Leisurely (au)</td>
<td>16 ± 9.4</td>
<td>25 ± 15.5</td>
</tr>
<tr>
<td>Moving (au)</td>
<td>9.0 ± 3.7</td>
<td>7.5 ± 1.6</td>
</tr>
<tr>
<td>Standing (au)</td>
<td>4.4 ± 1.7</td>
<td>4.0 ± 1.3</td>
</tr>
<tr>
<td>Sitting (au)</td>
<td>2.8 ± 1.1</td>
<td>2.0 ± 0.0</td>
</tr>
<tr>
<td>Stairs (au)</td>
<td>7.4 ± 5.9</td>
<td>8.2 ± 5.6</td>
</tr>
</tbody>
</table>

Values are means ± SD. * Significantly different from old; cm, centimeter; kg, kilogram; N, Newton; au, arbitrary units
**Force Steadiness**

The three way repeated measures ANOVA for steadiness did not reveal a significant interaction of wrist position, phase and age (p=0.50), but did reveal an interaction of age and phase (p<0.005) (Figure 9A) and significant main effects for phase (p<0.005) and age (p<0.005). Force steadiness in the old men (CV=0.073±0.040au) was approximately four times less in the first phase (17.5s-25s) than young men (CV=0.017±0.010au) and approximately three times less steady in the second phase (Figure 9A). No difference in force steadiness was observed in young men between the first and second phase (p=0.46) (Figure 9A) while old men increased force steadiness 33% in the second phase (p=0.03) (Figure 9A). A trend for force steadiness to differ between wrist positions (p=0.08, 1-β=0.5) was observed. Both young and old men were least steady in the neutral position (0.043±0.004au), followed by the pronated position (0.039±0.005au), and were steadiest in the supinated position (0.034±0.004au) (Figure 9B).

**Figure 9.** Force steadiness for the two phases in young and old men (A) and for the three wrist positions (B). (A). Force steadiness in young men (filled bars) did not differ between phases but old men (open bars) demonstrated significant improvement (p=0.0210^-4) in force steadiness in the second phase. Force steadiness differed between young and old men in the first phase (p=0.0610^-4) and second phase (p=0.03). (B). Force steadiness for the three wrist positions of neutral (horizontal bars), pronated (filled bars) and supinated (diagonal bars) demonstrated no main effect of wrist position (p=0.08), however the neutral position (CV=0.0430±0.004au) tended to be least steady whereas the supinated position (0.034±0.004au) was steadiest. Values are means + SEM. * p<0.05, + p=0.08.
Surface EMG

Surface EMG was analyzed for neutral (n=55), supinated (n=36), and pronated (n=28) positions for the first phase and second phase of the tracking task. The 2 (age) x 4 (muscle) x 3 (wrist position) x 2 (phase) repeated measures ANOVA was not significant (p=0.56) for average EMG (AEMG). The three way interaction between phase, age and muscle (p=0.02) was significant with a main effect for age (p=0.001). Post hoc analysis indicated that the AEMG was greater in the old men compared with young men for the SBB (63%), LBB (57%) and triceps (35%), whereas the brachioradialis did not differ between old and young men (10%) (p=0.27). The three way ANOVA for phase, age and wrist position was significant (p=0.04). Average EMG did not change between the first phase and the second phase for the SBB, LBB, brachioradialis, and triceps brachii (p=0.64, p=0.77, p=0.14, and p=0.97, respectively). In the young men the supinated position had higher activity than the neutral (p=0.001) and pronated position (p=0.03) for the SBB (Figure 10A). No other differences between wrist positions were observed in the young men. However, in the old men for the SBB and the LBB the pronated position had higher muscle activity than the neutral (p=0.05 and p=0.02, respectively) and neutral also had higher AEMG than supinated (p=0.03) for the SBB (Figure 10A,B). There were no difference observed in the triceps AEMG between wrist positions (Figure 10C), but in the brachioradialis for old men the supinated position had higher EMG than the pronated position (p=0.02) (Figure 10D).
Figure 10. Average EMG for (A) the SBB, (B) LBB, (C), triceps brachii, and (D) brachioradialis. (A). The supinated position (diagonal bars) had higher activity in young men compared with the neutral (horizontal bars) (p=0.001) and pronated position (filled bars) (p=0.03). In the old men, the pronated position had higher muscle activity than the neutral (p=0.05) and supinated positions (p=0.03). (B). In old men, the pronated position had higher AEMG compared with the neutral position (p=0.02). (C). No differences between positions were observed in young and old men for the triceps brachii. (D). The AEMG for the pronated position was less than the supinated position in old men (p=0.02). Data are shown as means + SEM. * p<0.05.

Intramuscular EMG

MU Activity during First Phase

A total of 84 MU recordings were analyzed for the first phase of the task from both the short head (n=48) and long head (n=36) of the biceps brachii in the neutral (n=44), supinated (n=18), and pronated (n=22) wrist positions in young and old men. Young men (13.91±3.41Hz) had higher MU discharge rates compared with old men (10.90±2.86Hz) across all wrist positions and in both heads of the biceps brachii (p=0.02^{10.3}). The standard deviation (SD) of MU discharge was also higher in young men (3.65±1.10Hz) compared with old men (3.07±0.49Hz) (p=0.002) for both the SBB
(p=0.045) and LBB (p=0.09^{10-2}). The 2 (age) x 3 (wrist position) x 2 (head of biceps brachii) ANOVA for MU discharge rate and SD of MU discharge rate yielded a non-significant interaction (p=0.23) and there were no main effects observed. Because MU discharge rates responded similarly within each head of the biceps brachii to changes in wrist position, age was made a covariate in analysis of discharge rate and variability (L. Stitt, statistical consultation, July 12, 2007).

Two way ANCOVA for head of biceps and wrist position with age as a covariate identified a significant interaction between head of biceps brachii and wrist position (p=0.04), and main effects of head of biceps brachii (p=0.001) and wrist position (p=0.03) (Figure 11). MU discharge rates in the SBB did not differ between the neutral and supinated positions (p=0.25) but the pronated position (8.06±2.59Hz) was lower compared with the neutral (11.69±3.59Hz) (p=0.003) and supinated (12.78±4.09Hz) (p=0.003) positions (Figure 11). In the LBB, MU discharge rate was significantly greater in the neutral (14.70±2.39Hz) position compared with the pronated (13.32±2.02Hz) and supinated (11.96±1.91Hz) positions (p=0.02 and p=0.009, respectively). In order to assess task-dependency, the main effect of head of biceps brachii was investigated, and the LBB demonstrated greater MU discharge rates than the SBB (p=0.001) in the neutral and pronated positions, but not in the supinated position (p=0.28). The SD of MU discharge rates were assessed with a 2 (head of biceps brachii) x 3 (wrist position) ANCOVA with age as the covariate. No significant interactions (p=0.33) or main effects (p=0.35) were observed. The discharge variability in the LBB was 3.50±0.58Hz, whereas the SBB was 3.24±1.05Hz. In the neutral, pronated and supinated positions discharge variability was 3.4±0.90Hz, 3.3±0.70Hz, and 3.2±1.05Hz, respectively.
Figure 11. MU discharge rates of the SBB (open bars) and LBB (filled bars) in the neutral, pronated, and supinated positions. MU discharge rates of the LBB were greater in the neutral position compared with the pronated position (p=0.02) and the supinated position (p=0.009). In the SBB the pronated position had significantly lower MU discharge rates than both the neutral (p=0.003) and supinated (p=0.003) positions. Data are shown as means + SEM. * p<0.05.

Comparison of MU Activity between First and Second Phase

As a consequence of the recruitment and derecruitment of MU in response to a change in wrist position between the first and second phase, individual MU were coded for each phase as active or inactive. The units that were active were coded ‘one’, and when the unit was not present during the first phase, or became de-recruited during the second phase it was coded ‘zero’ (L. Stitt, statistical consultation, July 12, 2007). Active to inactive ratios were calculated for each head between the two phases. Following coding of MU, a 2 (head) x 3 (position) x 2 (phase) repeated measures ANCOVA with age as a covariate established a head by position interaction (p=0.004) and a main effect of head of biceps brachii (p=0.01). The active/inactive ratio for the SBB and LBB between the first phase and second phase did not differ (p=0.32) demonstrating that the number of MUs present for each head between phases was similar. In the SBB
active/inactive ratio was much greater in the neutral (0.79±0.42au) and supinated positions (0.66±0.49au) than the pronated position (0.17±0.42au) (p=0.002 and p=0.03, respectively) (Figure 12), indicating that fewer MU were active in the pronated position in the SBB. No differences between active/inactive ratio of the LBB were observed between wrist positions (Figure 12). Based upon the differential presence of MU between wrist positions in the SBB, these data support the premise that task-dependent MU activation exists in the biceps brachii for young and old adults.

Figure 12. Active to inactive ratio of MU for the SBB (open bars) and LBB (filled bars) in the neutral, pronated and supinated positions. Active/inactive ratio for the neutral and supinated positions were greater than pronated position for the SBB (p=0.002 and p=0.03, respectively). No differences were observed between wrist positions for active/inactive ratio of the LBB. Data are shown as means + SEM. * p<0.05.

MU discharge rate and variability also demonstrated task-dependency. A head by position interaction was observed (p=0.03) resulting from higher MU discharge rates in the pronated position in the LBB compared with SBB (p=0.002). There was a main effect of position observed for MU discharge rate (p=0.02). In the neutral (12.35±3.99Hz) and supinated (14.00±5.17Hz) positions, MU discharge rates were greater than the pronated (8.34±2.35Hz) position (p=0.09^{10-6} and p=0.05^{10-4}, respectively)
Repeated measures ANCOVA for head of biceps brachii, wrist position, and phase, with age as a covariate revealed a head x position interaction (p=0.03). In the SBB, MU discharge variability was less in the pronated position than in the neutral (p=0.0210^{-2}) and supinated (p=0.0310^{-2}) positions (Figure 14). No differences in MU discharge variability were observed between wrist positions for the LBB.

**Figure 13.** MU discharge rates for the neutral, pronated and supinated positions. MU discharge rates were significantly lower in the pronated position than in the neutral (p=0.0910^{-4}) or supinated (p=0.0510^{-4}) positions. Data are shown as means + SEM. * p<0.05.

**Figure 14.** MU discharge variability of the SBB (open bars) and LBB (filled bars) in three wrist positions. MU discharge variability in the neutral and supinated positions were greater than in the pronated position (p=0.0210^{-2} and p=0.0310^{-2}, respectively). Data are shown as means + SEM. * p<0.05.
MU Discharge Behaviour/ Force Steadiness Relationship

The relationship between MU discharge behaviour and force steadiness was evaluated by plotting the MU discharge rate and SD of MU discharge rate with respect to force steadiness (coefficient of variation of force) for each wrist position during each phase for the LBB and SBB. During the first phase ($r = 0.97$) and second phase ($r = 0.98$), an increase in MU discharge rate of the LBB was closely related with a reduction in force steadiness (Figure 15A,B), whereas no relationship was observed between MU discharge rate and force steadiness for either phase in the SBB (Figure 15A,B). A similar pattern emerged for the relationship between MU discharge variability and force steadiness. A strong positive relationship between SD of MU discharge rate and coefficient of variation was observed during the first phase ($r = 0.96$) and second phase ($r = 0.99$) for the LBB (Figure 15C,D), but no relationship was observed between MU discharge variability and force steadiness in the SBB for the first phase ($r = 0.39$) and second phase ($r = 0.65$) (Figure 15C,D).
3.7 Discussion

It is well established that old adults are weaker than young adults and that force steadiness is less in the former compared with the latter. However, very few studies have examined force steadiness in the elbow flexors in young and old adults (Graves et al., 2000) and no study has determined the influence of wrist position on isometric steadiness. This study confirms results of prior studies of age-related muscle weakness and decrease in MU discharge rates, and contributes to the equivocal literature of reduced force steadiness in old compared with young adults for the elbow flexors (Graves et al.,
2000; and Tracy et al., 2002). The new findings extend the aging and force steadiness literature to include: 1) MU discharge rates are dependent upon wrist position; 2) MU discharge rates subsequent to a change in wrist position adopt behaviour that is reflective of the new position; 3) force steadiness is closely related to MU discharge rates and MU discharge variability in the LBB but not the SBB; 4) based upon differences in MU discharge rate between the three wrist positions task-dependency is evident in young and old adults. These results of task-dependent MU activity were observed in both heads of a muscle that produces multi-directional forces which establishes that force steadiness is a product of multiple functional compartments and that non-uniform activation likely influences the extent of force steadiness.

Strength and MU Discharge Rates

Age-related loss of MVC force in the elbow flexors has been documented previously and the 47% loss observed in this study is similar to prior studies that have investigated men in the 9th decade (Allman & Rice, 2003; and Jakobi et al., 1999) and greater than studies that have considered old men in the 7th – 8th decade (Lavender & Nosaka, 2007; and Klein, Rice, & Marsh, 2001). The mean MU discharge rate in the young men (13.91 ± 3.4Hz) and old men (10.90 ± 2.8Hz) for the 10% of MVC target force differed (p=0.0113). The limited literature pertaining to MU discharge rates in the biceps brachii at 10% MVC suggests a depression of MU discharge rates in old men compared with young men (Jakobi et al., 1999). Although the underlying mechanism for the age-related decrease in MU discharge rates is equivocal (Rice, 2000), this study establishes that in both the short and long head of the biceps brachii an age-related difference exists in low-threshold discharge rates of a multi-directional muscle.
Force Steadiness in Young and Old Men

Steadiness has consistently been shown to increase as force increases for the first dorsal interosseous and knee extensors (Burnett et al., 2000; Galganski et al., 1993; Laidlaw et al., 1999; Laidlaw et al., 2000; Tracy & Enoka, 2002; and Tracy et al., 2002). Results are equivocal with respect to the relationship between contractile force and steadiness in the biceps brachii (Tracy et al., 2002; Semmler, Tucker, Allen, & Proske, 2007) and with respect to age-related differences in this muscle (Graves et al., 2000; Tracy, Dinenno, Jorgensen, & Welsh, 2007; and Lavender & Nosaka 2007). Typically, for elbow flexion tasks the wrist is placed in a neutral position, whereas in the present study force steadiness was measured in three wrist orientations. An age-related decrease in force steadiness was observed in the biceps brachii for all wrist positions, with the neutral position eliciting the greatest difference between young and old, followed by pronated and supinated positions. Thus, force steadiness is not only dependent upon age, type and intensity of the contraction (Enoka et al. 2003) but limb position, which influences the amount of force each muscle contributes to the task.

Familiarization to the tracking task was provided in order to eliminate a practice effect, and while steadiness in the old men improved in the second phase, it still remained more variable than young men. Steadiness did not change between phases in the young men. It has been demonstrated that visuomotor correction contributes to force fluctuation in old adults (Tracy et al. 2007) and it is possible that the old men may have used less visuomotor correction during the first phase thus improving force steadiness in the second phase. Tracy et al. (2007) has demonstrated that force fluctuations increase when
old adults use visuomotor correction but when no visual feedback was provided steadiness increased. Steadiness in old adults may also differ between the first and second phase because of the difficulty in transitioning from the ramp portion to the constant force position for the first phase of the tracking task. It has been demonstrated that when old adults step down from a platform antagonist muscle activation occurs earlier and at a higher level relative to young adults (Hortobagyi & DeVita, 2000). In this particular task the visual cue (cursor two) to change from a ramp contraction may have augmented antagonist activity in anticipation of the upcoming plateau in force and thereby reduced steadiness in the first phase. As a compensatory measure, older adults increased muscle activity of the biceps brachii, as demonstrated by the greater level of surface EMG recorded; this may have resulted in greater force fluctuations in the first phase.

**Force Steadiness and Task-Dependent Muscle Activity as a Function of Wrist Position**

No study to date has investigated the effect wrist position has on force steadiness. Graves et al. (2000) investigated force steadiness during isometric elbow flexion in a neutral hand position across a range of target forces and utilized surface EMG to study the SBB, LBB, brachioradialis, and triceps brachii. At 10% MVC, no age-related decline in force steadiness was evident and the relative activation of the SBB, LBB, or brachioradialis did not differ between old and young (Graves et al., 2000). In the present study, differential activation of the biceps brachii was observed and force steadiness declined in old adults compared with young adults. Disparate observations with respect to age-related declines in elbow flexion force steadiness likely result from the old men in the present study being 84 ± 2.9 years, whereas Graves et al. (2000) studied old men with
an average age of 71.2±7.8 years. McNeil, Doherty, Stashuk & Rice, (2005) reported that age-related adaptations in MU activity can be detected at 60 years of age, but the functional consequence of this adaptation with respect to absolute force does not manifest until the 9th decade. A second possible explanation for the age-related decline in force steadiness might relate to grasping the manipulandum. Greater reductions in force steadiness during grasp have been demonstrated in old adults compared with young adults due to an increase in grasp force in the old adults (Cole, 1991; and Kinoshita & Francis, 1996).

Generally, force steadiness increases as force increases (Enoka et al. 2003), and in this particular experiment a consistent pattern of steadiness was observed between young and old adults between the three wrist positions. The supinated position was the steadiest position, followed by the pronated and finally the neutral position in young and old adults alike. Surface EMG from the SBB and LBB elicited the greatest levels of activation in the supinated position compared with the neutral and pronated positions, which suggests that the levels of steadiness may be related to the amount of activation. This finding is in agreement with Buchanan et al. (1989) who observed increases in biceps brachii activation in a supinated position compared with neutral and pronated positions concluding with utilization of surface EMG techniques that muscle activation is position dependent in young adults. This study corroborates the situation dependent activity, but extends the literature to old adults. Nevertheless, because surface EMG is also highly dependent upon the amount of subcutaneous tissue and conduction velocity of the motor neurons any attempt at describing a relationship between surface EMG and force
steadiness would be premature and perhaps misleading (Merletti et al., 2002) without the combined utilization of single MU measures.

Utilization of indwelling electrodes placed inside the muscle to measure MU activity can be readily employed to understand contribution of the peripheral nervous system to force control due to the all or none principle of MU activation and continuity between the nerve and muscle. Furthermore, the embedded aspect of the electrode into the muscle under investigation enables isolation of activity between muscles that are anatomically and functionally related such as the short (SBB) and long head (LBB) of the biceps brachii. Prior investigation of recruitment thresholds of the biceps brachii during independent isometric elbow flexion as well as flexion coupled with supinated or pronated determined that the threshold of MU activation depends on which wrist position was assumed (van Zuylen et al., 1988), and in turn MUs were classed as task-dependent based upon the contribution to elbow flexion, or a combination of elbow flexion and supinated. The head from which the MU was recorded was not identified and therefore a comparison between heads is not possible. In the present study, both heads of the biceps brachii were studied and task-dependent MU behaviour was evident as the SBB had higher discharge rates during the supinated and neutral positions and much lower in the pronated position irrespective of age. In contrast, task dependency in the LBB was demonstrated via higher discharge rates in the pronated and neutral positions, compared with the supinated position. Considering the SBB originates on the coracoid process of the scapula and inserts onto the radial tuberosity greater MU discharge rates in the neutral and supinated positions are evident because this portion of the muscle is in direct anatomical alignment for force production and thus MU discharge rates would be higher.
to achieve the optimal level of control. In the pronated and neutral positions, contraction creates torsion as the muscle fibres of the SBB pull the radial tuberosity to the midline of the humerus. In this situation, additional activation would be required by a pronator to counteract the torsion created by contraction of the SBB resulting in an inefficient force production (Buchanan et al., 1989). Conversely, the LBB originates from the supraglenoid tubercle of the scapula and inserts onto the radial tuberosity and in the pronated and neutral position when LBB MU discharge rates are greatest, the line of force production of the LBB is more direct than during supinated. When MU discharge rates were compared between the LBB during pronated and SBB during supinated, which is the anatomical position where MU activation should be optimal there was no difference between the two heads (p=0.44) of the biceps brachii.

In addition to MU discharge rates differing between heads and wrist position, force steadiness also differed between positions. The neutral position was the least steady of the three positions, possibly because activation of a pronator in the neutral position was employed to minimize the extraneous supinated torque of the SBB. This would create a situation where the two opposing forces (supinated and pronated) would impair the ability to maintain a steady elbow flexion force. Another possible explanation for differences in force steadiness between positions is task-dependent MU discharge variability. Discharge variability has been reported to be a central factor in the reduction in force steadiness for isometric and anisometric contractions of the first dorsal interosseous (Laidlaw et al., 2000; and Tracy et al., 2005). The SD of MU discharge rates in the present study was found to be largest for the LBB in the pronated and neutral positions and significantly less in the supinated positions. In contrast, the SBB
demonstrated greater MU discharge variability in the supinated and neutral positions than during pronated. Based upon these observations and the association between MU discharge variability increasing with a rise in discharge rates (Vaillancourt, Larsson, & Newell, 2002) the neutral position should be the least steady due to the greater discharge variability in both heads during this type of contraction.

Elucidation of differences in force steadiness due to the contribution of each head of the biceps brachii was evaluated by the linear regression analysis between the SD of MU discharge of the SBB and LBB, and the coefficient of variation of force corresponding to each wrist position. It was determined that the SBB expressed no relationship to force steadiness (Figure 15C,D), whereas an increase in LBB SD of MU discharge was highly correlated with an increase in coefficient of variation and thus a reduction in force steadiness (Figure 15C,D). Consequently, the reduction in force steadiness in the neutral position compared with the supinated position was likely due to greater MU discharge variability in the LBB during neutral compared with supinated. It has been suggested that increases in MU discharge variability are associated with changes in the synaptic contribution of inputs to the motor neuron pool (Laidlaw et al. 2000), and recent investigation of elbow flexor activation via transcranial magnetic stimulation has revealed inhibitory input to the biceps brachii following contraction of a forearm pronator and excitatory input to the biceps brachii prior to initiation of supinated (Gerachshenko & Stinear, 2007). In this study discharge variability was lowest during supinated for the LBB, likely due to the decrease in pronator activity in this position resulting in less inhibitory input to the biceps brachii which in turn manifests as greater force steadiness in supinated.
Effect of Position Change on Task-Dependent MU Behaviour

The active/inactive ratio of MUs in the present study illustrates task-dependent behaviour of the SBB and LBB. When position change occurs MU activity for each 'new' position reflects the activity that would have occurred in the first phase had the position been executed subsequent to the ramp-up in force. For example the supinated position produced the greatest active/inactive ratios in the SBB, whereas the pronated position was associated with reduced active/inactive ratios. Similarly, the LBB in the neutral and pronated positions displayed slightly larger active/inactive ratios than the supinated position. When evaluated with respect to force steadiness the LBB did not incur a large reduction in MU discharge rates or variability in its least active position (supinated) where steadiness was greatest. Thus, MU activity reflects the position of the wrist and influences force control.

Evidence of task-dependent recruitment following a change in wrist position in this study of old and young adults supports prior data from the study of young men (van Zuylen et al., 1988), but extends task-dependency to MU discharge rates and variability. Establishment of task-dependent MU behaviour during isometric elbow flexion provides information regarding the neural strategies employed when maintaining a constant position, but does not offer any insight into MU activity during functional movement. Investigation of MU behaviour during isometric contractions with a change in position provides an initial step to a better understanding of purposeful movement. Studies to date have been limited to MU recruitment during isometric elbow flexion and extension (Denier van der Gon et al., 1983; ter haar Romeny et al., 1982; ter haar Romeny et al., 1984; and van Zuylen et al., 1988) or MU recruitment and discharge rates during
isometric elbow flexion, and isotonic shortening and lengthening contractions of the biceps brachii (Denier van der Gon et al., 1985; Tax et al., 1989; Tax et al., 1990a; and Tax et al., 1990b) in young adults. Although the literature on task-dependency is narrow, it likely occupies a significant role in neural control of force production and possibly stems from alterations in the excitatory and inhibitory synaptic input in the spinal cord. Loeb (1985) identified differential activation of functional subunits of eight bifunctional thigh muscles in cats and hypothesized that cutaneous afferent pathways likely provide the excitatory or inhibitory input to subpopulations of MUs in order to achieve differential or task-dependent activation (Loeb, 1985).

3.8 Conclusion

The LBB and SBB of young and old men exhibit task-dependent MU discharge behaviour as observed when wrist position changes between neutral, pronated, and supinated positions during isometric elbow flexion. Force steadiness, which is greater in young men compared with old men, is also task-dependent for both age groups. The supinated position is the steadiest followed by the pronated position and finally the neutral position. Moreover, the relationship between force steadiness and MU discharge behaviour is exclusive to the LBB in that an increase in the MU discharge variability of the LBB is associated with a reduction in force steadiness. The results of this study emphasize that when force steadiness is considered, investigation of all muscles and their functional compartments is necessary.
3.9 References


Tracy, B.L., & Enoka, R.M. (2002). Older adults are less steady during submaximal isometric contractions with the knee extensor muscles. *J Appl Physiol, 92*(3), 1004-1012.


CHAPTER IV
CONCLUSION AND RECOMMENDATIONS

4.0 Conclusion

The previously described (Jakobi et al. 1999) reduction in MU discharge rate for
the biceps brachii in old men compared with young men was confirmed in this study. To
date MU discharge variability has not been reported in the biceps brachii, but in the first
dorsal interosseous and knee extensors variability is greater in old men compared with
young men (Laidlaw et al, 2000; Rice, 2000; and Tracy et al., 2005). This study which
evaluated both heads of the biceps brachii (LBB and SBB) refutes findings from other
muscles in that there is an age-related increase in MU discharge variability. Moreover,
in young men force steadiness is greater compared with old men and this observation is
consistent across the three wrist positions studied (neutral, pronated, supinated).
Irrespective of age, force steadiness appears to be related to MU discharge behaviour of
the LBB and not the SBB.

4.1 Summary of Specific Objectives (So)

1. To record MU discharge rates of the long head and short head of the biceps
   brachii during three different wrist positions.
   
   Achieved: MU discharge rates of the long head and short head of the biceps
   brachii were recorded in the neutral, supinated, and pronated
   positions

2. To assess task-dependent MU discharge in young and old adults.

   Achieved: Because MU discharge rates and MU discharge variability were
   unique to each wrist positions (neutral, pronated and supinated)
   task-dependent behaviour is evident in young and old men.

3. To measure MU discharge rates across subpopulations of the motor neuron
   pool in young and old adults.
Achieved: Within the long head and short head of the biceps brachii of young and old men, MU discharge rates were recorded.

4. To determine MU discharge rate variability in young and old adults for the long and short head of the biceps brachii.

Achieved: MU discharge variability was determined to be greater for young adults compared with old adults in the long head and short head of the biceps brachii.

5. To evaluate force steadiness in three different positions in the same young and old adults.

Achieved: An order of force steadiness (supinated>pronated>neutral) was demonstrated in young and old adults.

4.2 Summary of Research (H1) and Null (H0) Hypotheses

Note: Numbers correspond to specific objectives.

2. \( \text{H}_1: \) Motor unit task-dependency will be evident based upon differential MU discharge rates in three wrist positions during isometric elbow flexion in young and old adults.

Accepted

\( \text{H}_0: \) Task-dependency will not be observed because MU discharge rates will be similar between the three wrist positions.

Rejected: MU discharge behaviour of the long head of the biceps brachii was greater in the neutral position than in the pronated or supinated positions. In the short head of the biceps brachii, MU discharge rates in the neutral and supinated positions were greater than in the pronated position.

3. \( \text{H}_1: \) A reduction in mean MU discharge rate will be observed in old adults compared with young adults across subpopulations of the motor neuron pool.

Accepted

\( \text{H}_0: \) No difference in mean MU discharge rate will be observed between young and old adults across subpopulations of the motor neuron pool.

Rejected: Young men had greater MU discharge rates in both heads of the biceps brachii.
4. **$H_1$:** Old adults will exhibit more variable MU discharge rates than young adults.

Rejected: No differences between young and old men existed for MU discharge variability.

**$H_0$:** No difference in MU discharge rate variability will be observed between young and old adults.

Accepted

5(i). **$H_1$:** Old adults will demonstrate less force steadiness than young adults.

Accepted

**$H_0$:** No difference in force steadiness will be observed between young and old adults.

Rejected: Force steadiness was greater in young men compared with old men across all wrist positions.

5(ii). **$H_1$:** The order from least steady to most steady wrist position during elbow flexion will be the same in young and old adults.

Accepted

**$H_0$:** No difference in order of steadiness of wrist positions during elbow flexion will be observed between young and old adults.

Rejected: Young and old men were least steady in the neutral position and steadiest in the supinated position.

4.3 Limitations and Recommendations

The first and foremost limitation of the present study is the assumption that the sample population of MU recorded from the long and short head of the biceps brachii is representative of the entire population within each head of the biceps brachii. Although a large number of MU were recorded, the biceps generally has greater than five hundred MUs. Therefore, there is the possibility that the MU recorded from each head of the biceps brachii behave similarly to each other and differently from other MUs within the motor neuron pool.
The stability of recordings was acceptable for the analysis and provided interesting data regarding MU discharge behaviour, but use of fine wire intramuscular electrodes may have improved the clarity and stability of the recordings. Fine wire electrodes maintain similar bipolar configurations as the tungsten microelectrodes, but are more flexible and stable than tungsten microelectrodes. The tip of a fine wire electrode resembles a small hook which effectively maintains the position of the fine wire electrode during contraction. Moreover, the reference electrode for the tungsten microelectrode is located on the surface of the skin, while the reference electrode for the fine wire electrode is located intramuscularly nearer to the recording electrode providing greater clarity in the recordings.

Greater than expected brachioradialis activity was observed in the study and may have been a consequence of the design of the wrist apparatus. The subject was required to grasp a handle in order to produce an elbow flexion force. It is possible that the additional brachioradialis activity was a consequence of finger flexion in order to grasp the handle. Design of a wrist apparatus without a handle that still permitted elbow flexion in the three wrist positions may eliminate the presence of finger flexion and resolve the issue of greater than expected brachioradialis activity. However, there is the possibility that brachioradialis activity is in fact greater at the elbow angle studied. Insertion of a microelectrode and assessment of more than one elbow position would provide a better indication of the activity of the brachioradialis and offer greater insight as to the influence of finger flexion and elbow angle on brachioradialis activity.

As mentioned in the discussion, familiarization to the tracking task was provided to subjects prior to collection of data. Following familiarization, the tracking ability of
the old adults still improved as the tracking task continued. Thus, a practice effect may have been observed which was not accounted for in the design of the study. The period of familiarization may need to be extended in order for old adults to achieve similar levels of tracking ability throughout the entire tracking task.

The tracking task was performed at 10% of each subject's MVC and thus the results of this study are limited to low forces. MU discharge behaviour has been demonstrated to differ depending on force (Erim et al., 1999) and because the biceps brachii recruits up to 80% (Seki & Narusawa, 1996) it is possible that results would differ at high force levels. It is recommended that further investigation of task-dependent MU discharge behaviour include a range of target forces.

Isometric elbow flexion was only performed in the present study. Previous literature has demonstrated differences in MU discharge behaviour of the biceps brachii during isometric contractions, and isotonic shortening and lengthening contractions about the elbow joint (Tax et al., 1989; and Tax et al., 1990a). Although a change in wrist position provides information about MU discharge behaviour and force steadiness, it was limited to a joint angle of ~110° and stable wrist positions. Inclusion of a change in elbow joint angle and measurement of MU activity during the position change may offer greater insight into more functional movements of the biceps brachii.

Lastly, earlier studies have investigated the pronator teres of the forearm during elbow flexion, but never by combining MU discharge rates and force steadiness (Buchanan et al., 1989; and van Zuylen et al., 1988). A more comprehensive investigation of the elbow flexors, forearm supinators and pronators during force
production may provide a greater understanding of the interactions of these muscle
groups during dynamic force production.
Title of Study: Task dependent subpopulations of motor units in older adults.

You are asked to participate in a research study conducted by a student investigator: Brad Harwood and advisor: Dr. Jennifer Jakobi from the Department of Kinesiology, Faculty of Human Kinetics (x2473) at the University of Windsor. The results of this study will contribute to Brad Harwood’s thesis project to complete the candidacy for a Masters of Human Kinetics degree.

If you have any questions or concerns about the research, please feel free to contact the student investigator

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PURPOSE OF THE STUDY

The study aims at identifying neuromuscular control strategy differences between young and old adults.

PROCEDURES

If you volunteer to participate in this study, we would ask you to do the following things:
- Volunteer approximately two hours of your time in over 1-4 visits separated by 2 - 5 days.
- Allow the application/insertion of electrodes to your forearm and upper arm area while seated in a chair. Tungsten micro-electrodes are approximately the diameter of a horse hair and feel like a pin prick upon insertion. The sensation is similar to acupuncture.
- Perform both strong and weak contractions of the forearm.

POTENTIAL RISKS AND DISCOMFORTS

A possible risk associated with the use of tungsten micro-electrodes is infection. It is recommended to seek the advice of a physician or family doctor if an infection does occur. This risk will be reduced by the creation of a sterile environment and by following experimental precautions regarding data collection. To-date, no incidents of infection have been reported in a laboratory utilizing this technique.

POTENTIAL BENEFITS TO SUBJECTS AND/OR TO SOCIETY

You will not receive monetary gain from participation. Participants will benefit from exposure to neurophysiological techniques and gain a greater understanding of controlling force, as well as how and why it changes with age.

PAYMENT FOR PARTICIPATION

Participants will not receive payment for this study.

CONFIDENTIALITY

Any information that is obtained in connection with this study and that can be identified with you will remain confidential and will be disclosed only with your permission. All data from participants will be collected and coded for anonymity at the beginning of each study session.

PARTICIPATION AND WITHDRAWAL

You can choose whether to be in this study or not. If you participate in this study, you may withdraw at any time without consequences of any kind. The investigator may choose to withdraw you from his research if circumstances arise which warrant doing so. Any persons with musculoskeletal disorders, injury, other neurological disorders or painful neuropathy, myopathy, severe cardiovascular disease, have a pacemaker, recovering from surgery, alcoholism, pregnancy, or extreme physical activity patterns will not be considered suitable for this study and will be excluded.

FEEDBACK OF THE RESULTS OF THIS STUDY TO THE SUBJECTS

Following data collection, contact information will be recorded for later notification. Results from the study will be available on Dr. Jennifer Jakobi’s web site.
http://uwindsor.ca/ijakobi, or by mail. If you would prefer a copy of the manuscript be mailed to you, please provide mailing information.

SUBSEQUENT USE OF DATA

This data will be used in subsequent studies.

Do you give consent for the subsequent use of the data from this study?

☐ Yes  ☐ No

RIGHTS OF RESEARCH SUBJECTS

You may withdraw your consent at any time and discontinue participation without penalty. If you have questions regarding your rights as a research subject, contact: Research Ethics Coordinator, University of Windsor, Windsor, Ontario, N9B 3P4; telephone: 519-253-3000, ext. 3916; e-mail: lbunn@uwindsor.ca.

SIGNATURE OF RESEARCH SUBJECT/LEGAL REPRESENTATIVE

I understand the information provided for the study Task dependent subpopulations of motor units in older adults as described herein. My questions have been answered to my satisfaction, and I agree to participate in this study. I have been given a copy of this form.

______________________________
Name of Participant

______________________________  ________________________
Signature of Participant  Date

SIGNATURE OF INVESTIGATOR

These are the terms under which I will conduct research.

______________________________  ________________________
Signature of Investigator  Date
APPENDIX B

University of Windsor Research Ethics Board Approval

This is to inform you that the University of Windsor Research Ethics Board (REB), which is organized and operated according to the Tri-Council Policy Statement and the University of Windsor Guidelines for Research Involving Human Subjects, has granted approval to your research project on the date noted above. This approval is valid only until the Project End Date.

A Progress Report or Final Report is due by the date noted above. The REB may ask for monitoring information at some time during the project's approval period.

During the course of the research, no deviations from, or changes to, the protocol or consent form may be initiated without prior written approval from the REB. Minor change(s) in ongoing studies will be considered when submitted on the Request to Revise form.

Investigators must also report promptly to the REB:
1) changes increasing the risk to the participant(s) and/or affecting significantly the conduct of the study;
2) all adverse and unexpected experiences or events that are both serious and unexpected;
3) new information that may adversely affect the safety of the subjects or the conduct of the study.

Forms for submissions, notifications, or changes are available on the REB website: www.uwindsor.ca. If your data is going to be used for another project, it is necessary to submit another application to the REB.

We wish you every success in your research.

Dr. Maurie Mixson

Research Ethics Board

c: Dr. Jennifer Jakobi, Kinesiology
Research Ethics Coordinator

This is an official document. Please retain the original in your files.
APPENDIX C

Pictorial Representation of Wrist Positions

Supinated

Neutral

Pronated
Brad Harwood  
539 Country View Drive, Petrolia, Ontario  
519-816-2516  
bradharwood@hotmail.com

EDUCATION  
University of Windsor, Windsor, ON  
M.H.K. Applied Human Performance  
Thesis: "Task-dependent subpopulations of motor units in older adults"  
August 2007

University of Windsor, Windsor, ON  
B.H.K. Honours Human Kinetics  
Areas of concentration: Neuromuscular physiology, Dynamic systems in motor control
Honours independent study project: Central and peripheral contributions to rhythmic coordination.  
June 2005

PRESENTATIONS  
American College of Sports Medicine Annual Meeting, New Orleans, LA  
Quantifying muscular activation and rest in a discrete functional task of older men and women: 1665: Board #155 May 30 2:00 PM - 3:30 PM.  
Harwood, Brad J.; Edwards, Darl L.; Jakobi, Jennifer M.

Canadian Society for Exercise Physiology Annual Scientific Meeting, London, ON  
Task-dependent motor unit activity in young and old adults (Submitted).  
2007

Ontario Exercise Physiology Conference, Barrie, ON  
Muscular activation and rest for a discrete task in young and old men and women.  
2007

Ontario Exercise Neuroscience Group, St. Catharines, ON  
Effect of strength differences on phasic muscle activation in older adults.  
2006

Harwood, Brad J.; Jakobi, Jennifer M.

AWARDS  
- Graduate Tuition Scholarship, University of Windsor  
- President’s Excellence Award, University of Windsor  
- Grace Lamoureux-Howitt-Pinfold Memorial Award  
- P.J. Gallasso “Joy of Effort” Award  
- Academic All-Canadian  
- Dean’s Honour Roll  
- Demarco Award  
2005-2007

TEACHING EXPERIENCE  
University of Windsor, Windsor, ON  
Graduate Assistant – Exercise Physiology  
Fielded inquiries, guest lecturer, assignment and exam marking  
2005-2006

Graduate Assistant – Applied Neurophysiology  
Fielded inquiries, special tutorial sessions, assignment and exam marking  
2006-2007
### RELATED EXPERIENCE

**Windsor-Essex Cardiac Rehabilitation Program, Windsor, ON**  
**Student Volunteer**  
Instruct exercise training sessions in persons with prior cardiac incidence, record heart rate, blood oxygen levels, and blood pressure  
2006-2007

**Clinical Orthodics Consultants, Windsor, ON**  
**Student Volunteer**  
Production of casts, plastic molding and shaping, and construction of custom foot, leg, and arm orthodics  
2004

**Neuroscience Conference, Atlanta, GA**  
**Spike 2 (Version 6.0) Training**  
Basic introduction, signal recording and processing, spike sorting and analysis  
2006

### MEMBERSHIPS AND EXTRACURRICULAR

**Canadian Society for Exercise Physiology**  
Graduate Student Member  
2006-2007

**University of Windsor Lancers Men’s Soccer Team**  
Team captain and two time Ontario University Athletics All-Star and Most Valuable Player  
2002-2006

**University of Windsor**  
Graduate Committee Student Representative  
2006-2007