

THE PHYSIOLOGICAL DETERMINANTS OF RATE  
OF TORQUE PRODUCTION ACROSS THE LIFE SPAN

By

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OF TORQUE PRODUCTION ACROSS THE LIFE SPAN

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Title of Study: THE PHYSIOLOGICAL DETERMINANTS OF RATE OF TORQUE PRODUCTION ACROSS THE LIFE SPAN

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Abstract: Abstract: The data collected in this study provides additional knowledge into the complex interplay between the neural, contractile and morphological variables that contribute to voluntary rate of torque development (RTD). Twenty younger (age:  $23 \pm 3$  years) and 17 older men (age:  $74 \pm 6$  years) performed multiple explosive voluntary and involuntary isometric and maximal effort dynamic knee extensions. The RTD contractions were examined in 50 ms sequential time frames from the onset of torque to 200 ms. Surface electromyography (EMG) was used to record and examine muscle activation in sequential 50 ms time frames from EMG onset and normalized to M-wave. Contractile properties were examined from evoked muscular twitch torque variables. Muscle size and quality were assessed using a diagnostic ultrasound. Individual isokinetic (ISK) and isotonic (ISOT) torque-velocity (T-V) slopes were collected to examine differences between younger and older men. After checking for normality, age differences in each sequential 50 ms RTD time frames, neural, contractile, and morphological variables were examined using either the Welch's test or ANOVA. Multiple linear regressions were used to investigate the determinants of RTD across age and within each age group. There were significant reductions in a number of neural, contractile, and morphological variables in the older men. Additionally, older men had a significantly less negative T-V slopes in the ISK and ISOT conditions. Regression analysis revealed that the physiological determinants for each RTD time frame changed throughout the contraction across age (RTD<sub>0-50</sub>, neural & morphological; RTD<sub>50-100</sub>, neural, contractile & morphological; RTD<sub>100-150</sub>, contractile & morphological; RTD<sub>150-200</sub>, morphological), in the younger (RTD<sub>0-50</sub>, neural; RTD<sub>50-100</sub>, neural & morphological; RTD<sub>100-150</sub>, neural, contractile & morphological; RTD<sub>150-200</sub>, contractile), and older men (RTD<sub>0-50</sub>, neural & contractile; RTD<sub>50-100</sub>, contractile; RTD<sub>100-150</sub>, contractile; RTD<sub>150-200</sub>, neural & contractile). Additionally, Pearson correlation coefficient analysis shows multiple relationships between ISK and ISOT slope and physiological variables across age. In conclusion, neural, contractile and morphological variables largely accounted for RTD across age and within each age group. Further, these data suggest that the determinants of RTD are a blend of neural, contractile and morphological variables across age and in younger and older men.

## TABLE OF CONTENTS

Chapter	Page
I. INTRODUCTION .....	1
1.1 Introduction.....	1
1.2 Purpose of the Study .....	5
1.3 Research Questions/Hypotheses .....	5
1.4 Significance of the Study .....	7
1.5 Delimitations.....	7
1.6 Limitations .....	8
1.7 Assumptions.....	8
II. REVIEW OF LITERATURE.....	10
2.1. Neuromuscular Determinants of Rate of Torque Development .....	10
2.1.1 Motor Unit Behavior During Rapid or Ballistic Contractions.....	10
2.1.2 Age-Related Changes in Motor Unit Behavior.....	11
2.1.3 Age-related Changes in Voluntary Muscle Activation.....	20
2.1.4 Age-Related Changes in Motor Unit Number .....	34
2.1.5 Age-Related Changes in Sensory-Motor Function .....	40
2.1.6 Summary of the Neural Determinants of Rate of Force Development .....	49
2.2 Contractile Determinants of Rate of Force Development.....	53
2.2.1 Age-Related Changes in Muscle Phenotype and Function.....	53
2.2.2 Age-Related changes in Skeletal Muscle Size, Quality and Architecture.....	62
2.2.3 Summary of the Contractile Determinants of the Rate of Force Development .....	75
2.3 Age-Related Changes in the Force-Velocity Curve.....	78
2.3.1 <i>Summary of Age-Related Changes in the Force-Velocity Curve</i> .....	86
III. METHODOLOGY .....	89
3.1 Participants.....	89
3.2 Research Design.....	90
3.3 Instrumentation and Procedures.....	91
3.3.1 Ultrasonography.....	91
3.3.2 Electromyography.....	93
3.3.3 Voluntary Maximal Strength Assessment .....	94
3.3.4 Voluntary Rapid Strength Assessment .....	95
3.3.5 Motor Unit Number Estimation and Electrically Evoked Twitches.....	96

Chapter	Page
3.3.6 One Repetition Maximum Assessments and Torque-Velocity Curves ...	98
3.3.7 Motor Nerve Function Assessments .....	100
3.4 Signal Processing .....	100
3.5 Statistical Analysis.....	101
 IV. RESULTS.....	 103
4.1 Descriptive Statistics.....	103
4.2 Effects of Age on the Rate of Torque Development.....	104
4.3. Effects of Age on the Neural, Contractile and Morphological Characteristics.....	105
4.3.1. Neural Characteristics.....	105
4.3.2. Contractile Characteristics .....	105
4.3.3. Morphological Characteristics .....	107
4.4 Relationships between neural, contractile, and morphological characteristics and the rate of torque development.....	110
4.4.1 Relationships between the determinant variables and each sequential 50 ms RTD time frame across age.....	110
4.4.2. Relationships between the determinant variables and each sequential 50 ms RTD time frame within each age group.....	116
4.5 Determinants of Rapid Torque production .....	124
4.6 Age related adaptations to the torque-velocity curves and relationship with the physiological variables.....	130
 V. DISCUSSION.....	 136
5.1. Neural Determinants of the Rate of Torque Development .....	137
5.2. Contractile Determinants of the Rate of Torque Development .....	140
5.3. Morphological Determinants of the Rate of Torque Development .....	145
5.4. Age-related changes to and the Relationships between the Physiological variables and the Torque-Velocity curves .....	147
5.5. Limitations .....	150
5.6. Future Research and Recommendations.....	151
5.7. Conclusions.....	152
 REFERENCES .....	 154
 APPENDIX A: IRB Approval Letter .....	 163

## LIST OF TABLES

Table	Page
<b>1. Demographic data for the Younger and Older men.....</b>	<b>103</b>
<b>2. Age differences in Strength, Morphological, Neural, and Contractile Variables .....</b>	<b>109</b>
<b>3. Relationships between Predictor Variables and RTD Time Windows Across Age (collapsed across age groups).....</b>	<b>115</b>
<b>4. Relationship between Predictor Variables and RTD Time Windows in the Younger Men .....</b>	<b>117</b>
<b>5. Relationship between Predictor Variables and RTD Time Windows in the Older Men .....</b>	<b>121</b>
<b>6. Relationships between the velocity and load controlled torque-velocity curve across age. ....</b>	<b>131</b>

## LIST OF FIGURES

Figure	Page
<b>1.</b> Age differences in explosive force production during each 50 ms time periods.....	104
<b>2.</b> Age differences in absolute peak twitch torque from a single and doublet electrical stimulus in the younger and older men. ....	106
<b>3.</b> Age differences in normalized peak twitch torque (PTT:MVT) following a single (SGL PTT) and doublet (DBL PTT) stimulus between younger and older men.....	106
<b>4.</b> Age differences in evoked twitch RTD from a single and a doublet stimulus between younger and older men.....	107
<b>5.</b> Age differences in the normalized twitch variables in the younger and older men.	107
<b>6.</b> Age differences in the morphological variables in the younger and older men ....	108
<b>7.</b> Significant relationships between predictor variables and torque produced during the first 50 ms of the explosive knee extension.....	112
<b>8.</b> Significant relationships between predictor variables and torque produced during the 50-100 ms of the explosive knee extension.....	112
<b>9.</b> Significant relationships between predictor variables and torque produced during the first 100-150 ms of the explosive knee extension .....	113
<b>10.</b> Significant relationships between predictor variables and torque produced during the first 150-200 ms of the explosive knee extension .....	114
<b>11.</b> Significant relationships between the determinants and $RTD_{0-50}$ in the younger men.....	119
<b>12.</b> Significant relationships between the determinants and $RTD_{50-100}$ in the younger men.....	120
<b>13.</b> Significant relationships between the determinants and $RTD_{100-150}$ in the younger men.....	120



<b>14. Significant relationships between the determinants and RTD<sub>150-200</sub> in the younger men.....</b>	<b>121</b>
<b>15. Significant relationships between the determinants and RTD<sub>0-50</sub> in the older men.....</b>	<b>123</b>
<b>16. Significant relationships between the determinants and RTD<sub>50-100</sub> in the older men.....</b>	<b>123</b>
<b>17. Significant relationships between the determinants and RTD<sub>150-200</sub> in the older men.....</b>	<b>124</b>
<b>18. Determinants of explosive torque production A) collapsed across age, in the B) older, and the C) younger men in the first 50 ms of the maximal, rapid contraction .....</b>	<b>125</b>
<b>19. Determinants of explosive torque production A) collapsed across age, in the B) older, and the C) younger men in the 50-100 ms of the maximal, rapid contraction. ....</b>	<b>127</b>
<b>20. Determinants of explosive torque production A) collapsed across age, in the B) older, and the C) younger men in the first 100-150 ms of the maximal, rapid contraction.</b>	<b>128</b>
<b>21. Determinants of explosive torque production A) collapsed across age, in the B) older, and the C) younger men during the 150-200 ms of the maximal, rapid contraction.</b>	<b>130</b>
<b>22. Age differences in A) relative load-velocity and B) torque-velocity curve. * = Significant difference between slopes to the 0.05 level.....</b>	<b>131</b>
<b>23. Significant positive relationships between the determinant variables and SLOPE-ISK across age .....</b>	<b>132</b>
<b>24. Significant negative relationships between SLOPE-ISK and the morphological variables.....</b>	<b>133</b>
<b>25. Significant negative relationship between MUNE and SLOPE-ISK across age .....</b>	<b>133</b>
<b>26. Significant negative relationship between Twitch responses and SLOPE-ISK across age .....</b>	<b>134</b>
<b>27. Significant negative relationship between Twitch responses and SLOPE-ISOT across age.....</b>	<b>135</b>

## CHAPTER I

### INTRODUCTION

#### *1.1 Introduction*

Age is associated with decreases in muscle mass, maximal strength and function, commonly known as sarcopenia (Cruz-Jentoft et al. 2010). However, rate of force development (RFD) has been shown to decline to a greater extent than max strength during the ageing process, and, therefore, has been suggested to be more functionally relevant to activities ranging from athletics to those encountered daily in the older adult population (Aagaard et al. 2007; Aagaard et al. 2002; Bento et al. 2010; Clark et al. 2013; Thompson et al. 2014; Thompson et al. 2013; Tillin et al. 2010). RFD analyses typically examine the initial portion of the contraction (i.e. first 200 ms following the onset of torque) (Aagaard et al. 2002; Jenkins et al. 2014). However, RFD achieved during different sequential time frames within 200 ms of force/torque onset (i.e. 0-50, 50-100, 100-150, 150-200) are influenced by different physiological characteristics within the neural and muscular systems (Andersen and Aagaard 2006; Folland et al. 2014).

Neuromuscular activation is an important component of maximum force production. The magnitude of force produced is reliant on the number and discharge rate of recruited motor units (MUs) (Maffiuletti et al. 2016). A MU, which consists of the motor neuron and all fibers innervated by that neuron, is considered the most fundamental aspect of force production (Duchateau and Enoka 2011; Piasecki et al. 2016a). Each MU usually consists of similar muscle fibers that follow a specific phenotype (i.e. type I or type II) and are distributed across a muscle in a mosaic fashion (Edstrom and Larsson 1987). During contractions that require a high level of force production, MU are recruited from smallest to largest to meet the force demanded (Desmedt and Godaux 1978; 1977; Fling et al. 2009; Milner-Brown et al. 1973). Larger, later recruited MUs are associated with type II muscle fibers, which are more powerful and are essential in producing high levels of force (Lexell et al. 1988).

These high-threshold MUs are especially important for older adults during movements that require rapid force production, such as recovering from a fall (Maffiuletti et al. 2016). Similar to maximum force production, RFD is highly dependent on muscle activation (Del Balso and Cafarelli 2007; Folland et al. 2014). Specifically, the rate of muscle activation has been shown to be highly related to the early portion of RFD (i.e. < 80ms)(De Ruyter et al. 2004). MU behavior during a rapid contraction is altered leading to reduced recruitment thresholds and firing rates to achieve a high level of force quickly (Desmedt and Godaux 1978; 1977; Folland et al. 2014; Klass et al. 2008). Older adults have been shown to have a slower RFD accompanied by a reduced MU firing rate when compared to younger adults (Klass et al. 2008). A reduction in available functional MUs has been related to a reduced force production leading to a reduced functional ability in

older adults (Doherty et al. 1993; Hunter et al. 2016). MU loss, especially the loss of high threshold MUs (i.e. Type II), leads to a restructuring of the remaining, surviving MUs (i.e. reinnervation of type II fibers by type I MUs) to compensate for the lost MU in an attempt to preserve strength (Campbell et al. 1973; Gilmore et al. 2017; McComas et al. 1971; Power et al. 2013). This MU restructuring phenomenon is known as the remodeling process and has been linked to the age-related reduction in maximal strength (Ward et al. 2014). Due to the lower number of functional high threshold MUs, altered MU behavior, and atrophy of surviving muscle fibers associated with the aging process (Larsson et al. 1979; Lexell et al. 1988; Power et al. 2013), it is reasonable to suggest that the remodeling process could be an additional overlooked mechanism for reduced RFD observed in older adults. However, there is little evidence to explain how the number of available functional MUs influence rapid force production in the older adult population.

Although muscle activation and available MU may be important determinants of strength and RFD, the intrinsic muscular and morphological variables have also been suggested to influence RFD (Andersen and Aagaard 2006; Folland et al. 2014). For instance, muscle fiber type has been shown to be strongly related to RFD (Andersen and Aagaard 2006; Hvid et al. 2010) where, a higher type II muscle fiber area and percentage has been associated with improved RFD (Hvid et al. 2010). This may be due to type II muscle fiber's increased  $\text{Ca}^{2+}$  handling leading to an increased rate of cross-bridging resulting in an improved twitch force per action potential (Baylor and Hollingworth 2003; Straight et al. 2018). Additionally, morphological factors such as muscle size, quality and architecture may significantly influence RFD (Radaelli et al. 2014). For example, larger, better quality muscles with increased pennation angle have been suggested as a

mechanism for improved RFD during the later phase of an RFD contraction (Gerstner et al. 2017).

It has been suggested that neural and contractile components each play a crucial role in RFD. However, the investigation of both neural, contractile and morphological mechanisms may provide a better understanding of the underlying components that ultimately influences RFD in older adults. Previous research has suggested that the age-related decrease in RFD is associated with both neural and contractile mechanisms (Gerstner et al. 2017; Klass et al. 2008), and the determinants of RFD may change as a result of aging. Klass et al. (2008) observed a decreased motor unit discharge rate during RFD contractions in the older adults when compared to younger counterparts, suggesting the age related decline in RFD could be due to the slowing of the contractile properties as well as a reduction of MU discharge rate. Further, McNeil 2005 found that older adults (i.e. > 80 years old) had a lower estimated motor unit number and lower max strength capacities when compared to younger adults. Additionally, previous studies have observed age-related changes in muscle morphology and architecture may lead to a reduced contractile capacities of the muscle leading to a decreased RFD (Aagaard et al. 2007; Gerstner et al. 2017; Roos et al. 1999). For example, Gerstner et al. (2017) observed that muscle quality, architecture and muscle activation play a significant role in the RFD, especially the later time periods (i.e. > 100ms).

Although previous studies have investigated the age-related changes in RFD, no previous studies have examined the neural, contractile and morphological determinants of RFD to this extent. Additionally, the underlying mechanisms of age-related reductions in RFD are still unclear, and little evidence is available about how the underlying

mechanisms of RFD may change as a result of normal aging. It has been suggested that the early and late phases of RFD are determined by different physiological characteristics, however, there are some additional physiological characteristics that may influence RFD in the older adult population. Therefore, analyzing the neural, contractile and morphological determinants of RFD, simultaneously may provide an improved insight into age-related effects of RFD and may lead to improved interventions resulting in reduced functional ability loss and fall risk.

### *1.2 Purpose of the Study*

Although previous research has examined the effects of age on RTD, the mechanisms of rate of torque development declines observed in older adults have not been completely elucidated. Therefore, the purpose of this investigation was three-fold: 1) to examine the effect of age on the neural, contractile and morphological determinants of rapid torque production; 2) to investigate how the determinants of RTD may change as a result of the aging process; and 3) to examine the effect of age on the torque-velocity curves.

### *1.3 Research Questions/ Hypotheses*

This study has the potential to build upon previous information and provide further insight into the effects of age on RTD. The following four research questions have the potential to be answered by the present investigation.

- Do the determinants of the rate of torque development change with age?
  - Hypothesis: The determinants of RTD will be different between older and younger adults

- Hypothesis: When made relative, neuromuscular function will be associated with the reduced RTD in older compared to younger adults.
- Hypothesis: Evoked peak twitch torque will be lower in older compared to younger adults
- Hypothesis: Evoked RTD will be lower in the old when compared to the younger adults
- Hypothesis: Older adults will produce a lower amount of torque in maximal and rapid knee extensions.
- Hypothesis: M-wave amplitude will be reduced in the older when compared to younger adults
- Hypothesis: Muscle size will be lower in the older adults when compared to the younger adults
- Hypothesis: Muscle quality will be reduced in older adults when compared to younger adults
- Hypothesis: Muscle pennation angle will be greater in the younger adults compared to older adults
- Does the number of functional motor units play a role in the rate of torque development?
  - Hypothesis: Older adults will have a lower motor unit number when compared to younger adults
  - Hypothesis: CMAP amplitude will be reduced in the older when compared to younger adults

- Hypothesis: SMUP will be larger in the older adults compared to the younger adults.
- Does the force-velocity curve shift due to age?
  - If so, how does the curve shift and what are the differences between age groups?
  - Hypothesis: The force-velocity curves will be sifted to the downward and to the left.

#### *1.4 Significance of the study*

This study has the potential to enhance our understanding of the effects of age on the determinants of RTD. Current literature has focused on investigating age group differences in RTD or various training methodologies to improve neuromuscular function in young and older adults, without first pin pointing the primary determinants of age related reductions in RTD. Previous research into the age related reduction in RTD has examined both neural and intrinsic contractile properties, however, to our knowledge, there has been no other study that has examined the neural, contractile, and morphological components of RTD in the older population this comprehensively. Additionally, no other study has examined how the determinants of RTD change due to the aging process. The proposed study could provide valuable information that could lead to improved training interventions to reduce the age-related decline in RTD observed in the older adult population.

#### *1.5 Delimitations*

1. Approximately 30-40 males will be needed to complete this study
2. Participants will be between the ages of 18-30 years old or 65 years and older



3. All participants will be healthy and free from any neuromuscular disease (self-reported)
4. The participants will perform both voluntary and evoked contractions and movements
5. Only three of the 4 muscles in the knee extensor muscle group will be collected (i.e. vastus lateralis, rectus femoris, vastus medialis)

#### 1.6 Limitations

1. Participants will respond to either a posted advertisement, informational announcement/email and chose to volunteer on a volunteer basis. Thus, the process of subject selection will not be truly random.
2. Differences in motivation levels between participants may produce varying levels of effort during the voluntary contractions.
3. This study will use a non-invasive method of collecting data, therefore external factors may produce an increased variability in the data collected.

#### 1.7 Assumptions

1. Participants will provide accurate and honest information when completing the health and exercise history questionnaire.
2. Participants will provide maximal voluntary effort on all voluntary contraction assessments
3. The equipment used to acquire all signals are calibrated and will be functioning properly
4. There will be no errors in the data collection, data analysis, data entry or statistical evaluation process

5. The samples of younger and older adults will be similar in terms of number and basic physical fitness level when compared to age-matched norms

## CHAPTER II

### REVIEW OF LITERATURE

The following literature review will include previous research studies that are relevant to the purpose of this study. Each study will be summarized and the results of the study will be provided along with the interpretations of the authors. The aim of this review of the literature is to focus on the age-related changes in the variables assessed in the methods section of the proposal. However, a few previous investigations have been included to highlight specific mechanisms related to the purpose of this proposed dissertation. After each section, there will be a brief summary of the articles.

#### ***2.1. Neuromuscular Determinants of Rate of Torque Development***

##### *2.1.1 Motor Unit Behavior During Rapid or Ballistic Contractions*

Desmedt and Godaux (1977)

In this original study, these authors are among the original authors to examine the neuromuscular response to a rapid force contraction. This study examined the differences in motor unit (MU) behavior in the tibialis anterior during a rapid and a controlled contraction in a group of younger males (age: 21 – 29 years old).

During rapid force contraction, a burst of MU activity was observed during the rapid contraction compared to a more organized recruitment of larger MUs to produce required force. Additionally, the authors observed that MU activation thresholds were lower and MU firing rates were higher during rapid force contractions. The authors suggest that this may be an important mechanism for the development of strength quickly.

Desmedt and Godaux (1978)

A follow up study to the previous study examined the differences in motor unit behavior between a ballistic and ramp muscle contractions in different muscles. In 5 young participants, 117 motor units were collected and examined during voluntary ballistic and ramp contractions in three different muscles. Muscles examined were the masseter, first dorsal interosseous and soleus in the same participant. Muscles were further characterized as fast (masseter and interosseous) and slow (soleus) contractors. In accordance with their previous studies, motor unit recruitment order was similar between contraction speeds and muscles. However, motor unit recruitment threshold was decreased to a greater degree in the fast contracting muscles (i.e. masseter and interosseous) compared with the slow contracting muscles. This result suggests that the motor unit behavior is muscle dependent, and the force produced by each type of muscle (i.e. slow vs fast) may be limited by the motor unit behavior.

### *2.1.2 Age-Related Changes in Motor Unit Behavior*

Kamen et al. (1995)

This examined the age-related changes in maximal motor neuron activation is a potential limiting factor in the production of maximal strength contractions. Motor unit

data was collected from the first dorsal interosseous using a fine wire needle electrode. Results from the study showed that older adults produced a significantly lower discharge rate of approximately 20 impulses/s when compared to younger adults ( $p < 0.05$ ) during maximal effort contractions. Additionally, force production was 19% lower in the older when compared to the younger adults ( $p < 0.01$ ). The authors suggested that a reduced muscle activation observed in the older adults may be a significant mechanism for reduced maximum strength.

Van Cutsem et al. (1998)

This study examined the effects of a three month dynamic training program on the neuromuscular adaptations in the tibialis anterior muscle when performing rapid force production contractions. Three females and 2 males (age: 18-22 years) performed engaged in a 12 week ballistic training intervention, consisting of five sessions per week performing ten sets of ten ballistic dorsiflexions with 30-40% of one repetition maximum. During the pre and post analysis, participants were required to complete two - three maximal voluntary isometric ramp and twenty –thirty voluntary ballistic contractions (performed as fast as possible). During each contraction, single motor units were collected and identified using the spike triggered averaging method and their recruitment threshold and discharge rates were recorded pre- and post-training. Similar to previous research, the motor unit recruitment order was not significantly different between ramp and ballistic muscle actions. However, the motor unit activation threshold was lower and firing rates were higher during rapid force contractions. Following the dynamic training protocol, participants produced an increased torque when compared to prior to the intervention, however there was no difference in muscular twitch force. The

authors also observed an increased motor unit firing rate of additionally recruited motor units, suggesting that following a ballistic training program, neural characteristics are likely the cause of the increased the speed of force production.

Connelly et al. (1999)

The purpose of this study was to investigate the age-related changes in motor unit behavior in the tibialis anterior muscle in young and older adults. Contractile characteristics were examined by maximal voluntary contractions (MVC), interpolated twitch, and evoked twitch contractions. Motor unit behavior was analyzed from intramuscular EMG of the right tibialis anterior muscle. The older adults produced a significantly lower MVC torque compared to the younger adults ( $p < 0.01$ ). There was no statistical difference between voluntary activation between the age groups. The older adults possessed a greater time to peak tension, lower half relaxation rate and a longer contraction duration when compared to younger adults. Motor unit firing rates in the older adults were shown to be significantly lower at each of the contraction levels (i.e. 10, 25, 50, 75 and 100% intensity) when compared to the younger adults. The lower firing rates observed in the older adults could be due to the reduction of higher threshold motor units that may be due to the remodeling process. Additionally, the reduction in motor unit firing rates are observed to be related to the reduction in muscle strength and slower contractile properties of the muscle. The authors suggest that this could be related to the remodeling of the neuromuscular system observed in the older adults.

Scaglioni et al. (2003)

The primary aim of the study was to examine the effects of age on the electrical and mechanical properties of the motor units activated by the H-reflex and the correlated motor response. The study was done on the tibialis anterior. The peak-to-peak amplitude and duration (peak-to-peak time) of the soleus Maximal H-reflex (Hmax) and maximal M-wave (Mmax) were collected for each participant. Hmax was normalized to Mmax to examine the proportion of motor units activated by the Ia afferents and minimize the influences of other peripheral factors. H wave latency was examined as well. Twitch torque associated with Hmax and Mmax variables included: Peak torque (Pt), highest tension related to Hmax (Pth), Compound action potential at Mmax (Ptm). Twitch forces at Mmax were twitch contraction time (CT), time to maximal twitch tension, twitch half relaxation time (HRT), time to recover half of maximal twitch tension and mean rate of twitch tension development (Pt/CT). Results show that Mmax was lower ( $p < 0.001$ ), peak-to-peak duration was longer ( $p < 0.01$ ) in the older compared to the younger adults. The peak twitch amplitude elicited from Mmax was lower in the older than the younger adults. When CT and peak twitch torque were combined, they accounted for the lower Pt/CT observed in the older adults. Hmax amplitude was significantly reduced in the older compared with the younger adults. The H wave latency was significantly longer in the older compared to the younger adults. The MatHmax was significantly higher in the older compared to the younger adults. The slope of the regression analysis showed that the older adults had a significantly higher mechanical response to electrical stimulation compared to the younger adults. Peak twitch was lower in the older compared to the younger. Pth-m (i.e. an index of mechanical contributions of MatHmax to Pth). There is

an increased mechanical influence of MatHmax during the aging process. The authors suggested that the reflex response was mainly attributable to the muscle phenotype in the young and neural age-related changes in the older adults. The authors continue to suggest that the increased reflex ratio observed in the older adults may suggest motor unit remodeling. Further, the reduction in the reflex mechanical efficiency and neural excitability decline observed in the older adults could lead to a reduced functional ability.

Kamen and Knight (2004)

The purpose of this study was to examine the age-related changes in motor unit discharge rate during and following a resistance training protocol in younger and older adults. Results of the study describe a 28% reduction in maximal isometric knee extensor force production in younger and older adults. During the resistance training protocol, muscle force was improved as early as the second testing session in both the young and the older adults. Motor unit discharge rates were observed to improve in association with increased muscular force. Vastus lateralis motor unit discharge rates were significantly lower during submaximal (i.e. 50%) ( $p = 0.02$ ) and maximal (i.e. 100%) ( $p = 0.005$ ) in the older adults when compared to the younger adults. Motor unit discharge rate was improved following the first week of the training intervention, although not statistically significant. However, an increased motor unit discharge rate was increased at 100% MVC ( $p = 0.04$ ) when all four sessions were pooled. From these data, the authors suggested that the increase in muscle strength in the beginning phase of the training intervention relied heavily on the increase in maximal motor unit discharge rate.



Klass et al. (2008)

This study sought to examine the relationship between rate of torque development and motor unit firing rates in the young and the older adults during submaximal rapid force contractions of the dorsiflexors. Statistical analysis revealed that older adults had a 26% ( $p < 0.01$ ) reduction in time to peak torque when performing rapid contractions. This decrease in time to peak torque was accompanied by a 48% ( $p < 0.01$ ) reduction in absolute rate of torque development and 33% ( $p < 0.01$ ) reduction in relative peak rate of torque production. Muscle activation was closer to maximal during the rapid torque contraction in the older ( $p < 0.05$ ). Older adults possessed a reduced twitch force and a reduction in maximal rate of torque production. Motor unit discharge frequencies were faster in both groups compared to maximal torque contractions, however, older adults motor unit discharge frequency was lower than the younger adults ( $p < 0.05$ ). Additionally, recruitment threshold assessed during ramp contractions were significantly reduced in the older adults compared to the younger adults ( $p < 0.001$ ). The authors suggest that the motor unit behavior (i.e. motor unit discharge rate) and contractile speed characteristics may be an important limiting factor in rate of torque development contractions.

Ling et al. (2009)

The purpose of this study was to examine the effect of age on motor unit characteristics (i.e. motor unit behavior). Motor unit size and firing rate was determined during submaximal knee extension at 10%, 20%, 30% and 50% of the max strength value. Statistical analysis revealed that maximal strength was lower in the older adults ( $p$

< 0.0001). Additionally, there was a significant difference in motor unit size and firing rate starting at approximately 60 years of age. Further, the older adults that were  $\geq 75$  years old possessed greater single motor unit action potential area in the younger adults compared to the younger adults. The older adults possessed a increased firing rates during all contraction levels compared to the younger adults. The authors suggest that the older adults have an altered motor unit activation method allowing them to produce the same level of force as their younger counterparts.

Fling et al. (2009)

The purpose of the study was to examine the relationship between motor unit size and recruitment threshold during isometric contractions between younger and older adults. Motor unit behavior was examined through needle and global EMG recordings during the isometric contractions. Isometric contractions were performed in the tibialis anterior and the first dorsal interosseous. The isometric contractions were performed in a gradual ramp-like manner up to 50% of maximum voluntary contraction strength. Interestingly, maximal force production was not significantly different between the young and the older adults. Macro EMG amplitude was significantly larger in the older compared to the younger adults. Specifically, motor units recruited up to 30% of maximum strength were significantly larger than those recruited by the younger adults to the same intensity. Additionally, the relationship between motor unit size and recruitment threshold was similar between the young and older adults. The larger EMG amplitudes observed in the older adults indicate that the older adults are undergoing the process of remodeling. Although the motor unit size may be enlarged due to the remodeling process

in the older population, the recruitment order of smaller to larger motor units associated with increased force production seems to still be intact.

Dalton et al. (2010)

The purpose of this study was to examine the age-related changes in motor unit behavior in the upper arm muscles in young and older adults. Contractile properties in the muscles were examined by administering evoked twitches. Additionally, voluntary strength (MVC) was assessed in both the elbow flexors and extensors. Additionally, maximal voluntary activation was assessed through the interpolated twitch technique. Motor unit behavior was examined by needle electrodes inserted into each of the muscles of interest. MVC in both the flexor and extensor muscle groups were significantly lower in the older compared to the younger adults. Additionally, motor unit firing rates were significantly lower in the old than in the young throughout the contraction. The authors suggest that age significantly affected the motor unit firing rates in the older adults. This reduction in motor unit firing rates are not related to contractile speeds, suggesting that the reduction in MVC could be due to the reduced firing rates observed in the older population.

Kallio et al. (2010)

The purpose of this study was to investigate the age-related changes in H-reflex excitability and motor unit behaviors in younger and older adults. Intramuscular EMG was examined during isometric, concentric, and eccentric muscle actions. H-reflex excitability was examined by determining the H/M-wave ratio. Maximal muscle strength was also investigated. Results of the study show that there was a 12.3% reduction in

muscle strength in the old compared to the young. Older adults produced lower absolute and relative torque in all muscle actions (i.e. eccentric, concentric, isometric). Motor unit firing frequency was higher in the young than in the old. Additionally, H-reflex amplitude was higher in the young when compared to the old. Although the answer could not be derived from the data collected, the authors speculated that the reduction in the H-reflex amplitude could be due to the increased inhibition in the older adults. The different motor unit behavior observed in the different contractions could be due to a different activation strategy adopted by the older adults to attain force requirements.

Hourigan et al. (2015)

The purpose of this study was to investigate the neuromuscular transmission stability in younger and older adults. Motor unit behavior was evaluated using the decomposition based quantitative electromyography method. The muscles tested were the tibialis anterior and the vastus lateralis. The motor unit transmission stability was investigated by near fiber analysis of jiggle. Jiggle assesses the motor unit potential shape variability. Additionally, compound muscle action potential was assessed through electrically evoked contractions. The results of the study show that there was a significant increase in the near fiber jiggle (i.e. motor unit potential variability) in the tibialis anterior and the vastus medialis. There was a significant correlation between age and near fiber jiggle in both the tibialis anterior ( $r = 0.68$ ) and the vastus medialis ( $r = 0.58$ ). Further, there was a negative relationship between near fiber jiggle and motor unit number estimation, and a positive relationship with single motor unit action potential amplitude, motor unit potential duration, motor unit peak-to-peak voltage, and motor unit potential area. The authors suggest that the increased motor unit jiggle was due to the loss of motor

units and consequential remodeling process. The authors suggest that these data present evidence that near fiber jiggle could be an important measure to assess the progression of the remodeling process.

Watanabe et al. (2016)

The purpose of this study was to examine the effects of age on motor unit firing rates in the older adult's vastus lateralis during a moderate to low force production levels. Motor unit behavior was examined using a multichannel grid and further decomposed to examine individual motor unit firing rates non-invasively. Motor unit firing rates in the older adults were significantly lower during submaximal isometric contraction compared to the younger adults. Maximum strength was significantly related to the motor units recruited at lower levels (i.e. < 20% of MVC) in the older adults ( $r = 0.884$ ,  $p < 0.0001$ ). The authors suggest that age significantly effects the motor unit firing rates at submaximal levels of force production.

Piasecki et al. (2016)

Refer to section *2.1.4 Age-Related Changes in Motor Unit Number*

### *2.1.3 Age-related Changes in Voluntary Muscle Activation*

Hakkinen et al. (1995)

The main objective of this study was to examine the influence of age on voluntary and electrically evoked muscle force production. The study consisted of 3 groups of men: young men (mean age: 29 years old), middle-age (mean age: 49.6 years old) and older (mean age: 67.2 years old. Unilateral and bilateral maximal voluntary strength and

strength development was examined in the knee extensors. Rate of force development was examined in consecutive 100 ms time window from the beginning of force production to 500 ms following onset. Additionally, relative rate of rise of force production was examined at 30, 60 and 90% of maximal force. Relaxation time was determined from the time it took to relax from an 85% contraction to 10% contraction. Muscle activation was examined from the vastus medialis, rectus femoris and the vastus medialis. EMG during max force and every 100 ms from onset of contraction to 500 ms were collected and analyzed. Maximum uni- and bilateral twitch force was determined and maximal muscle activation was collected during an evoked contraction at the top of a maximal contraction. Younger adults possessed a significantly higher uni- and bilateral maximal force production compared to the older adults. EMG from the three quadriceps muscles were not significantly different between groups for the maximal voluntary uni- and bilateral knee extension. The rate of force development was significantly greater in the young compared to the middle and older age adults. Further, middle aged adults produced a greater rate of force development than the older aged group. The rate of relaxation was greater in the young compared to the middle and older adults following both uni- and bilateral knee extension. Additionally, the time to relative force were lower in the young than the middle-age, and were both shorter than the older adults. Twitch forces elicited in the young were greater than those for the middle and older age groups. However, middle and older age groups were not significantly different. Muscle activation was greater in the younger compared the to the older adults in the unilateral plus evoked contraction. The authors suggest that age significantly influences the maximal voluntary and evoked force, rate of force development and relaxation ability. The authors attribute

the reduction in muscle performance to reduced peripheral muscle function and neural activation as a result of the aging process.

Hakkinen et al. (1996)

Refer to section 2.2.2 *Age-Related Changes in Skeletal Muscle Size, Quality and Architecture*

Doherty and Brown (1997)

The purpose of this study was to investigate the age-related effects on contractile and muscle activation properties of the thenar motor units. Results of the study showed that older adult's motor units produced a smaller twitch force compared to the younger adults. When the single motor unit action potential size was normalized to the max M-wave, older adults possessed significantly larger single motor units when compared to younger adults ( $P < 0.05$ ). Further, the authors found a significant increase in twitch contraction time ( $p < 0.01$ ) and half relaxation time ( $p < 0.01$ ). The authors suggested that the elongated duration of the twitch indicated that this was an adaptation to achieve a high level of force with a diminished motor unit firing rate. Additionally, the authors suggest that the increased motor unit twitch force and slower motor unit contraction speed is an adaptation to the reduced motor unit numbers commonly observed in older adults.

Hakkinen et al. (1998)

The purpose of this study was to investigate the age related changes in muscle, maximal and explosive force production in the leg extensors between middle and older

adult men and women. During maximal power movement (jumping with 50% 1RM weight), older adults (i.e. average age: 67 – 70) possessed a lower muscle activation when compared to the middle aged adults. Muscle size was greater in the middle age than the older adults. When compared together, the middle aged adults has a significantly better uni- and bilateral isometric knee extension production compared to the older adults. Muscle size of the quadricep femoris was significantly correlated with muscle strength in the men, but not the women. Together, the specific force (force per unit of muscle mass) was greater in the young compared to the correlated older counterparts. Further, maximal rate of force development (i.e. within the first 500 ms) was significantly greater in the younger adults compared to their respective older counterparts. Maximal strength and rate of force development was significantly related in the older group. Additionally, older adults had a lower muscle activation compared to the middle aged adults when performing an isometric knee extension. During the maximal jumping movements, the younger adults had significantly greater muscle activation in the first 500 ms of the movement compared to the older adults. The authors suggested that older adults experience a reduced neural input to the muscles and reduced muscle size that could lead to the decrease in muscle function, reduced strength and power production capacity.

Izquierdo et al. (1999)

The purpose of this study was to investigate the age-related differences of maximal strength, isometric-time curves, and force-velocity curves during a concentric and stretch shortening cycle movement in the upper and lower body in middle and older aged adults. Statistical analysis revealed that the younger group produced significantly more force than the middle and older groups, with the middle aged group producing



significantly more force than the older group. Maximal force and the amount of force produced during the first 500 ms were greater in the young than the old and middle and older groups. Jump performance was better in the young compared to the middle and older groups. Both the young and middle age groups performed better than the old group. There was a high antagonist muscle activation during isometric knee extension in the older compared to the younger adults. When the middle and older groups were combined, rate of force development was significantly related to max strength. The older adult group had significantly worse balance scores than the younger adults and RFD capabilities were significantly related to balance ability. The authors suggest that explosive force declines at a faster rate than maximal force production capabilities. Additionally, the authors suggest that the age-related reduction in RFD could be due to reduced neuromuscular activity that can lead to declines in balance performance.

Aagaard et al. (2002)

This study sought to examine the effect of resistance training on contractile and neural mechanisms for rate of torque development. Fifteen young men participated in a heavy-resistance training protocol consisting of 38 sessions lasting a total of 4 weeks. Contractile and neural physiological mechanisms were analyzed during 0-30, 0-50, 0-100, and 0-200 time frames were assessed pre- and post-training protocol. The authors observed an increased isometric muscle strength ( $p < 0.001$ ) and the rate of torque development ( $p < 0.01-0.05$ ) following the training protocol. Contractile rate of force development increased by 17-26% after the resistance training program. Specifically, contractile rate of force development was increased in the early (i.e. 0-50 ms) and later time frame (i.e. 0-100) by 23-36% and 17-20%, respectively. Rate of force development

and muscle activation amplitude are suggested to be linked, therefore, a rise in rate of force development is associated with a parallel increase in muscle activation, especially at the initial portion of a rapid force contraction. Additionally, rate of muscle activation ( $p < 0.01 - 0.001$ ) was significantly increased during the initial portion of the rapid contractions (i.e. 0-100). The authors further suggested that the increased muscle activation variables may be responsible for the increases in rate of force production in the initial portion of the rate of force contraction (i.e. 0-50).

Scaglioni et al. (2003)

Refer to section *2.1.1 Motor Unit Behavior During rapid or Ballistic*

*Contractions*

De Ruiter et al. (2004)

This study sought to examine the ability to produce torque and muscle activation at three different knee angles during fast voluntary isometric knee extension. Participants were characterized as individuals who possessed a voluntary activation of 90% or higher were included in the study. Each participant performed rapid voluntary knee extensions at three different knee angles (i.e. 30, 60 and 90 degrees). Additionally, evoked contractions were administered at the same knee angles to examine the contractile influence on rapid torque production. Evoked and voluntary knee extensions were not significantly different at each knee angles ( $p = 0.86$ ). However, the time to peak rate or torque development was significantly longer in the voluntary condition compared to the evoked condition with in the first 40 ms. The authors also observed that surface EMG was positively related torque

production ( $r^2 = 0.76$ ) when compared to the evoked condition, suggesting that the initial portion of the rate of torque development is highly dependent on muscle activation.

Barry et al. (2005)

The purpose of this study was to examine the age-related changes in electromyographic activity during the initial phase of a rapid force development contraction and adaptations following a progressive resistance training intervention. Rate of torque development (RTD) was calculated in time windows of 0-30, 0-50, 0-100 and 0-200 ms after torque onset and peak RTD was calculated as the highest mean torque developed during the full 200 ms time window. Additionally, rate of electromyography rise (RER) was calculated during 0-30, 0-50 and 0-75 ms following EMG onset. The root mean square (RMS) was calculated in time windows of 0-30, 0-50 and 0-100 ms relative to EMG onset. Additionally, the older adults produced a lower rate of EMG rise compared to the younger adults. Older adults produced a 23.2% lower MVC ( $p = 0.205$ ) and a 51.2% reduction in peak RTD and RTD during each time window ( $p < 0.01$ ). Following the resistance training protocol, older adults improved their RTD during the 200 ms time window ( $p < 0.01$ ). There was a significant EMG RMS increase in the 0-50, 0-100 window for the older adults ( $p < 0.05-0.01$ ). The increased RER produced by the older adults following the training protocol was significant for all time frames ( $p < 0.01$ ). However, the degree of improvement of the older adults was not as great as the younger adults. The authors suggest that there may be an age-related reduction in the neuromuscular performance that leads to the reduced magnitude of improvement of the EMG variables following the resistance training program.

Van Cutsem and Duchateau (2005)

In this investigation, the authors investigated the influence of prior muscle activity on ballistic contraction performance. Seven young participants (Age: 22-44; male: 6; female: 1) performed three maximal voluntary contractions (MVC) using the dorsiflexors and plantarflexors. Motor unit's recruitment threshold and firing rates were identified and recorded during ramp MVC and rapid MVC. Results of the study discovered that prior muscle activity reduces the rate of torque development ( $p < 0.001$ ) when compared to starting the contraction from rest. When a ballistic contraction was performed from rest, motor unit firing rates were elevated when compared to the contraction performed from pre-activation ( $p < 0.05 - 0.001$ ). Additionally, the authors observed that the higher threshold motor units were not recruited during the preactivation condition, suggesting that preactivation effect the total motor unit pool. The authors indicated that the muscle activation prior to the ballistic contraction can greatly influence the rate of torque development and the motor unit discharge rate.

Del Balso and Cafarelli (2007)

This study sought to examine the changes in muscle activation following a short-term exercise training. Twenty healthy young sedentary adults volunteered and were split into a control and training group. The training group participated in a 4 week isometric training protocol of the plantar flexor muscles. The authors examined motor unit excitability and maximal muscle activation during low submaximal contractions (10% of MVC). Following the 4 week training protocol, MVC was increased along with an increase in RTD. However, due to the short duration of the training protocol, there was

no training induced muscular hypertrophy. The elicited an increase in MVC and RTD was accompanied with an increase in muscle activation and rate of muscle activation ( $p < 0.001$ ). Further, the authors observed a 49% increases in rate of muscle activation and 60% muscle activation was evident within the first three days ( $p < 0.002$ ). The authors suggest that the voluntary RTD performance were dependent on the rate at which the muscle was activated at the beginning of the rapid contraction. Further, motor unit behavior (i.e. recruitment threshold and firing rate) may be responsible for the increased rapid force production as opposed to contractile hypertrophy.

de Ruiter et al. (2007)

The authors sought to investigate how much contractile and muscle activation of the knee extensors influence the rate of isometric knee extension and maximal jumping performance. Eleven male volleyball players (age:  $20 \pm 2$  years) volunteered to participate in this study. Muscle activation and rate of torque development during the first 40 ms and maximal rate of torque development were examined at a knee angle of  $120^\circ$ . Additionally, squat jumps and countermovement jump performance at a knee angle of approximately  $120^\circ$  was determined. Results showed that voluntary initial torque was highly dependent on muscle activation ( $r^2 = 0.83$ ). Additionally, the electrically evoked contractions were not significantly related to the early portion of the rate of torque development contraction (i.e. 40 ms). The authors suggested that the neural activation of the muscle groups was such a strong determinant of early rate of force development that contractile determinants may be less significant in the early phase of the rate of force development contraction.

Cannon et al. (2007)

The purpose of this study was to examine the age-related changes in muscle strength, hypertrophy, voluntary activation and muscle activation between younger and older women. Additionally, the authors examined the lean tissue cross-sectional area (LCSA) and lean tissue volume (LMV) prior to and following the resistance training protocol. Prior to the resistance training protocol, maximal muscle strength was higher in the young compared to the older adults ( $p < 0.05$ ). Following the resistance training protocol, muscle strength improved in both the young and older adults, while the magnitude of difference was not significantly different. Voluntary activation was not significantly different prior to the training protocol, however following the training intervention, voluntary activation improved in both age groups but did not reach statistical significance. Following the training protocol, muscle activation was significantly higher but not different between age-groups. The authors suggest that regular physical activity may decrease the rate of neuromuscular age-related decline usually observed in the older populations. The authors further suggested that the improvements in muscle activation were located peripherally because of the increase in muscle activation but no change in voluntary activation following the resistance training program.

Klass et al. (2008)

Refer to section *2.1.1 Motor Unit Behavior During Rapid or Ballistic Contractions*

Clark and Taylor (2011)

The purpose of this study was to examine the age-related effects on neuromuscular activation and muscle performance in middle, older, and older mobility limited (OML) adults. Results showed that the older adults produced significantly less power (-23%) during a 70% leg press than the middle aged adults, and the OML performed worse than the middle and older age groups. OML adults produced a significant lower amount of rate of EMG rise when compared to the middle and older age adults. There was no significant difference between the middle age and older adults. Further statistical analysis revealed that rate of EMG rise was significantly related to leg press acceleration ( $r = 0.80$ ,  $p < 0.0001$ ), power ( $r = 0.73$ ,  $p < 0.0001$ ) and functional ability tests in the middle and older adults ( $p = 0.02$ ). The authors suggest that the muscle activation rate was related to muscle function and functional ability in older adults. Additionally, the age-related slowing of muscle activation rate could be an indicator of future functional ability declines.

Clark et al. (2013)

This study's purpose was to examine the age-related changes in neuromuscular activation and the effects of these age-related changes in neuromuscular activation on the muscle strength, power and functional ability in older adults. Results following the second visit (i.e. 2.5 years later) displayed a 28% decreased in rate of EMG rise ( $p < 0.004$ ) and a 16.5% lower leg press power ( $p < 0.01$ ). Additionally, the reduced rate of EMG rise was strongly related to the loss of power accounting for 61% of the variance ( $p < 0.001$ ). Muscle size was reduced ( $p < 0.05$ ) at the follow up visit. The authors also

found that there was a 9% reduction in neuromuscular activation, measured by rate of EMG rise, per year. The authors suggested that the reduction in motor unit behavior may be the factor leading to the reduced EMG rise observed in this study. Additionally, the authors suggested that the reduction in rate of EMG rise may be an important mechanism for the reduction in muscle power associated with aging.

Jenkins et al. (2014)

The purpose of this study was to examine the age-related differences in rate of torque development and rise in muscle activation in younger and older adults. Additionally, the authors examined if the age-related differences were still present after normalizing to maximum torque produced during a maximal RTD contraction and rate of EMG rise was normalized to maximal M-wave amplitude. Voluntary rate of torque development and rate of EMG rise were calculated at similar increments during the rapid torque contraction (i.e. 0-30, 0-50, 0-100 and 0-200 ms after torque and EMG onset). Additionally, evoked RTD was examined at similar time frames (i.e. 0-30, 0-50, 0-100 ms after torque onsets). Normalized RTD was determined by the proportion of peak torque and peak evoked twitch torque, then examined at 10%, 20%, 30%, 40%, and 50% of peak voluntary torque and evoked contractions. Normalized rate of EMG rise was determined by expressing the evoked EMG signal as a proportion of the maximal M-wave. Statistical analysis revealed that absolute values for RTD were significantly lower in the older adults in peak RTD and all RTD time frames ( $p < 0.001 - 0.037$ ). Additionally, absolute rate of EMG rise, M-wave amplitude, evoked rate of EMG rise, and normalized EMG rise was lower in the older adults compared to the younger adults ( $p \leq 0.05$ ). However, when normalized to max strength and EMG, the age differences in



RTD and EMG rise disappeared. The authors suggested that the elimination of age-related differences in RTD and rate of EMG rise following normalization suggests that the reductions in RTD and rate of EMG rise were due to a decrease in muscle strength and M-wave amplitude.

Thompson et al. (2014)

The purpose of this study was to examine the age-related effects on rate of muscle activation, maximal and rapid strength characteristics of the plantar flexors in young, middle, and older men. Results from the study show that the older adults had a significantly reduced peak force ( $p < 0.001$ ) and rate of force development ( $0 < 0.028$ ) compared to the other, younger groups. Further, the older adults performed worse on the rate of force development variables compared to the younger groups. However, there was no significant reduction in the normalized rate of EMG activation between the groups, in fact, the middle aged men possessed a greater normalized rate of EMG activation than the younger and the older groups. Relative RFD was significantly reduced in the older compared to the younger adults. The authors suggest that the lower relative RFD and the non-significant differences in rate of EMG rise between young and older adults suggest that the older adults were suffering from a reduction in type II muscle fiber. The authors also suggested that there may be an age related change in muscle morphology, architecture or quality leading to the reductions in relative RFD.

Wu et al. (2016)

The primary purpose of this study was to investigate the age-related changes in neuromuscular and mechanical characteristics factors in the knee extensor and flexor

muscle groups. Statistical analysis revealed that the older adults produced significantly reduced maximal voluntary muscle force compared with the older adults. Additionally, there was a significant age-related reduction in rate of torque development (60%,  $p < 0.01$ ). Muscle thickness was significantly greater in the young than in the older adults, however there was no significant differences between fascicle length between the young and older adults. Neuromuscular activation was significantly lower in the old when compared to the younger adults ( $p < 0.05$ ). Additionally, older adults had a lower median frequency compared to the younger adults. The authors suggested that muscle activation and muscle architecture may be important mechanisms for age related RTD and maximum muscle strength observed in older adults.

Gerstner et al. (2017a)

The purpose of this study was to examine the age-related differences in rate of torque development (RTD) during an early (i.e. 0-50ms) and late (i.e. 100-200ms) time intervals from torque onset. Additionally, the authors sought to examine the contributions of neural and contractile mechanisms that may influence the RTD during the two different time windows in older and younger adults. Specifically, ultrasonography was used to assess muscle fascicle length (FL), pennation angle (PA), muscle size (mCSA) and muscle quality (EI; echo intensity). Additionally, absolute and normalized RTD and muscle activation during sequential 50ms time windows (i.e. 0-50, 50-100, 100-150 and 150-200) after onset of torque. Results showed that older adults were able to produce a lower amount of torque at peak ( $p < 0.05$ ), 100 ms ( $p < 0.05$ ) and 200 ( $p < 0.05$ ) after onset. Additionally, EI ( $p < 0.05$ ) was lower and PA was higher ( $P < 0.05$ ) in the old compared to the younger adults. Further, older adults had a lower EMG value during the

100-150ms ( $P < 0.05$ ) and 150-200ms ( $p < 0.05$ ) windows. There were significant relationships between normalized RTD 100-200 and EI, EMG 100-150 and EMG 150-200. However, there were no significant relationships between the normalized RTD 100-200 and PA and FL. The authors suggest that the age-related reductions observed in the older adults could be an important mechanism for the reduction in RTD seen through the aging process. Additionally, this study provides additional evidence that the neural and muscular systems that are subject to decline during the aging process can influence RTD.

#### *2.1.4 Age-Related Changes in Motor Unit Number*

Campbell et al. (1973)

The purpose of this study was to investigate the age-related changes in motor unit number estimates. In this study, M-wave amplitude and peak twitch torques were examined. The older adults possessed an increased motor unit size and a lower number of functioning motor units. The authors suggest that the findings show that advancing age increases the reduction of functional motor units. These changes in motor unit behavior and number indicate that older adults undergo a process of motor unit remodeling to compensate for the age-related reduction in functional motor units. This compensatory process attempts to maintain muscle function throughout life.

Doherty et al. (1993)

The main objective of this study was to examine the age-related effects of motor unit decline and muscle strength in younger and older adults. Using the spike triggered averaging method, the authors observed a 47 % decline in motor units in the older compared to younger adults ( $p < 0.001$ ). Additionally, the older adults possessed a greater

single motor unit amplitude compared to the younger counterparts ( $p < 0.01$ ). Further, older adults possessed significantly lower muscle strength compared to younger adults ( $p < 0.05 - 0.001$ ). The authors suggested that the decreased motor unit number may be a primary mechanism for the reduction in muscle strength observed in the older adults.

McNeil et al. (2005)

This study's purpose was to examine the age-related differences in motor unit number estimation and muscle strength in young, old and very old men. Statistical analysis observed a decrease in maximal voluntary peak torque ( $p < 0.05$ ), time to peak torque ( $p < 0.05$ ) and motor unit firing rate in the old and very old men. Additionally, older adults produced a greater muscle activation at a lower contraction intensity when compared to younger adults ( $p < 0.05$ ). Further, there was a decline in motor unit number in the older and very old adults compared to their younger counterparts. The authors suggested that the reduced motor unit number could be a mechanism for the increased weakness and functional decline observed in the very old adults.

Power et al. (2010)

The purpose of this study was to investigate the motor unit numbers in healthy, active older adults with age-matched non-active older and recreationally active younger adults. Motor unit number was estimated through the spike-triggered averaging method in each group. The active older adults produced 25% lower isometric dorsiflexion torque than the age-matched and younger active adults ( $p < 0.003$ ,  $ES = 0.482$ ). Voluntary activation, assessed through the interpolated twitch method, showed that all participants were able to activate the muscle to 99% or above. Evoked twitch torque was 23% lower

( $p < 0.010$ ,  $ES = 0.348$ ) than the young adults. Additionally, a larger single motor unit potential was observed in the age-matched old compared to the younger adults ( $p < 0.021$ ,  $ES = 0.539$ ). Active older adults possessed a greater motor unit number compared to the age-matched older ( $p = 0.050$ ,  $ES = 0.256$ ) and the age-matched old possessed a smaller motor unit number than the younger active younger adults ( $p < 0.009$ ,  $ES = 0.497$ ). The authors suggested that despite the lower twitch force observed in the active old group, chronic physical activity may be able to reduce the age-related decline in functional motor unit loss.

Kaya et al. (2013)

The purpose of this study was to examine the age-related differences in motor unit number would effect the maximal strength production. The authors used the MUNIX method to examine the motor unit number estimation in younger and older adults. Results of the study found that the older adults possessed a lower motor unit number and a lower muscle strength. The authors suggested that the age-related reduction in muscle strength may be due to a reduced number of motor units.

Mau-Moeller et al. (2013)

The purpose of the study was to examine the underlying neural mechanisms of strength and rate of strength development in the quadriceps during the aging process. Rate of torque development was assessed in sequential 50 ms time frames from onset to 200 ms after onset of torque production. Voluntary activation was assessed through the interpolated twitch technique examining the electromyography and maximal M-wave of the quadriceps. Additionally, H-reflex was assessed to examine the motor neuron

excitability via the Ia afferents. Muscle twitch force was used to examine the contractile components of the muscle. Results of the study discovered an age-related reduction in muscle strength, voluntary activation and normalized EMG amplitude. The reduction in muscle activation during the initial (i.e. 50 - 100ms), middle (i.e. 100-150ms) and late (i.e. 150 – 200ms) in the elderly was correlated with the reduction in RTD. However, the older adults produced a greater muscle activation in the middle (i.e. 100-150ms) and later (150-200ms) phases of the RTD when compared to the younger group. Additionally, the M-wave latency was longer in the older compared to the younger adults. The resting twitch responses were significantly lower in the older compared to the younger adults. The authors suggested that the reductions in RTD observed in the older adults might be due to the interplay between the neural and muscular systems. Age-related changes in the neural determinants may be more relevant to rapid torque development.

McKinnon et al. (2015)

This study sought to investigate the effect of age on motor unit properties and muscle strength and power in younger and older adults. The motor unit number analysis used in this study was decomposition-based quantitative electromyography. Similar to previous research motor unit number was lower ( $p < 0.05$ ) and single motor unit action potentials ( $p < 0.05$ ) were larger in the older compared to younger adults. Older adults produced a reduced maximum isometric strength ( $p < 0.05$ ) and muscle power ( $p < 0.05$ ) compared to younger adults. The authors suggest that the reductions in muscle strength and power may not be solely due to muscle atrophy but may be due to the complex process of the remodeling process.

Piasecki et al. (2016)

This study examined the age-related effects on motor unit number and organization in younger and older adults. The older adults possessed a smaller vastus lateralis (VL) and a reduction in maximal strength. Additionally, the older adults possessed a significantly larger single motor unit potential and lower number of motor units compared to the younger adults. Further, there was a significant lower muscle fiber count in the older adult compared to the younger adults. There was an increased variability at the neuromuscular junction examined by the enlarged jiggle value. The authors state that the majority of the motor units in the VL and were enlarged and less stable suggesting that these data could lead to future functional ability limitations.

Gilmore et al. (2017)

The purpose of this study was to investigate the differences in motor unit number estimations between younger (age = ~ 25) and very old (age = ~ 85) adults. Muscle activation (EMG RMS), torque, voluntary activation, compound muscle action potential (CMAP), motor unit number estimate (decomposition-enhanced spike-triggered averaging) were collected to examine the physiological differences between age groups. Additionally, the motor unit number estimation was collected during a contraction a 30% EMG RMS and 50% EMG RMS. The results show that the younger adults were significantly stronger than the younger adults. There was no significant difference between voluntary activation between the two groups. The older group possessed smaller CMAP amplitudes. Further analysis revealed that the older adults possessed significant fewer motor unit numbers at each contraction level. The authors suggest that the older

adults suffered from a reduction in motor units and have undergone age-related collateral reinnervation.

Piasecki et al. (2018)

The purpose of this investigation was to examine the effect of age on motor unit size and number in young, older, sarcopenic and non-sarcopenic adults. Motor unit behavior was assessed through surface and intermuscular EMG. Muscle strength was examined in each group. The compound muscle action potential (CMAP) was examined from the stimulation of the femoral nerve. Motor unit number estimation was achieved through spike triggered averaging. Muscle size decreased in each group from the young possessing a greater muscle size than the non-sarcopenic, pre-sarcopenic and sarcopenic older adult men. Younger men possessed a greater muscle strength value than the non-sarcopenic old (-34%), pre-sarcopenic (-39%), and sarcopenic (-49%) old. The intramuscular motor unit potentials were smaller in the non-sarcopenic (-26%) and pre-sarcopenic (-41%) when compared to the young. Additionally, the sarcopenic motor unit action potentials were smaller in the sarcopenic compared to the non-sarcopenic. Motor unit number estimation was significantly lower in the non-sarcopenic, pre-sarcopenic and sarcopenic old compared to the younger adults. The authors suggest that the loss of motor units begin before the onset of sarcopenia. This is confirmed by the enlarged motor unit action potentials in the non-sarcopenic older men compared to the pre-and sarcopenic old men. The authors indicate that the reduction and inability to recover motor units can indicate a difference between sarcopenic and non-sarcopenic muscle. The authors go on to suggest that the remodeling process is a survival mechanism that can lead to the onset of sarcopenia.



### *2.1.5 Age-Related Changes in Sensory-Motor Function*

Taylor (1984)

The purpose of this study was to examine the effects of aging on nerve conduction variables in adults. The results of the study found that the reduction in sensory and motor conduction velocity and sensory amplitude begin to decline at an increasing rate from the fifth decade on. The authors suggest that the loss of nerve axons seem to effect the sensory nerves before the motor nerves. The age-related decline in the motor nerve function is thought to be attenuated due to the collateral sprouting during the remodeling process.

Bouche et al. (1993)

The main purpose of this study was to examine the age-related effect on peripheral nerve function in younger and older adults. Results of the study showed that sensory nerve conduction velocity was decreased in participants older adults beginning around 60 years old. Additionally, participants who were 80 years old experienced declines in sensory and motor nerve conduction velocities. The reduction in sensory nerve function suggests that sensory nerve function may decline before the motor nerve.

Resnick et al. (2000)

The purpose of this study was to examine the relationships between peripheral nerve function and functional ability. Peripheral nerve disability was significantly related to poor balance ability, usual and fast gait speeds in women. Additionally, age was associated with reduced peripheral nerve function. The reduction in usual and fast gait

speeds became more apparent as age increased. The authors suggest that there is an association between peripheral nerve function and reduced functional ability in older adults.

Rivner et al. (2001)

The purpose of this study was to examine the relationship between age and height on nerve conduction. Participants in the study ranged in age from 20 – 95 years old. The peroneal motor, ulnar motor, palmar motor and sural sensory nerve function were examined. The motor nerve function was analyzed by the compound action potential (CMAP) and the sensory nerve function was assessed by analyzing the sensory nerve action potential (SNAP). Additionally, nerve conduction velocity was examined. Statistical analysis revealed that nerve conduction velocity was inversely related to age in the sural, peroneal motor, and ulnar motor nerves, however, there was a small positive relationship between age and distal latencies of the same nerves. Age only accounts for approximately 10% of the variability in nerve conduction velocity. Height explained for more of the variability in nerve conduction velocity (~7%) than age alone, and when age and height were combined, the accounted variability was improved. Approximately 16% of the variance in SNAP was accounted for by age and adults older than 60 years old possessed a lower number of high amplitude SNAP. Additionally, when height and age are combined, height and age account for about 22% of the variance in sensory sural nerve amplitude. The authors suggest that these data indicate an age-related reduction in peripheral nerve function.

Resnick et al. (2001)

The purpose of this study was to examine the age-related effects on peripheral nerve function. Additionally, the authors examined if peripheral nerve functional decline was associated with diabetes independent of age. Participants who participated in the study ranged in age from 65 – 85 years old. Sensory nerve function was examined by measuring vibration perception threshold (VPT). Results of the study show that there is an age-related decline in peripheral sensory nerve function in older adults. The younger old adults (i.e. 65-74 years old) had 56% of participants score normal, as opposed to 43% for middle old (i.e. 75-84 years old) and 20% for the oldest group (i.e.  $\geq 85$  years old). Further, the older adult population had a significant percentage of adults possessed a severe peripheral nerve dysfunction (31%.  $p < 0.001$ ). Regression analysis revealed that increasing age was significantly associated with increased risk of developing peripheral nerve dysfunction. The authors suggest that the results presented provide additional evidence for the age-related decline in peripheral nerve.

Scaglioni et al. (2003)

Refer to section *2.1.1 Motor Unit Behavior During Rapid or Ballistic*

*Contractions*

Gregg et al. (2004)

The purpose of this study was to examine the existence of peripheral arterial disease (PAD), lower extremity disease (LED) and peripheral neuropathy (PN) in the United States adult population  $\geq 40$  years of age. Peripheral neuropathy was assessed by self-reporting touch sensation on the foot. The participant indicated when they felt the

pressure from a monofilament in three different places on the foot. The monofilaments, each have a different weight and stiffness, was pushed against the skin until it bent. There was an increase in PN prevalence from 8.1% in the younger adults (i.e. 40-49 years old) to 34.7% in the older (i.e.  $\geq 80$  years old) groups of adults. PN was more prevalent in men (18.2%) than women. PN and PAD were seen to be linked in the participants where PN was 23.1% higher in those adults with PAD than those without PAD (14.2%) ( $p > 0.05$ ). The authors suggest that it is difficult to compare results to previous studies due to the different methodological approaches, however, the study's results could provide a baseline for future research.

Tong et al. (2004)

The purpose of this study was to examine the influence of age on peripheral nerve function in healthy adults. Additionally, the authors sought to examine if other physiological or anthropometrical measures influence peripheral nerve function over time. Peripheral nerve function was assessed at two different time points separated by approximately 5.4 years. Peripheral nerve function variables included onset latency, peak latency, and baseline to peak amplitude, sensory nerve action potential (SNAP) amplitude distal latencies and conduction velocities were examined in the median and ulnar nerves. Results of the study showed that there SNAP amplitude decreased 1.75 – 2.3  $\mu\text{V}$ , peak latencies were longer by 0.06 – 0.11 ms, conduction velocity decreased by 0.71 – 1.1 m/s and onset latencies were longer by 0.043 – 0.072 ms at the follow up assessment (i.e.  $\sim 5$  years). Additionally, statistical analysis revealed that the change in peripheral nerve function is not linear over time. There was a 0.13 m/s decline in conduction velocity per year. Further analysis indicated that the rate of change between the nerve function

variables were significantly different, suggesting that the nerve function changes at different rates across time.

Lauretani et al. (2006)

The purpose of this study was to examine the effect of age on peroneal nerve function in older and younger adults. Compound muscle action potential (CMAP) was assessed to examine the motor nerve amplitude. Nerve conduction velocity was examined by dividing the length of the fiber and the time for the stimulus to travel from one point to the next. Muscle size and density was examined in the calf. Additionally, plantarflexion strength was assessed to determine muscle strength for each participant. Results of the study showed that there was a negative relationship between age and nerve conduction velocity. CMAP, muscle size and muscle density were lower as age increased. The age-related reduction in CMAP, muscle size and muscle density decline was faster for the women than the men. Additionally, a smaller CMAP was associated with a high probability of having a lower muscle density. The authors suggest that the reductions in muscle volume and density could be primarily due to the reduction in the number of motor axons, leading to a reduction in continual stimulation of those fibers.

Saeed and Akram (2008)

The purpose of this study was to examine the effects of age, sex, height, weight, and BMI on the sensory sural nerve function. Participants who were included in the study ranged in ages from 40 – 70 years of age. Results of the study showed that age was significantly related to sural nerve conduction velocity ( $r = -0.401$ ,  $p < 0.05$ ).

Additionally, the results of a regression analysis revealed that there was a reduction of 2.4

m/s in nerve velocity per ten years. Although insignificant, there was a relationship ( $r = 0.361$ ,  $P > 0.05$ ) between sensory latency and age. The authors suggest that the reduction in conduction velocity and increased latency could be due to a reduction in myelination of the peripheral nerves.

Strotmeyer et al. (2009)

The purpose of this study was to examine the effects of sensory-motor nerve function on muscle strength in older adults. Muscle strength in the quadriceps and ankle were measured for muscle strength. Sensory nerve function was assessed with monofilament touch sensitivity and vibration threshold. Additionally, motor nerve function was assessed in the peroneal nerve by assessing the nerve amplitude and conduction velocity. Results of the study showed that those older adults who had low sensory vibration thresholds and low motor nerve conduction amplitude were also associated with low quadriceps and ankle strength compared to those with high levels of peripheral nerve function. Further analysis revealed that monofilament insensitivity, vibration threshold, and motor nerve amplitude each contributed to the reduction in quadriceps strength. Monofilament and motor nerve amplitude were also independent predictors of ankle strength. The author suggest that the reduction in quadricep and ankle strength may be due to the relationship it has with sensory and motor nerve function declines in the older adults.

Thakur et al. (2010)

The purpose of this study was to examine the age-related effects on nerve function in younger and older adults. Motor nerve function was assessed by examining

the compound muscle action potential (CMAP). Sensory nerve function was assessed by examining the sensory nerve action potential (SNAP). Statistical analysis revealed that the older adults had a lower CMAP amplitudes were smaller in the bilateral median, right ulnar, right tibial, le tibial, and bilateral common peroneal nerve ( $p < 0.05$ ). CMAP durations were shorter in the right median, right ulnar, le ulnar, right tibial, le tibial, le common peroneal nerve ( $p < 0.05$ ). Older adults had a smaller CMAP latencies compared to the younger adults ( $p < 0.05 - 0.01$ ). SNAP amplitudes were lower in the older adults in the bilateral median nerve, right ulnar and right radial nerves ( $p < 0.05 - 0.01$ ). SNAP durations in the older adults were shorter when compared to the younger adults ( $p < 0.05 - 0.01$ ). SNAP latencies were longer in the older adults compared to the younger adults ( $p < 0.05$ ). The authors suggest that these data provide evidence of reduced sensory and motor nerve function in older adults.

Werner et al. (2012)

The primary aim of this study to examine the age-related changes in peripheral sensory nerve function in healthy adults. The study examined the distal median and ulnar nerves of the dominant hand of each participant. Additionally, the study had a longitudinal component to it where participants were examined at two or more time points over a 9 year span following baseline assessments. Peripheral nerve function variables included sensory nerve action potential (SNAP) amplitude, peak latency, onset latency and sensory conduction velocity (SCV). Results of the study show that onset and peak latencies increased over time and conduction velocities and amplitude declines with age ( $p \leq 0.002$ ). The rate of reduction in conduction velocity was 0.41 m/s per year for the median sensory nerve and 0.29 m/s per year for the ulnar sensory nerve. The

reduction in amplitude was 0.70 m/s  $\mu$ V per year for the median nerve and 0.89  $\mu$ V per year for the ulnar sensory nerve. The authors suggest that there is a significant change in peripheral nerve function with advancing age and that nerve function may differ between nerves.

Ward et al. (2014b)

The purpose of this study was to investigate the effects of peripheral nerve function on muscle power in older men. This longitudinal study examined older adults peripheral nerve function and muscle power over a 2 year span. Nerve function was examined in the peroneal motor nerve. Sensory nerve function was examined by monofilament touch perception and sural sensory nerve. Results of the current study found that a lower motor nerve amplitude ( $p < 0.05$ ) and sensory nerve ( $p < 0.05$ ) and monofilament sensitivity ( $p < 0.05$ ) was associated with muscle power. A lower sensory and motor amplitude was associated with a 1.4 – 1.8 fold aging effect. Additionally, insensitivity of 1.4 – 10-g monofilaments was associated with 2.2 – 3.4 year aging effect. Insensitivity to the smaller monofilament (1.4-g) was a significant predictor of reduced power production. The authors suggest that poor sensory nerve function was related to a reduced muscle power production in the older adults, and could lead to a reduced functional ability.

Ward et al. (2015)

The purpose of this study was to examine if sensorimotor function is a determinant for the reduction in strength associated with the aging process. This longitudinal study examined the isokinetic strength and sensory nerve function over a



span of 6 years. Peroneal motor nerve conduction velocity and amplitude were assessed. The sural sensory nerve function was assessed by monofilament and vibration detection. Results of the study show that poorer sensory and motor function predicted the lower strength and power capabilities. Additionally, a lower initial sensory function predicted lower strength in men and women and a faster reduction in strength in women. The authors suggested that poor nerve function (i.e. sensory and motor) was able to predict declines in strength and rate of decline in strength.

Palve and Palve (2018)

The purpose of this study was to examine the influence of aging on peripheral nerve function and determine the point where significant changes are apparent in younger and older adults. Peripheral nerve function was completed on the median, peroneal and tibial nerves in adults aged 18-60 years old. The distal motor latency (DML), motor nerve conduction velocity (NCV), and compound muscle action potentials (CMAP) were collected for the motor nerves. For the sensory nerves, sensory nerve action potential (SNAP) and sensory nerve conduction velocity (SNCV) were examined in the sensory nerves. Late responses were examined in H-reflex studies and the F-wave in the median, peroneal and tibial nerves. Results of the study show that with advancing age there was a significant increase in latency, smaller amplitude and slower conduction velocity in the sensory median nerve and the common peroneal nerve. The motor peroneal and tibial nerve showed a lower amplitude, longer latency, slower conduction velocity, and a greater H-reflex response (tibial nerve) with advancing age. There was significant negative correlations between tibial motor and sensory nerves with age. Additionally, H-reflex was positively associated with aging. The authors suggest the results provide

additional evidence that the older adults possess lower number of nerve fibers, smaller nerve diameter and change in fiber membrane properties. The authors also suggested that age significantly influences peripheral nerve function and delayed responses in multiple peripheral nerves.

#### *2.1.6 Summary of the Neural Determinants of Rate of Force development*

The aging process has been associated with changes in the neuromuscular system and has been linked to reductions in muscle strength (Piasecki et al. 2016), power (Clark et al. 2013) and functional ability (Izquierdo et al. 1999). Previous research has suggested that the body experiences the process of remodeling to compensate of the reduction in functional motor units to maintain muscle strength and function (Scaglioni et al. 2003). When performing a ballistic contraction, motor unit recruitment decreases and firing rates increase to provide adequate stimulation to produce elevated levels of force quickly (de Ruiter et al. 2007; Del Balso and Cafarelli 2007; Desmedt and Godaux 1978; 1977; Van Cutsem et al. 1998). During the aging process, high threshold motor units are preferentially lost, and the corresponding muscle fibers begin to atrophy. However, to preserve strength, the adjacent surviving lower threshold motor units begin to reinnervate those recently denervated fibers, commonly known as the remodeling process (McNeil et al. 2005). Although this process is a protective mechanism to preserve strength and function, it is associated with functional limitations. The rate of decline in motor unit number increases with advancing age and can lead to a reduction in muscle strength, power, functional ability and sarcopenia (Piasecki et al. 2018).

Motor unit number estimation (MUNE) is an assessment that non-invasively examines the surviving motor units in the neuromuscular system (Campbell et al. 1973). Although there are many methods used to examine MUNE in older adults, most studies have the same trend in common, a reduction in MUNE associated with advancing age (Doherty and Brown 1993; Gilmore et al. 2017; Kaya et al. 2013; McKinnon et al. 2015; McNeil et al. 2005; Piasecki et al. 2016). Additionally, older adults have larger, low threshold motor units thought to be caused by the collateral sprouting and reinnervation of recently vacated muscle fibers (Piasecki et al. 2016). For example, Piasecki et al. (2016) found that older adults had significantly larger single motor unit potentials (SMUP) and smaller compound action potential (CMAP) than younger adults in the vastus lateralis. The increased SMUP is thought to be due to the reinnervation of neighboring high threshold fibers, and the decreased CMAP is thought to be due to the reduction in number of fibers or available motor units (Doherty and Brown 1997). Due to the remodeling process, older adults are left with fewer larger, low threshold motor units that can precede the diagnosis of sarcopenia (Piasecki et al. 2018).

The remaining remodeled motor units have been shown to have an altered morphology, behavior and variability (Hourigan et al. 2015; Klass et al. 2008; Piasecki et al. 2016). Specifically, older adult motor units have been shown to have a lower discharge rate and reduced recruitment threshold when compared to younger adults during maximal contractions (Connelly et al. 1999; Dalton et al. 2010; Fling et al. 2009; Kallio et al. 2010; Kamen and Knight 2004; Kamen et al. 1995; Watanabe et al. 2016). This reduction in recruitment threshold and increased firing rate has been suggested to be the result of the remodeling process (Kamen et al. 1995; Ling et al. 2009). Klass et al.

(2008) observed the motor units recruited during a maximal RFD contraction had a significantly lower firing rate compared to the younger adults. Additionally, the altered motor units exhibit changes in the motor unit action potential shape and size. Previous research has observed larger single motor unit potential (SMUP) resulting in an increased force production per SMUP in older adults (Fling et al. 2009; Ling et al. 2009; Power et al. 2010). The larger SMUP is thought to be due to collateral sprouting of the surviving motor unit to include the more powerful neighboring muscle fibers leading to the increased force production per SMUP (Ling et al. 2009; Power et al. 2010). However, when maximally stimulated, older adults produce a reduced compound muscle action potential (CMAP) and lower corresponding twitch force (Fling et al. 2009; Scaglioni et al. 2003). The combination of increased SMUP and lower CMAP could be due to a lower number of functional high threshold motor units as a product of the remodeling process (Doherty and Brown 1997).

Muscle activation, assessed using electromyography (EMG), has been used to examine muscle activation. Previous research has shown that muscle activation during the initial phase of a rapid contraction is extremely important for producing high levels of force quickly (Aagaard et al. 2002; Hakkinen et al. 1998; Van Cutsem and Duchateau 2005; Van Cutsem et al. 1998) and has been shown to be highly related to the early production of force (i.e.  $\leq 80 - 100$  ms) (Klass et al. 2008; Mau-Moeller et al. 2013). Although some older adults may be able to voluntarily activate their muscles to a similar degree (Cannon et al. 2007; Power et al. 2010), older adults produce lower EMG amplitude than younger adults during a maximal RFD contraction (Gerstner et al. 2017a; Hakkinen et al. 1996; Hakkinen et al. 1995). This reduction in EMG amplitude has been

related to RFD in older adults. This suggests that neural activation within a limited time frame may be a limiting factor in RFD performance in the older adults (Barry et al. 2005; Clark et al. 2011; Wu et al. 2016). Additionally, the rate of muscle activation (i.e. rate of EMG rise) has been shown to be slower in the older adults and associated with a reduced RFD capacity (Barry et al. 2005; Clark et al. 2011). Additionally, Clark et al. (2013) found that the rate of EMG rise was related to leg press power and was observed to decrease about 9% per year. This observation is in agreement with Klass et al. (2008) who observed the reduced RFD in the older adults was accompanied by a reduction in motor unit discharge rate in the initial phase of the contraction. Further, the reduction in rate of EMG rise was associated with a reduced RFD and muscle power, strength and functional ability in older adults (Clark et al. 2011). These age-related reductions in voluntary muscle activation amplitude and rate is extremely important because RFD has been linked to functional ability and a better quality of life (Clark et al. 2011). However, other authors have observed no such age difference in rate of EMG rise. For instance, Thompson et al. (2014) found that there was a significant reduction in RFD in the older adults without a corresponding reduction in rate of EMG rise. Additionally, Jenkins et al. (2014) found differences in absolute rate of EMG rise and RFD, however when RFD and rate of EMG rise were normalized to max strength and EMG, the age differences disappeared. However, in Jenkins et al study, there was still a significant difference in M-wave amplitude and max strength. Therefore, taken together, the impaired ability to activate the musculature may be a significant limiting factor in RFD observed in the older adults.

Reduction in peripheral nerve function is another piece to the age-related changes in neuromuscular function. Age-related alterations to both sensory and motor peripheral nerve function has been observed to increase with advancing age (Bouche et al. 1993; Gregg et al. 2004; Palve and Palve 2018; Resnick et al. 2001; Resnick et al. 2000; Taylor 1984). Previous research has shown a distinct decline sensory and motor nerve conduction velocity and amplitudes on the older adults (Rivner et al. 2001; Saeed and Akram 2008; Strotmeyer et al. 2009; Thakur et al. 2010; Tong et al. 2004; Ward et al. 2015; Werner et al. 2012). Sensory nerve amplitudes have been shown to decline prior to motor nerves during the aging process (Taylor 1984). Further, declines in either sensory or motor nerve function could lead to have been linked to poor quadriceps strength and increased rate of strength decline (Ward et al. 2015). Specifically, motor amplitude has been shown to be reduced in older adults and is linked to a reduction in strength over time (Ward et al. 2015). It has been suggested that the reduction in motor nerve amplitude is due to the reduction in axonal availability (Lauretani et al. 2006). Previous research has shown that peripheral nerve function, mainly lower amplitudes, is related to muscle strength and power (Strotmeyer et al. 2009; Ward et al. 2015; Ward et al. 2014b).

## ***2.2 Contractile Determinants of Rate of Force Development***

### ***2.2.1 Age-Related Changes in Muscle Phenotype and Function***

Larsson et al. (1979)

The purpose of this study was to investigate the age related changes in the mechanical properties in the quadriceps, muscle strength and movement speed. The authors discovered that there was a significant age-related reduction in muscle strength

and movement speed. The decline in muscle strength and knee extension velocity began around the age of 50 years old. Further, Type II muscle fiber area was reduced in the older compared to the younger adults. This age-related reduction in type II muscle fibers was significantly related to maximum muscle strength. The authors suggested that the age-related decrease in powerful type II muscle fibers was a primary mechanism for the reduction in muscle strength.

Lexell et al. (1988)

In this cadaveric study, the authors sought to examine the effect of age on muscle fibers. Forty three previously healthy men were included in this study and separated into 5 age groups: 20 (n = 9, mean age: 19, age range: 15-22 year old), 30 (n = 9, mean age: 32, age range: 26-37 year old), 50 (n = 8, mean age: 51, age range: 49-56 year old), 70 (n = 9, mean age: 73, age range: 70-75 year old) and 80 (n = 8, mean age: 82, age range: 80-83 year old). Muscle fiber size, number, area, proportion and distribution of type I and type II fibers were collected and recorded. Results of the study found that after the age of 25 muscle area ( $p < 0.001$ ), total number of fibers ( $p < 0.001$ ) begins to decreased at an accelerated rate ( $p < 0.001$ ). Additionally, there was a significant decrease in type II fiber size associated with age ( $p < 0.01$ ). Age was shown to decrease the number of fibers that composed the whole muscle from 70% in the young and 50%. The authors suggested that the age-related atrophy of muscle is dependent on multiple complex reductions in muscle fibers and muscle fiber related variable (i.e. fiber size, and proportion).

Lexell and Downham (1991)

The purpose of this study was to examine the age-related changes in muscle fiber distribution and arrangement. Previously healthy males aged from 15-83 years old were included in this study and the fiber type distribution and arrangement was examined in the vastus lateralis muscle. In younger adults, fiber types are observed to be segregated, however, from the years of 30-60, there was considerable amounts of random fiber groupings. Above the age of 60, there was an excessive amount of random fiber grouping. The authors suggest that the muscle undergoes continual change (i.e. remodeling process) over the life span.

Hakkinen et al. (1995)

Refer to section *2.1.3 Age-Related Changes in Voluntary Muscle Activation*

Connelly et al. (1999)

Refer to section *2.1.3 Age-Related Changes in Voluntary Muscle Activation*

Roos et al. (1999)

The purpose of this study was to investigate the age related changes in isometric voluntary and evoked contractile properties and motor unit behavior in the quadriceps in younger and older adults. Results of the study described a 48% ( $p < 0.05$ ) decrease in muscle strength in the older adults. Further, there was no significant differences between voluntary muscle activation in the young and older adults. The slower contractile properties observed in the older adults shifted the force-time curve to the left ( $p < 0.05$ ). Older adults were weaker than the young and possessed a lower evoked twitch force and



slower contractile speeds. However, there was no age-related changes in motor unit firing rates at any contraction intensity. The main finding of the study was that stimulated twitch and voluntary forces were significantly lower in the older adults compared to the younger adults. The authors suggested that the changes in muscle strength is related to the reduction in contractile properties due to the non-significant differences in voluntary activation observed between the young and the older adults.

Aagaard et al. (2002)

Refer to section *2.1.3 Age-Related Changes in Voluntary Muscle Activation*

Scaglioni et al. (2003)

Refer to section *2.1.1 Motor Unit Behavior During Rapid of Ballistic Contractions*

D'Antona et al. (2003)

The purpose of this study was to examine the underlying mechanisms of reduced force and shortening velocity in older and younger muscle fibers. Results show that there was a reduction in type II muscle fibers associated with aging. Additionally, type I muscle fibers were 16% more frequent in the old compared to only 9% in the young. There was a significant atrophy of type I (-22%) and type IIa (-12%) following the aging process. Older adult's type I and type II muscle fibers produced significantly less specific strength compared to the younger adults, -22% and -16%, respectively. Shortening velocity of both fiber types (i.e. type I and type II) were slower in the older adults compared to the younger adults. The authors suggest that age effects the mechanical

properties of the muscle fibers. Specifically, the reduction in number of muscle fibers and the slowing of the muscle fibers observed in the older adults could lead to reductions in strength and muscle power.

Baudry et al. (2005)

The purpose of this study is to examine the age-related reduction in contractile properties with an electrically evoked contraction in the tibialis anterior in younger and older adults. Twitch response following a maximal strength contraction was assessed and used to examine the contractile properties of the muscle between ages. Statistical analysis revealed that muscle strength (MVC) was greater in the young compared to the older adults ( $p < 0.05$ ). There was an age-related reduction in the potentiated twitch torque following the maximal contraction observed in the old compared to the younger adults. This reduction in potentiated twitch force has been linked to an age-related change in muscle fiber (i.e. reduction in type II fibers). The authors suggest that the reduction in potentiated twitch force is linked to a reduction in muscle contractile performance.

Andersen and Aagaard (2006)

The authors sought to examine the voluntary and evoked contractile components related to the rate of force development (RFD). Specifically, the authors examined the relationship of contractile components in multiple 10 ms time increments from the start of a explosive force contraction. Twelve young healthy sedentary males (Age:  $23 \pm 3$  years old) performed voluntary and evoked maximal rapid force contractions with the knee extensors. During the evoked contractions, peak twitch RFD (tRFD; determined as the peak slope of the rising phase of the twitch curve), twitch time to peak torque (TPT;

defined as the time between the onset of torque to peak torque), Peak torque (PT), half relaxation time ( $1/2RT$ ; defined as the time from peak twitch torque to 50% peak twitch torque) and twitch peak torque (PT; defined as the time from onset to peak twitch amplitude torque). During voluntary RFD contraction, peak torque (MVC) was determined and contractile RFD was defined as the slope of the torque time curve during sequential 0-10 ms windows from 0 (onset) to 250 ms. Statistical analysis revealed that as the contraction continued the voluntary RFD relied more heavily on the MVC rather than the muscle twitch properties, and visa versa. Maximal muscle strength accounted approximately 80% of the variance in the later phase of the contraction (i.e. 150 – 250 ms) and voluntary RFD was only moderately related to the contractile twitch properties in the earlier portion of the RFD contraction (i.e. < 40 ms). Moreover, the relationship between the contractile twitch characteristics and voluntary RTD became insignificant after 50 ms from contraction onset. The authors suggested that different portions of the RFD contractions are dependent on different physiological mechanisms. Additionally, the moderate correlation observed between the contractile twitch properties and voluntary RFD suggest that there may be another physiological mechanism that could account for the unaccounted variance in the early portion of the RTD contraction.

Cannon et al. (2008)

The purpose of this study was to investigate the age-related changes in the contractile characteristics in younger and older adult women. Contractile properties were assessed through maximal voluntary and evoked twitch contraction force prior to and following a resistance training protocol. Max voluntary torque (MVC), peak twitch torque (PT), time to peak torque (TPT) and rate of torque development (RTD) were

collected prior to and following the resistance training protocol. Prior to the resistance training protocol, MVC ( $p < 0.05$ ), PT ( $p < 0.05$ ) and RTD ( $p < 0.05$ ) were significantly lower in older compared to the younger women. Following the resistance training protocol, twitch properties remained unchanged and there was no significant group differences following the training protocol despite an increase in MVC. The authors suggested that there is an age-related reduction in contractile properties. Additionally, the changes in strength following the resistance training protocol without significant changes in twitch properties suggest that there was no contractile properties adaptations.

Hvid et al. (2010)

This study examined the age-related effects of short-term immobilization on muscular function and fiber morphology. In a sample of twenty healthy younger ( $n = 11$ ,  $24.4 \pm 0.5$  years old) and older ( $n = 9$ ,  $67.3 \pm 1.3$  years old) men, mechanical function and muscle morphology was assessed prior to and following a short-term immobilization and again after a retraining period. Maximal isometric muscle strength (MVIC), dynamic muscle strength (MVC), rapid force development (RFD), relative RFD (relRFD; absolute RFD  $\div$  MVIC), contractile impulse, and contraction time (CT; defined as the time to reach  $1/6^{\text{th}}$ ,  $1/2$ , and  $2/3^{\text{rds}}$  of MVC from contraction onset) were examined. For the RFD variables, the slope of the torque-time curve during the 0-50 ms window and 0-100 ms window was used as early and late phases of the RFD contraction, respectively. Muscle samples were harvested from the vastus lateralis following the immobilization and retraining protocols and variables examined were: fiber type cross-sectional area (CSA), fiber type percentage and percent area. Correlations and changes between age following the two different time points were examined. Statistical analysis demonstrated

a significant reductions in RFD in the older adults compared to the young prior to the interventions (40-43%,  $p < 0.05$ ). Following the immobilization protocol, RFD was lower in the initial (i.e. 0-50) (36.2%,  $p < 0.05$ ) and later (i.e. 0-100) (24.9%,  $p < 0.05$ ) portion of the RFD curve in the older compared to the younger adults. Following the retraining, the RTD improved in both the young and the older men, however, RFD during the initial portion of the contraction remained reduced in the older adults from prior RFD. Type II muscle fiber area was lower in the old prior to immobilization (31.9%,  $p < 0.05$ ). Following the immobilization protocol, type II area was significantly reduced (13.2%,  $p < 0.05$ ). Further analysis observed a nonsignificant relationship between type II muscle fiber area and the initial phase of the RFD. The authors suggested that the retraining following the immobilization lead to a recapturing ability of the muscle fiber area in the young men, but not in the old. This suggests that older adults may be more at risk for decline in muscle function that can lead to a reduction in RFD.

Mau-Moeller et al. (2013)

Refer to section *2.1.4 Age-Related Changes in Motor Unit Number*

Nilwik et al. (2013)

The purpose of the study was to examine the effects of age-related changes in muscle size and if the age-related reduction in muscle size is attributed to the changes in muscle fiber size. Fifty one participants (young;  $n = 25$ ; Old;  $n = 26$ ) volunteered to participate in this study. Results of the study found that there was a significant decrease in CSA with age. Additionally, the older adults possessed a smaller type II muscle fiber size ( $p < 0.001$ ). The age differences in type II muscle fiber size fully explained the

differences in quadriceps size. The authors suggested that the reduced muscle size is mainly dependent on the reduction in type II muscle fiber size and can lead to a further loss of muscle fibers.

Power et al. (2016b)

The main goal of this study was to examine the effects of age on the contractile function of a single muscle fiber from young, old and old master athletes. Results of the study showed that, even when normalized to fiber size, the muscle fiber biopsied from the older and the older masters athletes were weaker than the younger muscle fibers. On top of the reduction in strength, the older groups fibers possessed a slower shortening velocity compared the younger adults. The rate of force development was significantly lower in the older groups compared to the younger groups. The authors suggest that the observed reduction in muscle contractile performant is not negated by physical activity.

McPhee et al. (2018)

The purpose of this study was to investigate the age-related effects and contributions of muscle size, specific force, muscle activation on weakness and sarcopenia. The results from the investigation showed that there was a 37% reduction in maximal muscle force (MVC), 25% decline in physiological cross-sectional area (PCSA), and in situ force was 83% lower in the older compared to the younger adults. Quadriceps volume was the primary predictor in the reduced MVC (76%,  $p < 0.001$ ). There was not significant contribution from pennation angle (PA), voluntary activation (VA), moment arm length (MAL) or gender to the regression model. During the 5 year follow up assessments, MVC decreased by 12%, quadriceps volume was lower by 6%, PCSA was

reduced by 5%, and voluntary activation was 4% lower. Following the regression analysis, quadriceps volume remained the main determinant (51%,  $p < 0.001$ ) for the reduction in MVC, however, voluntary activation accounted for an additional 21% ( $p < 0.001$ ) of the variance in max torque production. There was no significant difference between fiber type percentage of type I or type II muscle fibers, however, the old possessed a significant reduction in type II muscle fiber area (26%,  $p < 0.001$ ). Further analysis revealed, when all fibers were examined, older adults fibers (i.e. combination of type I and type II) was 15% lower and VL PCSA was smaller in the old compared to the younger adults. This result suggests that fiber atrophy accounts for over 50% of the reduction in muscle size. This leads to the older adults possessing less muscle fibers in the VL. The authors suggest that these data indicate that the reduction and loss of muscle fibers, especially the reduction in type II muscle fiber size, is primarily related to the age-related reduction in force and weakness.

### *2.2.2 Age-Related changes in Skeletal Muscle Size, Quality and Architecture*

Hakkinen and Hakkinen (1991)

The main goal of this study was to examine the effect of age on muscle size, maximal and explosive voluntary force production in women. Maximal force was determined as the highest force value achieved during the full isometric voluntary knee extension. The rate of force development (RFD) and rate of relaxation were also examined. Muscle cross-sectional area (mCSA) of the quadriceps femoris was determined. The younger and middle aged women had significantly larger mCSA, greater maximal force production, increased RFD, and shorter time to relative torque compared

to the older women. mCSA and maximal voluntary force were significantly related in all age groups. When force was normalized to muscle size, there were no significant differences in maximum voluntary force between any age group. The authors suggest that because the significant differences in muscle strength disappeared when made relative to muscle size, the reduction in explosive force production may be more related to neural activation than muscular properties. However, the authors do not rule out the possibility that age-related atrophy of powerful type II muscle fibers could lead to the observed declines in maximum and explosive strength observed in the older women.

Hakkinen et al. (1996)

The main objective of this study was to examine the influence of age on muscle cross-sectional area, maximal and explosive force production in knee extensor muscle in middle and older adults. Uni- and bilateral isometric maximal and explosive knee extension force was examined in both groups of adults. Voluntary peak torque, force-time, and relaxation time were assessed and analyzed to determine group differences. The force time variable was assessed in consecutive 100 ms windows from force onset. The maximal rate of force development was examined in each age group and uni- and bilaterally. Muscle activation was assessed through surface EMG from the vastus lateralis, rectus femoris and the vastus medialis. Peak muscle activation was assessed during the 500 – 1500 ms window following the initiation of contraction. Additionally, muscle activation during consecutive 100 ms windows following the onset of the contraction was examined. Muscle cross-sectional area (mCSA) was assessed from all three of the quadriceps muscles tested. Statistical analysis revealed that the maximal voluntary bilateral and unilateral knee extension was greater in the middle aged group



compared to the older adults. mCSA was significantly larger for the middle aged group compared to the older group. Additionally, mCSA was significantly related to muscle maximum voluntary strength in the middle and the older adults. However, when force was made relative to mCSA, only the older women produced significantly less torque than the other groups. EMG was not significantly different in any group during maximal uni- or bilateral knee extension. The middle age group had a larger RFD within the first 500 ms than the older groups during the unilateral, not in the bilateral knee extension. The authors suggest that the reduction in maximal strength and rate of rise in force could be due to the reductions in muscle size observed in the older population. The authors continue to suggest that the increased rate of decline in explosive force could be due to the age related reduction in fast twitch muscle fibers.

Hakkinen et al. (1998)

Refer to section *2.1.3 Age-Related Changes in Voluntary Muscle Activation*

Frontera et al. (2000)

These authors sought to examine the changes in skeletal muscle function over a 12 year longitudinal study. Each participant was assessed twice; once at the beginning of the study, and again at the end of the 12 years. Twelve older men voluntarily participated in the first testing session (age:  $65.4 \pm 4.2$  years old) and only nine returned for the second session (age:  $77.6 \pm 4.0$  years old) the study. Maximal isokinetic muscle strength and an index of local muscle endurance of the knee and elbow extensor and flexors were assessed at each time point. Computerized tomography (CT) scans of each of the muscle groups examined were used to determine the muscle cross-sectional area (mCSA).

Muscle biopsies were collected and analyzed to examine the percent distribution and area of type I and type II muscle fibers were calculated. Results from the study showed a 23.7 – 29.8% decrease in muscle strength in the knee extensor strength, and 9 participants showed a reduction in elbow extension and flexion strength. Additionally, the participants showed a significant reduction in muscle strength at higher velocities. Local muscle endurance showed a decrease of 2.3% following the 12 year follow up assessment. mCSA was 12.5 – 16.1% (reduced following the 12 years between testing sessions). The authors discovered that the loss of mCSA predicted 90% of the reduction in muscle strength produced at the second testing session. There was a significant reduction in type I fibers and capillary density following the 12 years of aging. From these results, the authors suggested that the mCSA was a significant contributor to the reduction in muscle strength associated with advancing age.

Kent-Braun et al. (2000)

The main purpose of this study was to examine the effects of age and physical activity on muscle quality in young and older adults. Twenty three young (Males; n = 12, age:  $33.7 \pm 5.3$ ; Females; n = 11, age:  $29.4 \pm 4.0$ ) and 21 older (Males; n = 11, age:  $72.2 \pm 5.9$ ; Females; n = 10, age:  $73.2 \pm 5.6$ ) volunteered to participate in the study. Muscle size and composition was assessed with a magnetic resonance imaging (MRI) machine. Men possessed a larger total contractile and non-contractile composition when compared to women ( $p < 0.001 - 0.003$ ). Younger adults possessed a larger contractile area and smaller non-contractile area when compared to older adults ( $p < 0.001$ ). Statistical analysis observed a significant inverse relationship between non-contractile and physical activity in the older adult ( $r = -0.68, p < 0.01$ ). These results suggest that the physical

activity levels in the older adults are related to the non-contractile components of the thigh. The results from this study found that older adults have a higher percentage of non-contractile tissue and a lower muscle size compared to younger adults, suggesting that there is a reduction in muscle quality as a result of aging.

Kubo et al. (2003)

The purpose of the study was to investigate the age-related differences in muscle architecture in young and older adults. Muscle architecture was examined by muscular ultrasound. Specifically, muscle architecture variables collected included muscle thickness, pennation angle and fascicle length. In the vastus lateralis, younger men had significantly greater absolute and relative muscle thickness compared to the older men. Younger adults had a significantly increased pennation angle compared to the older adults. Absolute fascicle length was lower in the young compared to the older men in the VL. Additionally, relative fascicle length was significantly longer in the older compared to the younger adults. The authors suggest that there is a significant effect of age on muscle architecture.

Narici et al. (2003)

This study sought to investigate the effect of age on muscle architecture. Twenty healthy adult men (young:  $n = 14$ , age range: 27 – 42 years old; Older:  $n = 16$ , age range: 70 – 81 years old) participated in this study consisting of analyzing anatomic cross-sectional area (ACSA), muscle volume (VOL), resting muscle fascicle length (Lf), pennation angle (PA) and physiological muscle cross-sectional area (PCSA) of the gastrocnemius medialis (GM). Computerized tomography (CT) was used to measure

ACSA, PCSA was measured as the ratio between VOL and Lf, pennation angle and fascicle length were assessed with an ultrasonography machine. Results showed that there was a significant decrease in ACSA (19.1%,  $p < 0.005$ ) and VOL (25.4%,  $p < 0.001$ ) compared to younger adults. Additionally, Lf and PA were reduced in the older adult compared to the young by 10.2% ( $p < 0.01$ ) and 13.2% ( $p < 0.01$ ), respectively. Further analysis observed a significant relationship between ACSA and PA ( $p < 0.05$ ) and a 15.2% reduction in PCSA in the older adults ( $p < 0.05$ ). The author suggested that the aging process significantly effects the muscle size and architecture. Additionally, the authors suggest that the reduction in the variable examined may lead to declines in muscle function which could lead to losses in functional ability.

Morse et al. (2005)

The purpose of this study was to investigate the age-related changes in muscle architecture in the triceps surae (i.e. soleus, lateral and medial gastrocnemius) and the functional implications of the observed changes in younger and older men. Magnetic resonance imaging was used to examine the muscle volume of each participant. Muscle architecture (i.e. fascicle length and pennation angle) was assessed using a B-mode ultrasound machine. Statistical analysis revealed that the muscle volume of all three muscles were lower in the old compared to the young. Older adults possessed a significantly reduced pennation angle compared to the younger adults. In the older adults, only fascicle length was significantly shorter in the medial gastrocnemius when compared to the young. Physiological cross-sectional area was significantly smaller in the old compared to the young in the lateral and medial gastrocnemius. The authors suggest that the reduction in the physiological cross-sectional area (i.e. ratio of muscle volume

and fascicle length) is a natural mechanism for the maintenance of force per cross-sectional area.

Goodpaster et al. (2006)

The purpose of this study was to examine the age-related changes in muscle size, strength and quality over a 3-year longitudinal study. Body and muscle composition was analyzed using a DXA. Quadriceps strength and muscle quality (torque per unit of muscle mass) were examined isokinetically and isometrically, respectively. Strength was lost at a faster rate than muscle mass. Age was independently associated with strength decline in both men and women. Muscle quality was decreased over the three years in both men and women. Interestingly, there was no strength maintenance associated with an increase in lean mass. The authors suggest that the reduction in muscle mass is related to muscle strength and quality decline in older adults.

Thom et al. (2007)

Refer to section 2.3 *Age-Related Changes in the Force-Velocity Curve*

Hvid et al. (2010)

Refer to section 2.2.1 *Age-Related Changes in Muscle Phenotype and Function*

Fukumoto et al. (2012)

The main purpose of this study was to examine the relationship between muscle echo intensity, muscle strength and body composition. Participants in the study ranged in age from 51 – 87 years old. Maximal knee extensor strength was used as muscle strength.

B-mode ultrasound assessments were completed to examine the muscle thickness, fat thickness and echo intensity of the rectus femoris. Body composition was assessed with a bioelectrical impedance analysis machine. EI and muscle thickness was significantly related to age and muscle strength. Age and BMI were also related to muscle strength. Further statistical analysis showed that EI and muscle thickness were independently related to muscle strength. Specifically, EI had a negative relationship with muscle strength. The authors suggest that muscle quantity and quality independently contribute to the age-related reduction in muscle strength and could be used to examine functional ability status in older adults.

Stenroth et al. (2012)

This study examined the age related differences in Achilles tendon properties and triceps surae muscle architecture in vivo. One hundred healthy younger ( $n = 33$ ; age:  $24 \pm 2$  years old) and older ( $n = 67$ ;  $75 \pm 3$  years old) volunteered to participate in this study. This study consisted of assessing Achilles tendon cross sectional area (CSA) and length, gastrocnemius medialis (GM) and soleus (SOL) anatomical CSA (ACSA), fascicle length (FL) and pennation angle (PA) using a ultrasonographic machine. Additionally, max plantarflexion force was assessed. Statistical analysis observed an age related decrease in Achilles tendon stiffness ( $p < 0.01$ ), lower muscle thickness in the SOL and GM (9%,  $p < 0.05$ , 13%,  $p < 0.001$ ), GM muscle size was 15% smaller ( $p < 0.01$ ), smaller tricep surae muscle size ( $p < 0.05$ ), shorter FL ( $p < 0.05$ ) in older adults when compared to the younger counterparts. Plantarflexion max force was significantly associated with tendon stiffness ( $r = 0.580$ ,  $p < 0.001$ ). The authors suggest that older adult's tendons may adapt

alongside the GM during the aging process. They further suggested that the tendon properties adapted to the reduced level of activity intensity observed in the older adults.

Strasser et al. (2013)

The aim of this study was to examine the reproducibility and age differences in muscle size and architecture in young and older sarcopenic adults. Anthropometric, knee extension strength and hand grip strength measures were collected for each participant and used for future analysis. A 2 dimensional B-mode ultrasound was used to examine the muscle architecture of the rectus femoris, vastus intermedius, and vastus lateralis. From these images the authors analyzed the pennation angle and echo intensity of the muscle. Results showed that the older adults had a significantly reduced muscle strength and handgrip strength compared to the younger adults. All muscles assessed were thinner in the younger compared to the older adults. Pennation angles in the vastus lateralis were lower in the older adults compared to the younger adults. Echo intensity was significantly greater in the old compared to the younger group. Muscle strength was significantly related to muscle thickness. Muscle strength was observed to be related to increased pennation angles in the young group. The authors suggest that the data shows that muscle thickness is a reliable method of monitoring sarcopenia.

Thompson et al. (2013)

The purpose of this study was to examine the effects of age on maximal and rapid torque production. Participants were split into 3 groups; a young, middle-aged, and older group. Rate of torque development (RTD) was calculated in 4 different time intervals (0-30, 0-50, 0-100 and 0-200 ms after torque onset). Additionally, relative RTD was

collected (10-50% of max torque) was assessed. PT, peak RTD and the later phase RTD (i.e. 0-100 and 0-200ms) variables were significantly reduced compared to the younger participants ( $p \leq 0.05$ ). Early phase RTD (i.e. 0-30 and 0-50ms) was lower for the older men when compared to the younger and middle aged men. Estimated thigh cross-sectional area (eCSA) was also lower in the middle and older men compared to the younger adults ( $p = 0.001 - 0.016$ ). The authors suggested that the reduction in eCSA and RTD variables observed in the older adults indicated that muscle mechanisms may be an important factor in the reduction in the age related declines in strength and RTD.

Watanabe et al. (2013)

The purpose of this study was to examine the associations between muscle quality and strength in older adults. Participants in the study ranged in age from 65-91 years old. Echo intensity (i.e. based on the pixel intensity in the region of interest in the muscle) was determined based on the gray scale analysis. Maximum isometric torque of the knee extensors was completed to assess muscle strength. Statistical analysis showed that the echo intensity score was significantly related to muscle strength. Muscle thickness was negatively related to muscle strength. Echo intensity was shown to have a positive relationship with age and fat thickness. Echo intensity was negatively associated with muscle strength. The authors suggest that muscle quality (assessed by echo intensity) was independently related to muscle strength and the age-related changes in muscle quality (assessed by echo intensity) play a role in strength decline.



Nishihara et al. (2014)

The purpose of this study was to examine the echo intensity (EI) and motor functions in young and older adults. Each participant's motor function was assessed by undergoing a battery of functional ability tests (i.e. normal and fast gait, TUG and maximum knee extension strength). Ultrasound images of the quadricep femoris (i.e. rectus femoris and vastus intermedius) were collected using a B-mode ultrasound machine. Muscle thickness and echo intensity was assessed from the same images. The older adults had a lower functional ability than the younger adults. The older adults also had a lower quadricep femoris thickness and a greater EI than the young in both rectus femoris and vastus intermedius. There was a significant positive correlation between rectus femoris thickness and muscle strength in both the young and the older adults. EI was negatively correlated with vastus intermedius and quadricep femoris thickness. The mean frequency in the region of interest (MFROI) of the rectus femoris was negatively correlated with quadricep femoris thickness. The authors suggest that the examination of the MFROI could provide valuable information about functional declines during the aging process.

Rech et al. (2014)

Although this study did not examine the age-related differences in muscle quality, echo intensity and rate of torque development, the study highlights important relationships between skeletal muscle and rate of torque development. In this study 40 older women volunteered to participate. This study examined muscle quality (specific tension = knee extensors peak torque ÷ muscle size), echo intensity (EI), muscle

thickness (MT), hand grip strength (HG), 30 second sit to stand test (30SS), usual gate speed (UGS), knee extension peak torque (PT) and rate of torque development (RTD) during different time frames (0-50, 0-100, 0-250, 0-300 ms). All muscle variables (i.e. EI, MT, CSA) were collected from the quadricep femoris using an ultrasound. Statistical analysis revealed a significant relationship between EI and 30SS ( $r = -0.505$ ,  $p < 0.01$ ), UGS ( $r = -0.347$ ,  $p < 0.05$ ) and isometric peak torque ( $r = -0.314$ ,  $p < 0.05$ ). Further, quadriceps EI was negatively associated with 30SS ( $r = -0.493$ ,  $p < 0.01$ ) and peak torque ( $r = -0.409$ ,  $p < 0.01$ ). However, the EI of the quadriceps femoris was found to be significantly related to RTD 0-100, 250, and 300 time frames. This suggests that the morphological characteristics may play an increased role in the later phases on the RTD contraction in the older adults. The authors suggested that EI might be a significant characteristic in functional performance and RTD in older adults.

Wilhelm et al. (2014)

Similar to the previous study by Rech et al. (2014), this study examined the relationships between morphological characteristics and RTD in the older adult population. Although this does not describe any age-related changes, it does however provide evidence about how the morphological characteristics effect RTD and functional performance. Specifically, the authors examined the effects of whole quadriceps echo intensity (EI) on muscle power, strength and function. Fifty sedentary older men (age:  $66.1 \pm 4.5$  years) volunteered to participate in this study. The quadriceps echo intensity (QEI), knee extension one repetition maximum (1RM), peak isometric knee extension torque (PT), rate of torque development during 0-50 (RTD<sub>0-50</sub>) and 0-200 (RTD<sub>0-200</sub>) ms (RTD), muscle power (MP), 30 second sit to stand functional assessment (30SS), and

countermovement jump performance (CMJ) were collected and analyzed. Statistical analysis revealed that QEI was significantly related with 1RM ( $r = -0.657$ ,  $p < 0.05$ ), PT( $r = -0.628$ ,  $p < 0.05$ ), RTD<sub>0-50</sub> ( $r = -0.320$ ,  $p < 0.05$ ), and RTD<sub>0-200</sub> ( $r = -0.501$ ,  $p < 0.05$ ). Specifically, QEI was more related to the later time point than the early RTD time point. The authors suggested that muscle EI may be a significant component on functional ability and muscular performance.

Fukumoto et al. (2015)

The purpose of this study was to examine the age-related changes in muscle quality in women. Muscle thickness and echo intensity were examined in the biceps brachii, quadriceps femoris, rectus abdominus external oblique, internal oblique and transversus abdominis by transverse ultrasound imaging. Specifically, the young-old (i.e. 65-74 years old) and the old-old (i.e. 75-92 years old) had significantly thinner quadricep femoris values compared to the younger group. The old-old group possessed significantly thinner quadricep femoris values than the middle-aged group ( $p < 53-64$ ). The younger group had significantly lower echo intensity scores compared to the middle, young-old, and old-old groups. The authors suggest that the data presented indicate that declines in muscle quality may occur prior to reductions in muscle quantity.

Wu et al. (2016)

Refer to section 2.1.3 *Age-related Changes in Voluntary Muscle Activation*

Gerstner et al. (2017a)

Refer to section 2.1.3 *Age-related Changes in Voluntary Muscle Activation*

Magrini et al. (2018)

The purpose of this study was to investigate the age-related differences in muscle size and strength, specific tension, echo intensity and functional performance in physically active younger and older adults. Additionally, the authors examined the age differences between the same variables listed above. Maximal isometric muscle strength (MVIC), a maximal functional ability test (i.e. maximal one repetition sit to stand test), muscle cross-sectional area (mCSA), specific strength (i.e. strength per unit of muscle mass), and muscle quality of the rectus femoris were collected and used for analysis. Statistical analysis revealed that MVIC was significantly related to mCSA in the older women. Additionally, there was a significant association between specific strength and echo intensity in the older adults and not in the younger adults. The authors suggested that the physical activity observed in the older adults may have maintained specific muscle strength (i.e. strength per unit of muscle mass). The authors go on to suggest that the significant relationship between specific strength and echo intensity in the older adults, but not in the younger adults, suggest that muscle quality assessed by echo intensity may be a more beneficial muscle quality test in the older than younger adults.

### *2.2.3 Summary of the Contractile Determinants of the Rate of Force Development*

Previous research has shown that intrinsic contractile, fiber content and morphological variables significantly influence RFD (Gerstner et al. 2017a; Hakkinen et al. 1996; McPhee et al. 2018). One explanation for this relationship is that the later phase of a maximal voluntary RFD contraction is dependent on the contractile variables in the muscle. Specifically, muscle size and muscle strength has been shown to be highly

related, however maximal strength does not occur until well after 200ms from contraction onset (Aagaard et al. 2002; Andersen and Aagaard 2006; Hakkinen et al. 1998). Once the muscle is activated, it relies on the intrinsic contractile properties to produce force. However, with advancing age, these intrinsic contractile properties have been shown to degrade leading to a reduced RFD.

The aging process has been associated with a reduction in muscle mass and function, which is partially due to the age related remodeling process (Frontera et al. 2000; Lexell et al. 1988). Previous research has shown that older adults tend to lose powerful type II muscle fibers with advancing age (Larsson et al. 1979; Lexell and Downham 1991; Lexell et al. 1988). The reduction in type II muscle fibers has been associated with a reduction in muscle size, quality, strength, and power and contraction velocity (Larsson et al. 1979). The percentage of type II muscle fibers in a muscle is positively associated with maximal strength and RFD capabilities (Nilwik et al. 2013; Power et al. 2016b). Muscle fiber type has been associated with the rapid rise in force during a maximal RFD contraction (Hvid et al. 2010), therefore a reduction in the proportion of type II muscle fibers will have a significant effect on RFD.

In addition to the change in muscle fiber composition and organization, aging has been shown to influence the contractile properties in the muscle (Andersen and Aagaard 2006). Directly stimulating the motor nerve can provide valuable information about the contractile properties of the muscle without the influence of voluntary neural activation. Older adults have been shown to produce a greater force at lower evoked intensities (Baudry et al. 2005). However, the RFD achieved during an evoked contraction has been shown to be lower in the old than the young indicating significant reductions in the

contractile speed of the muscle (D'Antona et al. 2003; Hakkinen et al. 1995). Older adults also have a prolonged twitch duration and reduced relaxation time compared to younger individuals (Cannon et al. 2008; Mau-Moeller et al. 2013), further suggesting that older adult contractile properties are effected by the remodeling process (Connelly et al. 1999; Scaglioni et al. 2003). The increased force production per motor unit activated, increased contraction time and rate of half relaxation time has been suggested as a compensatory mechanism to counteract the decline in type II muscle fibers and to achieve required levels of force during the aging process (Cannon et al. 2008).

Both the fiber type proportion and the intrinsic contractile properties of skeletal muscle play a significant role in the RFD contractions, however, the morphological and architectural structure of the muscle also plays a part in the development of force (Gerstner et al. 2017a; Roos et al. 1999; Strasser et al. 2013; Thom et al. 2007; Thompson et al. 2013; Wu et al. 2016). Muscle size and quality have been shown to be related to strength and RFD capabilities in the older adult populations (Fukumoto et al. 2012; Hakkinen and Hakkinen 1991; Kent-Braun et al. 2000; Kubo et al. 2003; Nishihara et al. 2014; Stenroth et al. 2012; Watanabe et al. 2013). Specifically, older adults have been shown to have a lower amount of muscle mass and muscle quality, which is undoubtedly due to the remodeling process associated with advancing age (Goodpaster et al. 2006; Rech et al. 2014). Muscle size and quality are both negatively correlated with the RFD production and functional ability in older adults (Fukumoto et al. 2015; Magrini et al. 2018; Rech et al. 2014; Wilhelm et al. 2014). Additionally, previous research has observed a smaller pennation angle and fascicle length in the older population was significantly related to RFD capabilities (Morse et al. 2005; Narici et al. 2003; Stenroth et

al. 2012), however other investigations only report a significant reduction in pennation angle and no age differences in fascicle length (Gerstner et al. 2017a).

### ***2.3 Age-Related Changes in the Force-Velocity Curve***

Harries and Bassey (1990)

The purpose of this study was to examine the relationship between muscle strength and movement velocity in a knee extension movement in young and older women. Seven different movement velocities were examined from 0 rad/s<sup>-1</sup> to 300 rad/s<sup>-1</sup>. Maximum torque was examined at each movement velocity and used for statistical analysis. The younger adults were significantly stronger at every movement velocity compared to the older adults. As velocity increased torque decreased in a similar fashion, however the degree of decline was faster for the older adults compared to the younger adults. Average torque produced at the fastest angular velocity was significantly lower in the older group compared to the younger group. Additional analysis revealed that the influence of angular velocity on torque production was significantly different between age groups. The authors suggest that these data indicate that older women may be limited by their ability to produce force rapidly. Further, the authors suggest that the reduction in physical activity may lead to the reduction of high threshold motor units which may be an important factor contributing to the reduction in torque at high velocities.

Lanza et al. (2003)

The purpose of this study was to examine the age comparison of torque production during isokinetic contractions and the torque-velocity and power-velocity relationships in the ankle dorsiflexors and knee extensors in younger and older adults.

Isometric knee extension and ankle dorsiflexion was assessed to determine muscle strength. During the isovelocity contractions each participant performed a series of contractions from 30°/s - 240°/s for the dorsiflexors and 60°/s - 400°/s for the knee extensors. Torque produced at peak isovelocity was used for statistical analysis. Statistical analysis revealed that younger adults produced significantly more isometric torque compared to the older adults in both the knee extensors and ankle dorsiflexors. Some participants in the older groups were unable to reach the target velocity, thus not producing any torque. This was especially relevant during the high velocity knee extension  $\sim 270^\circ/\text{s}$  and  $\sim 210^\circ/\text{s}$ . Young were able to reach target velocity faster than the older group. Across all velocities, the older adults produced less torque than the younger adults. Normalized torque developed at isovelocities (normalized to max strength), the older adults produce lower torque at all velocities compared to the younger adults. Specifically, at the highest velocity achieved, the older adults produced less torque than the younger adults. Further, older adults had an impaired ability to produce power at higher velocities when compared to the younger adults in the knee extensors. At the highest velocity achieved, the power produced was significantly lower in the older adults compared to the younger adults. The authors suggest that these data provide valuable information about the reduced capacity to produce torque and power at high velocities in older adults. The authors suggest that the results may be due to the reduction in the contractile properties due to the aging process.

Petrella et al. (2007)

The purpose of this study was to examine the influence of age on the determinants of the force-velocity curve in younger and older adults. Body composition was assessed



using DXA and thigh lean mass was collected and used to determine specific strength and power. Each participant's one repetition maximum load was determined and used to calculate the required loads that needed to be lifted for the load-power and load-velocity assessments. Muscle activation was assessed using EMG RMS at a specific knee angle during a sit-to-stand task. The EMG RMS was normalized to EMG RMS collected during the isometric strength testing. One repetition max strength, specific strength increased from week one to week 8 in both young and older adults. In the older adults, neural activation was significantly lower during the sit-to-stand task at week 8 compared to baseline. The load-power curve improved in the old and young group at week 8, and peak concentric velocity improved in the older adults. Interestingly, after the training protocol, there was no significant difference between the young and older adults in movement velocity at any load. The authors suggest that these results provide evidence that training at high velocities can lead to neuromuscular adaptations in older adults. These changes could be observed as early as 8 weeks of resistance training.

Thom et al. (2007)

The purpose of this study was to examine the influence of muscle architecture on the age-related differences in torque-velocity and power-velocity relationships of the plantarflexors in the younger and older adult men. Muscle volume was assessed by magnetic resonance imaging. Muscle strength was measured isometrically and isokinetically. Muscle architecture was assessed by examining ultrasound images and analyzing the fascicle length. The physiological cross-sectional area (PCSA) was determined by the ratio between muscle volume and fascicle length. Results of the study showed that older adults possessed a lower muscle volume, smaller fascicle length and

smaller PCSA compared to the younger participants. Isometric strength and shortening velocity of the younger adults was greater than that of the older adults. The older adult produced significantly lower torque at all contraction velocities. The torque-velocity plots were significantly shifted to the left (i.e. lower torque at specific velocity) compared to the younger adults. Absolute peak power and optimum velocity at peak power were lower in the older adults. When peak power was normalized to muscle volume, the younger adults produced 72% higher peak power compared to the older adults. When torque was normalized to PCSA, older adults still produced less torque compared to the younger adults. When normalized to fascicle length max velocity produced by the older adults was ~77% of the max velocity produced by the younger adults. Further analysis revealed that fascicle length accounted for less than 20% of the difference between young and older max velocity production. The authors suggest that muscle architecture is an important component in the torque- and power-velocity curves in the older adults. The authors also indicate that the intrinsic muscular properties may influence power production in the older adults.

Yamauchi et al. (2010)

The purpose of this investigation was to examine the age-related difference in maximum force, unloaded velocity and power production in the leg muscles in young and older adults. Participants of the study ranged in ages from 18 – 82 years old. Muscle function was examined using an isokinetic dynamometer leg press. The participants were instructed to press the force plate away from the starting position to full extension as fast and strong as possible. In order to examine the force velocity relationships, the dynamometer was set in an isotonic mode and the participant pressed against it to

examine the force power relationship. Results of the study show that there was a significant negative relationship between age and max force production. When max force was normalized to body weight, the negative correlations between age and max force increased. Max velocity nor normalized max velocity with body weight was not correlated with age. Max power and normalized max power to body weight was negatively related to age and was seen to decline with advancing age. The authors suggested that these data presented displayed a significant reduction in the force-generating ability with advancing age. However, there was no age-related reduction in muscle shortening velocity. The authors suggest that the reduction in the force generating ability in the muscles could lead to the reduction in muscular power production associated with the aging process.

Callahan and Kent-Braun (2011)

The main purpose of the study was to examine the age differences in and contributions of the force-velocity curve and the ability to maintain force during a fatiguing task in younger and older women. Maximal strength was assessed isometrically and dynamically. Voluntary activation was assessed by the interpolated twitch protocol to examine the central voluntary activation. Magnetic resonance imaging was used to determine the quadricep cross-sectional area (CSA). Peak strength was normalized to CSA to provide a relative strength value. Statistical analysis revealed that the older adults produced significantly less isometric torque compared to the younger adults. Additionally, the older adults were able to produce significantly less torque during the dynamic force-velocity assessment at each force increment. Specifically, there was a progressively increased decline in torque as velocity increased in the older adults. The

stimulated rate of torque development was not significantly different between age groups, however the half relaxation time was slower in the older adults. CSA was highly correlated with muscle strength in both age groups. However, CSA was not significantly related to the torque production during the dynamic contractions. The authors suggest that other physiological factors may be more important to the production of dynamic torque at high velocities.

Pojednic et al. (2012)

The purpose of this study was to investigate the age-related relative importance of force- and velocity-based measures of muscle performance could explain power production in middle, healthy old and older mobility limited adults. Torque and power were assessed using an isokinetic dynamometer. The stair climb and chair rise functional assessments were used to examine functional ability. Computed tomography (CT) was used to examine the cross-sectional area (CSA) of the thigh. Results show that in the middle-aged adults, torque, not velocity, was positively associated with power production. In the older healthy adults, torque and velocity were associated with power. In the older mobility limited adults, velocity was associated with power production, not torque. Velocity production accounted for the chair rise and stair climb inter-individual variability across all subjects. Velocity production was only associated with chair rise performance in the older mobility limited older adults. The authors suggest that the data presented in the article indicates that velocity is an important determinant of power production. Further, the authors suggest that the neural and muscular mechanisms needed for velocity production may be compromised to a greater degree than those of force production.

Jenkins et al. (2015a)

The purpose of this study was to investigate torque, power, rate of velocity development and muscle activation during isometric and dynamic knee extension tasks in younger and older adults. Further, the authors intended to examine the effects of normalization on peak torque, rate of velocity development, and EMG amplitude in the vastus lateralis and rectus femoris muscles during isokinetic knee extension at 1.05 and 3.14  $\text{rad}\cdot\text{s}^{-1}$ . Additionally, the authors sought to examine the percent decrease or increase in peak torque or mean power, respectively. Statistical analysis revealed that isometric peak torque was lower in the older compared to the younger adults. Additionally, peak torque was lower in both isokinetic velocities compared to the younger adults. The percent decrease of peak torque was greater in the older adults compared to the younger adults from 1.05 to 3.14  $\text{rad}\cdot\text{s}^{-1}$ . Absolute mean power was greater in the younger at 1.05 and 3.14  $\text{rad}\cdot\text{s}^{-1}$ . Additionally, when mean power was normalized, the percent increase in mean power from 1.05 to 3.14  $\text{rad}\cdot\text{s}^{-1}$  was greater in the young compared to the older adults. EMG was greater during the isometric knee extension in the young compared to the older adults. The authors suggested that when peak torque and mean power were normalized to max strength, there were no more age differences. However, there still was significant differences in torque- and power-velocity relationships between the young and the older adults. The authors go on to suggest that there may be other physiological determinants to explain the magnitude of the percent differences.

Alcazar et al. (2017)

The purpose of this study was to investigate the reliability of force-velocity testing in the older adult population. The force velocity assessment began by instructing the participants to lift 40% of their body weight as fast as possible on a leg press machine. The load was then increased in 5 kg increments until the participant was unable to move the weight. The velocity was recorded during each maximal effort contraction. The highest mean velocity was recorded for each of the repetitions. Additionally, 2 sets of three repetitions were performed at 60% of the max value. This was done to examine the reliability of power production. Results of the study showed that there was a significant relationship in force and velocity in all of the older participants. Max power was shown to explain a moderate amount of functional ability variability in the older adults. The results indicated that force-velocity assessments were reliable in the older populations.

Alcazar et al. (2018)

The purpose of this investigation was to examine the force-velocity profile, muscle power, mental and physical function and quality of life in the older adults. Additionally, the authors examined the underlying mechanisms of the force velocity profile that may lead to a reduction in muscle power. Each participant performed a series of functional ability, mental and quality of life tests. Maximum power was assessed on a leg press machine. Muscle composition was assessed by the use of DXA. The study examined if force or velocity was the limiting factor in the production of power during the leg press exercise and determined that a reduction of either force production or

velocity production would lead to a reduction in maximum power. Results showed that relative max power was significantly related to physical function and health related quality of life score. Absolute max power was associated with cognitive function and frailty. Although, the authors observed force and velocity deficits in the participants, neither force nor velocity produced a significant reduction in max power production. However, when compared to the non-deficit group, the velocity and force deficit groups showed a significant harmful effect on maximum power. Additionally, when compared to the non-deficit group, the force and velocity deficit groups scored lower in physical functioning, health related quality of life and higher frailty scores. The main underlying mechanisms for the force deficit group were skeletal muscle mass and specific force (i.e. force produced per unit of muscle mass). However, there were no significant relationships between muscle mass and the velocity deficit group. The authors suggest that the results of the study indicate that muscle power deficits are caused by reductions in either force or velocity, and deficits in force or velocity were associated with lower cognitive, functional and physical quality.

### *2.3.1 Summary of Age-Related Changes in the Force-Velocity Curve*

As previously discussed, aging is associated with significant alterations in the neural and muscular systems leading to a reduction in force, velocity and power production (Harries and Bassey 1990). Because of these physiological changes observed during the aging process, previous research has shown an alteration in the force-velocity relationship in older adults (Alcazar et al. 2017; Alcazar et al. 2018; Callahan and Kent-Braun 2011; Jenkins et al. 2015a; Lanza et al. 2003; Petrella et al. 2007; Pojednic et al. 2012; Thom et al. 2007; Yamauchi et al. 2010). Muscle power has been shown to

decrease at a faster rate than just muscle strength along (Izquierdo et al. 1999). Therefore, it would be logical to examine the components that create power (i.e. force x velocity) (Alcazar et al. 2018).

Previous research shown that the force-velocity relationship shifts downward and to the left during the aging process (Lanza et al. 2003). Movement velocity between the young and the older adults have been shown to be significantly different (Jenkins et al. 2014; Lanza et al. 2003; Pojednic et al. 2012). Specifically, at low isokinetic speeds, older adults are unable to produce the same amount of torque as their younger counterparts (Thom et al. 2007). The decline in torque production is even higher at high velocities, in fact some older adults are unable to move fast enough to produce torque (Frontera et al. 2000; Lanza et al. 2003). These observations in the older adults suggests that some age-related physiological mechanisms (i.e. contractile or neural) that may be limiting the torque production. Even though normalization can eliminate the age differences in strength and power production, Jenkins et al. (2015a) observed significant age differences in the magnitude of decline in strength and power production at each velocity tested between the young and older adults. This result could be due to the shift in fast twitch to slow twitch muscle fibers leading to a reduction in torque and power.

However, the specific contributions of force or velocity to the production of power are disputed (Pojednic et al. 2012; Yamauchi et al. 2010). Recently, Alcazar examined the reliability of an individualized force velocity profile in the older adults and found that it is an efficient method to determine either force or velocity deficits (Alcazar et al. 2017). Previous research has suggested that power production is dependent on the velocity characteristics of the muscles. On the other hand, others have suggested that



force is the limiting factor in power production in older adults. To end the dispute, Alcazar et al. (2018) found that deficits in either force or velocity can contribute to the reduction in power. However, an individualized force-velocity profile could be extremely beneficial to developing more efficient exercise programs aimed at improving power and, as a result, functional ability (Alcazar et al. 2018).

## CHAPTER III

### METHODOLOGY

#### *3.1 Participants*

Twenty young (18-35 yr old) and 17 older (65+ yr old) men volunteered for this investigation. All participants were independent and community dwelling individuals who were able to visit the laboratory for each testing session. This study was approved by the Oklahoma State University Institutional review board for human participant research. Prior to any testing, all participants completed an informed consent, pre-exercise health and exercise status survey. Further, participants completed a customized physical activity questionnaire to quantify what physical activities the participant engages in and the frequency of participation in those activities. Participants included in the study were free from any musculoskeletal dysfunctions or circulatory/edema pathologies involving the hip, knee, or ankle joints. Additionally, participants were free from any neurological disorders. All musculoskeletal and neurological disorders were self-reported.

### ***3.2 Research Design***

The study consisted of 3 separate visits to the lab each lasting approximately 90 minutes. Each session was separated by at least 48 hrs within  $7 \pm 2$  days. Participants were instructed to refrain from any lower body exercise 24-36 hours prior to each testing session. On the first visit, following the informed consent and completion of the required paperwork, each participant will complete a short familiarization session consisting of all of the movements required during that testing session. Then the participant completed the motor unit number estimation (MUNE) and evoked twitch assessments of the quadriceps muscle group. Then the participant's motor nerve function was assessed. Following the MUNE, evoked twitch, and motor nerve assessments, participants performed a series of maximal voluntary isometric contraction (MVIC) and rapid (rMVIC) knee extensions. The muscles that were examined were the vastus lateralis (VL), rectus femoris (RF), and the vastus medialis (VM) on the right leg. On the second visit, participants completed a one repetition maximum (1RM) unilateral knee extension assessment on the right leg where the load that was lifted was adjusted in ~10 lb increments until a maximum load is reached. On the third visit, ultrasound (US) assessments were performed to quantify the muscle size, quality and architecture. Following the US assessments, the participant's height, and weight was measured. Following the anthropometric testing, participants completed an isokinetic assessment on the right leg. Below is a summary of each visit:

1. First Visit (in order):
  - a. Familiarization session
    - i. Practice each movement required in the session
  - b. MUNE and Evoked Twitch assessments

- c. Motor nerve function
  - d. Three MVIC knee extensions
  - e. Three rMVIC knee extensions
2. Second Visit (in order):
- a. 1 RM testing with load-controlled torque velocity curve
3. Third Visit (in order):
- a. US assessment
  - b. Height and weight
  - c. Isokinetic 1RM knee extension

### ***3.3 Instrumentation and Procedures***

#### ***3.3.1 Ultrasonography***

Ultrasound (US) images of the right thigh muscles including the vastus medialis (VM), rectus femoris (RF) and vastus lateralis (VL) muscles was obtained using a diagnostic US imaging device (GE Logic S8, Milwaukee, WI, USA) with a linear array probe (model ML6-15-D, 4-15 MHz, 50-mm field view). Participants were instructed to lay supine and on their left side on an adjustable padded plinth with their legs completely relaxed and knees bent at approximately 10°. Participants were required to rest for 5 minutes prior to the collection of the US images. Panoramic US images of the right VM, RF, and VL were taken at 80%, 50% and 50% of the distance between the right anterior superior iliac spine (ASIS) and the medial femoral epicondyle, superior portion of the patella and lateral femoral epicondyle, respectively. During each panoramic US scan, the investigator placed the probe perpendicular to the skin and advanced the probe laterally along the skin above the muscles in a slow, consistent manner. During each scan, great

care was taken to limit muscle compression beneath the probe. A generous amount of water-soluble transmission gel was applied to the skin to enhance acoustic coupling (Wilhelm et al. 2014). Muscle cross-sectional area (mCSA) and echo intensity (EI) were optimized for image quality using musculoskeletal mode prior to all image acquisitions using a gain of 50 dB and a frequency of 12Hz. Depth was constant between each participants and muscles to keep the pixels per cm standard between participants. Panoramic US images were captured until two uniform scans with acceptable image quality were collected (Jenkins et al. 2015b). Additionally, panoramic US images of muscle architecture were collected. The US probe was placed on the skin in a similar fashion as the mCSA and EI measurement, however, the probe was oriented in line with the femur. Pennation angle (PA) of the VL was determined as the angle between the fascicle and the deep aponeuroses (Franchi et al. 2015). The US settings will be held constant between participants.

One investigator (M.A.M.) performed all US scans. US image analysis was performed using Image-J software (National Institutes of Health, USA, Version 1.50i). Each image was individually calibrated from pixels to cm using the straight-line function in image-J. mCSA and EI of each of the quadriceps muscles (i.e., VL, RF, and VM) for the two images were analyzed by defining a region of interest that included as much muscle as possible, without including any bone or fascia, using the polygon function in the image-J software. EI was determined using computer-aided gray scale analysis using the standard histogram function and was measured in arbitrary units (au) with values ranging from 0 (black) to 255 (white). mCSA, EI, and VL PA values will be recorded, averaged and used for further analysis.

The muscle mCSA for each of the quadriceps muscle were added together to create a composite mCSA (PmCSA) that was used for further analysis. Additionally, muscle quality (MQ<sub>EI</sub>) was determined as a weighted value that took into account mCSA and EI of each muscle assessed. MQ<sub>EI</sub> was determined as a weighted value by calculating the relative contribution of each muscle (VL, RF, VM) to the total quadricep mCSA and multiplying each muscle's mCSA by the same muscle's EI (Jenkins et al. 2018). The formula is below:

$$MQEI = \left[ \left( \frac{VL \text{ mCSA}}{\text{composite mCSA}} \right) \times VL \text{ EI} \right] + \left[ \left( \frac{RF \text{ mCSA}}{\text{composite mCSA}} \right) \times RF \text{ EI} \right] \\ + \left[ \left( \frac{VM \text{ mCSA}}{\text{composite mCSA}} \right) \times VM \text{ EI} \right]$$

Finally, a total mCSA (TmCSA) that accounted for each muscle's EI (i.e., VL, RF, VM) was calculated by dividing the PmCSA and the MQEI. This, in theory, provides a better measure of muscle size accounting for the EI assessed physiological variables.

### 3.3.2 Electromyography

Surface electromyographic (EMG) signals were collected from the VL, RF, and VM muscles using a signal acquisition system (MP150WSW, Biopac Systems, Inc.; Santa Barbara, CA, USA). In an effort to minimize skin impedance and optimize signal quality, the skin was shaved, abraded and cleansed with isopropyl alcohol prior to the placement of the surface electrodes (Beck and Housh 2008). Two pre-gelled surface electrodes (Ambu A/S, Baltorpbakken, Denmark) were placed on the skin directly over the muscle belly in line with the muscle fiber orientation in a bipolar fashion (Lieber and

Friden 2000) on each muscle. The surface electrodes were placed at a standardized percentage of thigh length from the anterior superior iliac spine (ASIS) to the knee joint space (VL: 66%, RF 50%, VM: 80%) to avoid the innervation zone of the each of the muscles (Hermens et al. 1999). A reference electrode was placed on the center of the patella of the same limb.

### *3.3.3 Voluntary Maximal Strength Assessment*

For all voluntary isometric testing, participants were seated with straps securing the trunk, hips and left thigh on a calibrated isokinetic dynamometer (Biodex system 3; Biodex Medical Systems, Inc. Shurley, NY, USA). The participant's lower right leg was secured to the dynamometer lever arm approximately 1 inch above the lateral malleolus. The axis of rotation of the dynamometer head was aligned with the lateral epicondyle of the right femur. Each participant's hip angle was held constant at 120° between the thigh and the trunk. The lower leg was positioned at 90° of knee flexion. Participants warmed-up by performing 2, 3 second contractions at 50% and 75% of their perceived effort with 30 seconds of rest between contractions. Following the warm up and 2 minutes of rest, 2, 3-4 second maximal voluntary isometric contractions (MVIC) of the knee extensors were performed and recorded with 2 minutes of rest between each contraction. For each MVIC contraction, the participants were instructed to kick out "as hard as possible" for the full 3-4 second contraction. Max voluntary torque (MVT) was defined as the highest average instantaneous torque produced during any of the MVIC contractions.

### *3.3.4 Voluntary Rapid Strength Assessment*

Following the MVIC contractions and a 5 minute rest period, 2 rapid maximal voluntary isometric contractions (rMVIC) were performed separated by 1 minute of rest to reduce the effect of fatigue on performance. During the rMVIC, the participant was instructed to kick out “as hard and as fast as possible” and hold the contraction for approximately 3 seconds. The peak torque produced during the rMVIC was defined as the highest average instantaneous torque produced during the rapid maximal voluntary contraction (rMVT). Torque and EMG measurements were collected simultaneously and were averaged across the two rMVIC contractions. Torque was measured at 50, 100, 150, and 200 ms from onset of torque. The RTD during each of these time periods was defined as the change in torque divided by the change in time ( $\Delta\text{torque}/\Delta\text{time}$ ). RTD was measured at separate, consecutive 50 ms time windows following the onset of torque, 0-50 (RTD<sub>0-50</sub>), 50-100 (RTD<sub>50-100</sub>), 100-150 (RTD<sub>100-150</sub>), and 150-200 (RTD<sub>150-200</sub>). The RTD was expressed in absolute terms. The EMG RMS was collected during each rMVIC contraction in consecutive 50ms time windows from EMG onset. Additionally, the rate of muscle activation (RER) was examined during the first 50 ms of each rMVIC and averaged between contractions. EMG measurements were normalized to M-wave and were expressed as a percentage of maximal muscle activation (%Mpp). Additionally, electromechanical delay (EMD) was assessed from the time difference from the onset of EMG to the onset of torque. For all MVIC and rMVIC contractions, participants were instructed to avoid any countermovement prior to the maximal effort voluntary contractions. If the torque produced during the second knee extension for both the MVIC and rMVIC was 10% higher than the first contraction, a third contraction were



completed. The two most similar, and best contractions were used for further analysis. However, none of the participants needed completed more than two attempts for each contraction.

### *3.3.5 Motor Unit Number Estimation and Electrically Evoked Twitches*

Motor unit number estimation (MUNE) was collected using the incremental method. This method examines MUNE by obtaining the maximal compound muscle action potential (CMAP) and a single motor unit potential (SMUP) (McComas et al. 1971; McComas et al. 1993). MUNE was quantified by dividing the maximal CMAP by the size of the mean surface-recorded SMUP. Formula is presented below:

$$MUNE = \left( \frac{CMAP}{SMUP} \right)$$

To collect each of these variables, transcutaneous electrical stimuli was delivered via a cathode-anode arrangement using high voltage (maximal voltage = 100 mA) stimulus from a constant-current electrical stimulation cart (Cadwell Sierra Summit, Cadwell Industries, Inc., Kennewick, WA, USA). The cathode probe (Cadwell Stimtroller *Plus*, Cadwell Industries, Inc., Kennewick, WA, USA) was pressed into the femoral triangle over the femoral nerve and the anode was a disposable surface electrode (40 x50mm, Technomed Medical Accessories, Amerikalaan 71, Netherlands) fixed over the right greater trochanter. Recording electrode (20x27mm, Cadwell Industries, Inc., Kennewick, WA, USA) was placed next to the surface EMG sensors (66% of the distance between the ASIS and lateral femoral epicondyle). The reference and the ground electrodes were placed on the quadriceps tendon and on the medial malleolus, respectively. The optimal stimulation probe position was determined by delivering single

low-voltage exploratory stimuli (20-30 mV) with the cathode probe. Probe location was selected based on visual inspection of the twitch force and the CMAP amplitudes. Once the optimal probe position was attained, the spot was marked and was used for all motor evoked twitches. The MUNE protocol consisted of several submaximal manual step-wise increases in stimulation from baseline (no M-wave produced). Any similar M-waves, indicative of alternation, were deleted from analysis using a cross-correlation of the difference between the current stimulation and the previous stimulation. Each stimulation was administered every 15 seconds to ensure neuromuscular recovery. MUNE was derived by the software included with the stimulation cart using the equation provided above. The CMAP, SMUP and MUNE values will be presented on the monitor and recorded.

Following the MUNE protocol, additional step-wise increases in a single stimulus (a single square wave impulse) stimulation were delivered from baseline (no M-wave) until M-wave reaches a plateau. During each of the step-wise increases in electrical stimulation, torque, and EMG were simultaneously collected and recorded. Once the M-wave plateau was achieved, two supramaximal single electrical (i.e. 120% of maximal M-wave stimulation, single square wave impulse at 100 Hz) stimulations were administered. The last maximal evoked twitch was used to examine the peak twitch torque (SGL PTT), rate of torque development during the first 50 ms of torque response (SGL RTD<sub>0-50</sub>), peak rate of relaxation (SGL pRR), and EMD (SGL EMD) of the quadriceps muscles. SGL PTT was defined as the highest torque achieved following torque onset and was examined as absolute (Nm) and relative to MVT (%MVT). SGL RTD<sub>0-50</sub> was defined as the slope of torque production for the first 50 ms following torque

onset and was examined in absolute ( $\text{Nm}\cdot\text{s}^{-1}$ ) and relative ( $\text{nSGL}_{0-50}$ ) to the single peak twitch torque (% PTT). The SGL pRR was defined as the steepest negative 50 ms slope following PTT and was examined in absolute ( $\text{Nm}\cdot\text{s}^{-1}$ ) and relative ( $\text{nSGL pRR}$ ) to single peak twitch torque (% PTT).

Following the single step-wise increases in stimulation and short rest period, an additional two evoked contractions were administered with a doublet stimulus (200 ms duration square-wave impulse at 100 mA) to examine maximal muscle activation and maximal twitch torque. The mean M-wave peak-to-peak (Mpp) amplitude of the two stimulations was defined as the maximal M-wave (Mmax). Mmax was used for the normalization of the voluntary EMG variables. Variables collected from the doublet stimulations included the peak doublet torque (DBL PTT), doublet rate of torque development for the first 50 ms (DBL RTD<sub>0-50</sub>), and doublet peak relaxation rate (DBL pRR). The DBL PTT, DBL RTD<sub>0-50</sub>, and DBL pRR were analyzed the same as the singlet twitches. The doublet twitch responses were examined in absolute (Nm) and a normalized ratio of PTT to MVT (nDBL PTT). For DBL RTD<sub>0-50</sub> and DBL pRR, the variables were expressed in absolute (Nm) and relative (nDBL RTD<sub>0-50</sub> and nDBL pRR) to peak twitch torque (% PTT). The ratio of PTT and MVT in the nSGL PTT and nDBL PTT was used to isolate and examine the peripheral properties of the quadriceps muscle groups without central nervous system influence (Jenkins et al. 2017).

### *3.3.6 One Repetition Maximum Assessments and Torque-Velocity Curves*

Each participant completed a 1 repetition maximum (1RM) knee extension on a calibrated isokinetic dynamometer set in isotonic mode. The participant was seated in the machine with their waist and torso secured to the seat and their knee flexed to 90°. From

this position, the participant was instructed to kick out against the padded lever arm of the dynamometer “as hard and as fast” as they can until the participant reaches the top of the range of motion (180° of knee extension). The weight was increased in a step-wise fashion from a low load (~20 lbs) to a maximal load where the participant is unable to extend the leg to the top of the range of motion. Each contraction was separated by a 2 minute rest period to prevent the effect of fatigue on performance. The velocity produced during at each load was collected from the calibrated isokinetic dynamometer. Each participant continued the stepwise increase in load until they were unable to complete the full range of motion.

Once a maximal load is achieved, a force-controlled torque-velocity curve was completed where each participant performed 4 different knee extensions with different loads. Participants were be instructed to lift a randomly assigned load “as fast and as hard” as they can at 5 different intensities (20%, 40%, 60%, 80%, and 100%) relative to the previously determined 1RM. The torque (Nm) and velocity (Deg/s) was collected from a calibrated isokinetic dynamometer set in isotonic mode.

On a different testing session, a velocity-controlled torque-velocity curve was also be collected. Participants completed 4 different speeds of isokinetic knee extensions with two minutes of rest between each repetition on the same calibrated isokinetic dynamometer. Participant’s knee angle was positioned at 90° and strapped into the dynamometer. Then, the participants was asked to kick against the lever arm as “hard and as fast” as possible to move the lever arm to the top of the range of motion (180°). Participants performed 2 repetitions of each muscle action at 5 different speeds: slow (60°/sec), medium slow (180°/sec), medium (180°/sec), medium fast (240°/sec) and fast

(300°/sec). Isotonic torque-velocity relationships have been shown to be reliable and valid when using multiple loads (Alcazar et al., 2017). Loud verbal encouragement was provided during all the 1RM and force velocity curves assessments.

### *3.3.7 Motor Nerve Function Assessments*

The motor nerve function assessment was conducted on the right femoral nerve using an automated nerve conduction study device using the same stimulation cart detailed previously. For the femoral motor nerve function, a surface recording electrode (20x27mm, Cadwell Industries, Inc., Kennewick, WA, USA) was placed on the belly of the VL. The reference electrode (20x27mm, Cadwell Industries, Inc., Kennewick, WA, USA) was placed on the lateral portion of the patella. The same stimulation probe (kept identical to the evoked twitch and MUNE protocol) was placed in the femoral triangle, just lateral to the femoral artery over the femoral nerve. Motor nerve conduction velocity (CV) was assessed from the time difference between the electrical stimulus and the onset of CMAP.

### *3.4 Signal Processing*

All torque and EMG signals were sampled simultaneously at 2 kHz with a data acquisition system (MP100WSW, Biopac Systems, Inc.; Santa Barbara, CA, USA), stored on a personal computer and processed off-line with a custom written analysis program (Labview v. 17.0, National Instruments, Austin, TX, USA). EMG signals were amplified (gain = 1000) using a differential amplifier (MP100WSW, Biopac Systems, Inc.; Santa Barbara, CA, USA) with a common mode rejection ratio of 110 dB min. The EMG signals were rectified, zero-meaned and digitally filtered using a zero-phase shift

4<sup>th</sup>-order Butterworth filter with a band pass of 10 – 499 Hz. To determine RER, the rectified EMG signals were linear enveloped by applying a zero-phase shift, 4<sup>th</sup>-order, low-pass Butterworth filter with a cut off frequency of 10 Hz (Beck and Housh 2008; Jenkins et al. 2014). EMG RER was calculated as the slope of the EMG-time curve in during the first 50 ms following EMG onset. EMG variables were expressed as absolute and relative to M-wave (%Mpp). The torque signals were zero-meaned, low-pass filtered using a zero-phase shift 4<sup>th</sup>-order Butterworth filter with a 15 Hz cutoff. All subsequent analyses were completed using these filtered signals. Torque and EMG onset were manually detected by the same investigator (M.A.M) from the filtered signals to provide a more accurate analysis of torque and EMG variables (Tillin et al. 2013).

### ***3.5 Statistical analysis***

Descriptive statistics of the participants are displayed in a table as means  $\pm$  standard deviations (SD). RTD values were expressed in absolute (Nm and Nm/s) terms to better examine age related adaptations. Statistical analysis will be performed using SPSS v. 22 (SPSS Inc., Chicago Illinois, USA), and the type-I error rate will be set a priori at 5%.

A 2 x 4 way mixed model ANOVA (group x RTD time window [RTD<sub>0-50</sub>, RTD<sub>50-100</sub>, RTD<sub>100-150</sub>, RTD<sub>150-200</sub>]) was completed to examine the differences between age-groups in the predictor variables (PmCSA, VL PA, MQ<sub>EI</sub>, MUNE, EMG<sub>0-50</sub>, EMG<sub>50-100</sub>, EMG<sub>100-150</sub>, EMG<sub>150-200</sub>, nEMG<sub>0-50</sub>, nEMG<sub>50-100</sub>, nEMG<sub>100-150</sub>, nEMG<sub>150-200</sub>, nRER<sub>0-50</sub>, EMD<sub>V</sub>, SGL PTT, SGL pRR, SGL EMD, DBL PTT, DBL pRR, MVT, CMAP, SMUP, Motor CV). Significant interactions were decomposed with follow up, multiple one-way ANOVAs. If the data was not normally distributed and/or spherical, a Welch's test was

used to examine age differences for all variables. Pearson correlation coefficients were used to examine the relationships between the predictor variables and each RTD time frame collapsed across age. Additionally, separate correlations were run to examine the relationship between the predictor variables and each RTD time window in each age group. Following the Pearson correlation coefficients, stepwise multiple regression analysis was used to examine which of the predictor variables (PmCSA, VL PA, MQ<sub>E1</sub>, TmCSA, MUNE, EMG<sub>0-50</sub>, EMG<sub>50-100</sub>, EMG<sub>100-150</sub>, EMG<sub>150-200</sub>, nEMG<sub>0-50</sub>, nEMG<sub>50-100</sub>, nEMG<sub>100-150</sub>, nEMG<sub>150-200</sub>, nRER<sub>0-50</sub>, EMD<sub>v</sub>, SGL PTT, SGL pRR, SGL EMD, DBL PTT, DBL pRR, nSGL PTT, nSGL pRR, nDBL PTT, nDBL pRR, MVT, CMAP, SMUP, Motor CV) independently explained a significant proportion of the total variance in RTD variables (RTD<sub>0-50</sub>, RTD<sub>50-100</sub>, RTD<sub>100-150</sub>, RTD<sub>150-200</sub>) across age and for each age group. Only variables that were significantly related to each RTD time window in across age and within each age groups were used in the regression analysis. This was done in an attempt to improve the statistical value of each stepwise regression.

For the torque-velocity curves, linear regression analysis was used to examine the line of best fit for the load controlled and the velocity controlled torque-velocity curves. Once the best fit is determined, separate one-way ANOVAs were used to examine the age differences in the slope for each of the force velocity curves (velocity controlled vs. load controlled). Following the one-way ANOVAs, Pearson's correlation coefficients were used to examine the relationships between the predictor variables and the slope for each force-velocity curve across age.

## CHAPTER IV

### RESULTS

#### *4.1 Descriptive Statistics*

Twenty young men and seventeen older men completed all three testing sessions. Demographic data for the two age groups are presented in table 1. Older men were significantly weaker when compared to the younger men ( $p \leq 0.001$ ). However, there were no significant differences in height or weight between ages (Table 1).

**Table 1. Demographic data for the Younger and Older men**

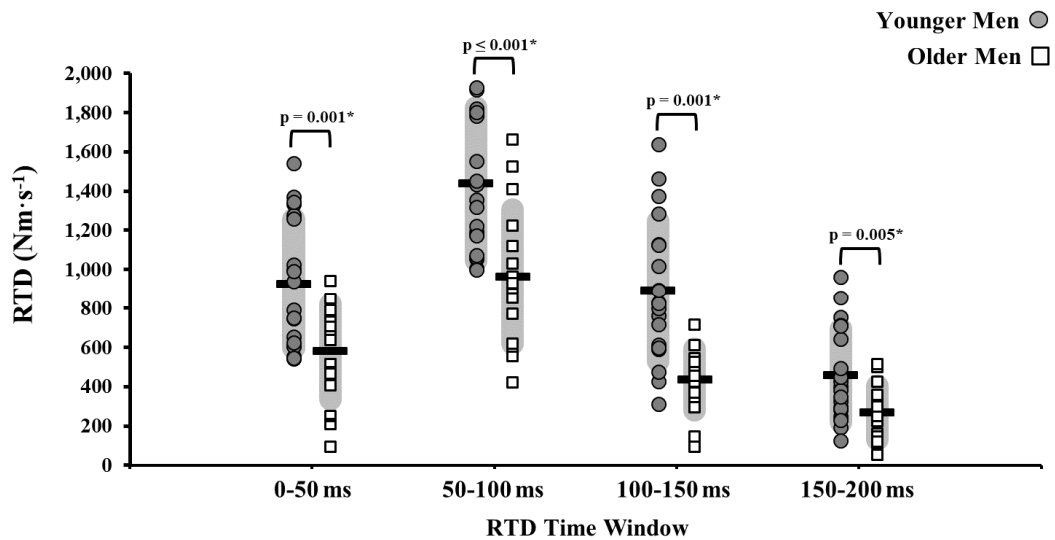
	<b>Younger Men (n = 20)</b>	<b>Older Men (n = 17)</b>	
	<b>Mean <math>\pm</math> SD</b>	<b>Mean <math>\pm</math> SD</b>	<b>p-value</b>
<b>Age (yrs)</b>	23 $\pm$ 3	74 $\pm$ 6.2	$\leq 0.001^*$
<b>Height (cm<sup>2</sup>)</b>	176.83 $\pm$ 7.29	175.39 $\pm$ 4.89	0.505
<b>Weight (kg)</b>	87.49 $\pm$ 15.63	85.12 $\pm$ 13.86	0.754
<b>MVT (Nm)</b>	259.97 $\pm$ 99.05	132.66 $\pm$ 22.38	$\leq 0.001^*$

\* = Significant differences to the 0.05 level



#### 4.2 Effects of Age on the Rate of Torque Development

The two-way ( $2 \times 4$ ) mixed model ANOVA (age-group x RTD time window [RTD<sub>0-50</sub>, RTD<sub>50-100</sub>, RTD<sub>100-150</sub>, RTD<sub>150-200</sub>]) showed that the data was not spherical ( $p = 0.002$ ) or equally distributed. Specifically, RTD<sub>100-150</sub> and RTD<sub>150-200</sub> was not equally distributed ( $p = 0.005$  and  $p = 0.030$ , respectively). Therefore, a Welch's test was used to examine the age differences in RTD time window. Each obtained Welch's F ratio was examined at the significance level of 0.05. The older adults produced significantly less torque during RTD<sub>0-50</sub> ( $F_{(1,34.33)} = 13.707$ ,  $p = 0.001$ ), RTD<sub>50-100</sub> ( $F_{(1,34.33)} = 15.550$ ,  $p \leq 0.001$ ), RTD<sub>100-150</sub> ( $F_{(1,26.792)} = 26.141$ ,  $p = 0.001$ ), and RTD<sub>150-200</sub> ( $F_{(1,34.33)} = 6.531$ ,  $p = 0.005$ ) (Figure 1).



**Figure 1.** Age differences in explosive force production during each 50 ms time periods. \* = Significant relationship to the 0.05 level.

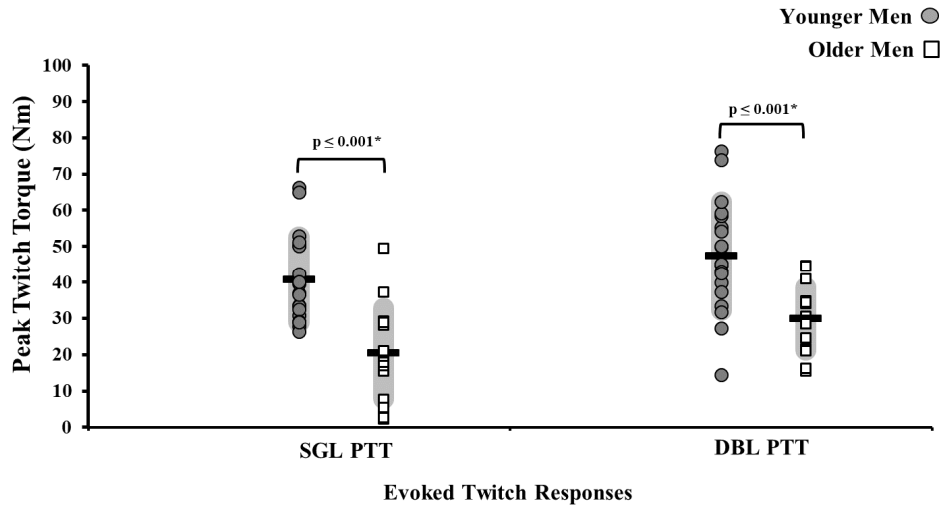
### ***4.3. Effects of Age on the Neural, Contractile and Morphological Characteristics***

#### *4.3.1. Neural Characteristics*

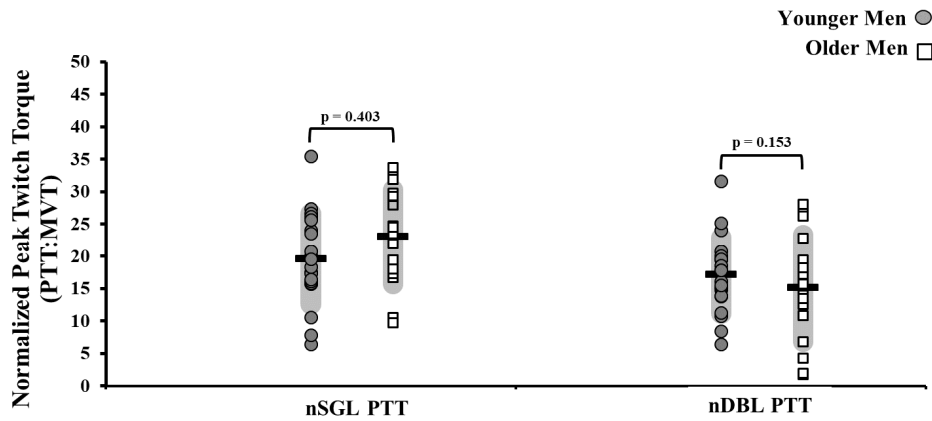
The statistical analysis revealed that older adults had a slower Motor nerve CV ( $F_{(1,35)} = 33.043$ ,  $p \leq 0.001$ ), smaller aEMG<sub>50-100</sub> ( $F_{(1,35)} = 5.914$ ,  $p = 0.020$ ), aEMG<sub>100-150</sub> ( $F_{(1,32.027)} = 7.999$ ,  $p = 0.008$ ), aEMG<sub>150-200</sub> ( $F_{(1,35)} = 4.234$ ,  $p = 0.047$ ), and larger nEMG<sub>50-100</sub> ( $F_{(1,35)} = 16.536$ ,  $p = 0.001$ ) amplitude. Additionally, older men had a higher nEMG<sub>0-50</sub> ( $F_{(1,21.661)} = 6.357$ ,  $p = 0.020$ ) and nEMG<sub>150-200</sub> ( $F_{(1,35)} = 14.186$ ,  $p = 0.001$ ). Older men had a lower MUNE ( $F_{(1,35)} = 65.630$ ,  $p \leq 0.001$ ) and a smaller CMAP ( $F_{(1,35)} = 45.584$ ,  $p \leq 0.001$ ). Interestingly, there was no significant differences in SMUP ( $F_{(1,35)} = 0.043$ ,  $p = 0.843$ ), suggesting that the lower MUNE observed in the older men is due to the lower CMAP since MUNE is the ratio of SMUP and CMAP.

#### *4.3.2. Contractile Characteristics*

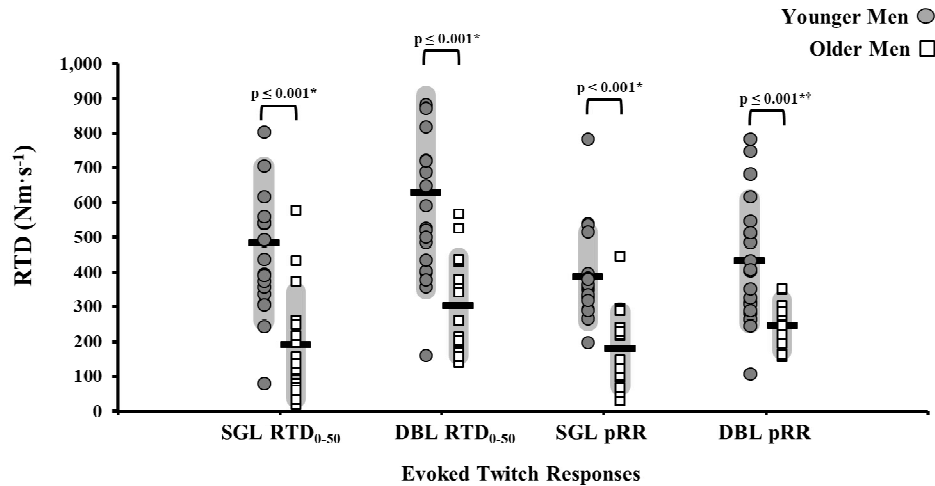
Further, older adults produced a lower SGL PTT ( $F_{(1,35)} = 26.137$ ,  $p \leq 0.001$ ), slower SGL RTD<sub>0-50</sub> ( $F_{(1,35)} = 21.317$ ,  $p \leq 0.001$ ), slower SGL pRR ( $F_{(1,35)} = 28.134$ ,  $p \leq 0.001$ ), and longer SGL EMD ( $F_{(1,24.321)} = 6.615$ ,  $p = 0.017$ ) when compared to the younger adults (Figure 2, 4). For the doublet evoked contraction condition, the older men produced significantly lower DBL PTT ( $F_{(1,35)} = 17.626$ ,  $p \leq 0.001$ ), reduced DBL RTD<sub>0-50</sub> ( $F_{(1,29.066)} = 21.182$ ,  $p \leq 0.001$ ), and slower DBL pRR ( $F_{(1,25.740)} = 18.072$ ,  $p \leq 0.001$ ) compared to the younger men (Figure 2, 4). When normalized, there were no longer any age differences in the DBL and the SGL twitch responses (Figure 3) between younger and older men, except for a significantly higher nDBL RTD<sub>0-50</sub> ( $F_{(1,8.968)} = 19.139$ ,  $p = 0.007$ ) (Figure 5). Age-related differences in predictor variables are presented in table 2.



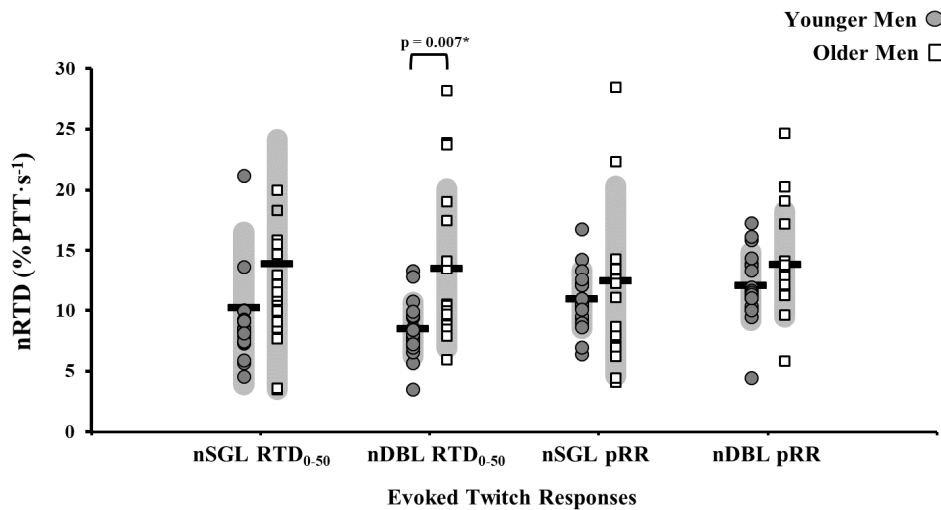
**Figure 2.** Age differences in absolute peak twitch torque from a single and doublet electrical stimulus in the younger and older men. \* = Significant relationship to the 0.05 level.



**Figure 3.** Age differences in normalized peak twitch torque (PTT:MVT) following a single (SGL PTT) and doublet (DBL PTT) stimulus between younger and older men. \* = Significant relationship to the 0.05 level.



**Figure 4.** Age differences in evoked twitch RTD from a single and a doublet stimulus between younger and older men. \* = Significant relationship to the 0.05 level.

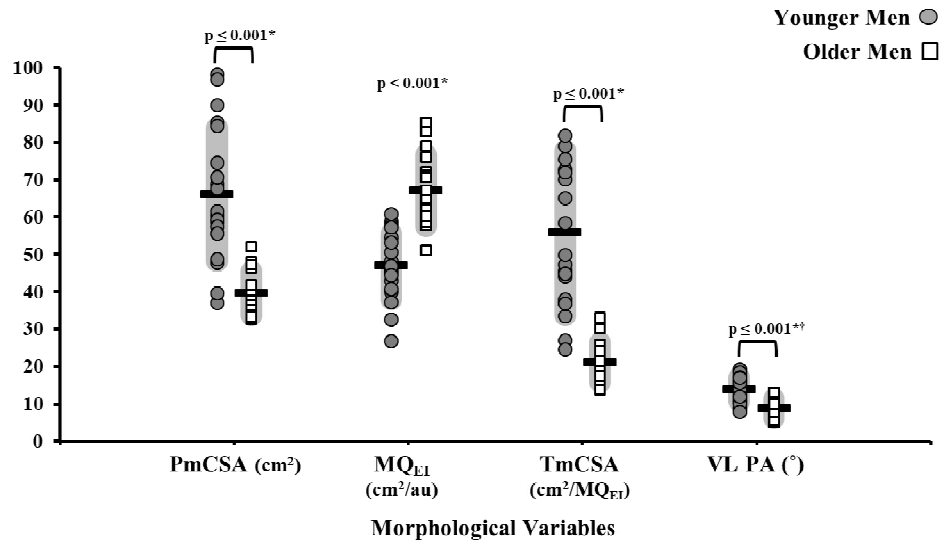


**Figure 5.** Age differences in the normalized twitch variables in the younger and older men. \* = Significant relationship to the 0.05 level.

#### 4.3.3 Morphological Characteristics

For the morphological determinants, Welch's test revealed that the younger men possessed significantly larger PmCSA ( $F_{(1,23.836)} = 39.226$ ,  $p \leq 0.001$ ), better MQ<sub>EI</sub> ( $F_{(1,32.896)} = 43.915$ ,  $p \leq 0.001$ ), TmCSA ( $F_{(1,21.478)} = 45.948$ ,  $p \leq 0.001$ ), and greater VL

PA ( $F_{(1,34.902)} = 28.811, p \leq 0.001$ ). Group mean age differences in the morphological determinants are displayed in figure 6.



**Figure 6.** Age differences in the morphological variables in the younger and older men. \* = Significant relationship to the 0.05 level.

**Table 2. Age differences in Strength, Morphological, Neural, and Contractile Variables**

		<b>Younger Men (n = 20)</b>
		<b>Means ± SD</b>
	<b>MVT (Nm)</b>	259.97 ± 99.05
<b>Morphological</b>	<b>PmCSA (cm<sup>2</sup>)</b>	66.04 ± 17.76
	<b>TmCSA (cm<sup>2</sup>/MQ<sub>EI</sub>)</b>	55.83 ± 22.14
	<b>MQ<sub>EI</sub> (cm<sup>2</sup>/au)</b>	46.83 ± 8.85
	<b>PA (°)</b>	13.88 ± 3.19
<b>Neural</b>	<b>MUNE (#)</b>	261.43 ± 41.01
	<b>CMAP (μV)</b>	18034.12 ± 4356.29
	<b>SMUP (μV)</b>	70.10 ± 17.56
	<b>aEMG<sub>0-50</sub> (mV)</b>	171.68 ± 93.53
	<b>nEMG<sub>0-50</sub> (%M<sub>pp</sub>)</b>	72.64 ± 44.83
	<b>nRER<sub>0-50</sub> (%M<sub>pp</sub>·s<sup>-1</sup>)</b>	861.71 ± 484.83
	<b>aEMG<sub>50-100</sub> (mV)</b>	301.86 ± 130.43
	<b>nEMG<sub>50-100</sub> (%M<sub>pp</sub>)</b>	121.35 ± 72.78
	<b>aEMG<sub>100-150</sub> (mV)</b>	261.65 ± 112.19
	<b>nEMG<sub>100-150</sub> (%M<sub>pp</sub>)</b>	69.42 ± 35.42
	<b>aEMG<sub>150-200</sub> (mV)</b>	259.29 ± 93.65
	<b>nEMG<sub>150-200</sub> (%M<sub>pp</sub>)</b>	86.42 ± 44.24
	<b>Motor CV (m/s)</b>	67.20 ± 8.74
	<b>Contractile</b>	<b>SGL PTT (Nm)</b>
<b>SGL pRR (Nm·s<sup>-1</sup>)</b>		385.72 ± 126.86
<b>SGL RTD<sub>0-50</sub> (Nm·s<sup>-1</sup>)</b>		482.06 ± 189.58
<b>SGL EMD (ms)</b>		14.03 ± 5.99
<b>nSGL TPT (PTT:MVT)</b>		17.05 ± 5.89
<b>nSGL pRR (%SGL PTT)</b>		10.89 ± 2.42
<b>nSGL RTD<sub>0-50</sub> (%SGL PTT·s<sup>-1</sup>)</b>		10.19 ± 6.32
<b>DBL PTT (Nm)</b>		47.24 ± 15.03
<b>DBL pRR (Nm·s<sup>-1</sup>)</b>		431.87 ± 178.93
<b>DBL RTD<sub>0-50</sub> (Nm·s<sup>-1</sup>)</b>		628.98 ± 278.73
<b>nDBL PTT (PTT:MVT)</b>		19.59 ± 7.06
<b>nDBL pRR (%DBL PTT)</b>		12.01 ± 2.83
<b>nDBL RTD<sub>0-50</sub> (%DBL PTT·s<sup>-1</sup>)</b>		8.44 ± 2.25

\*= Significant age difference to the 0.05 level between younger and older men from the mixed models ANOVA

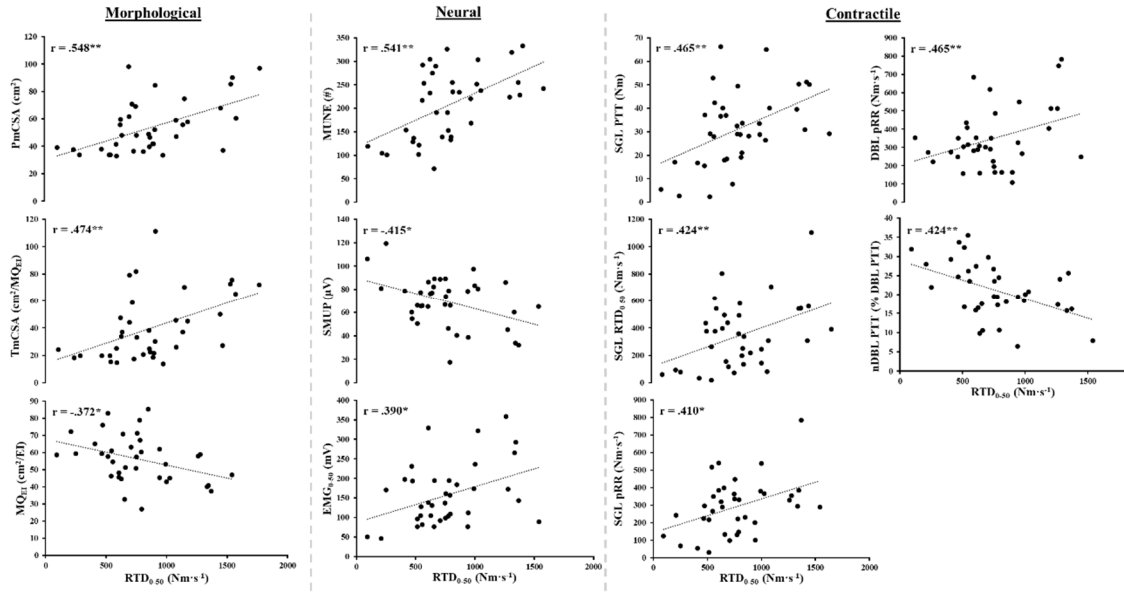
†= Data violated assumptions of equality and sphericity, therefore, signifies significant age differences to the

#### *4.4 Relationships between neural, contractile, and morphological characteristics and the rate of torque development*

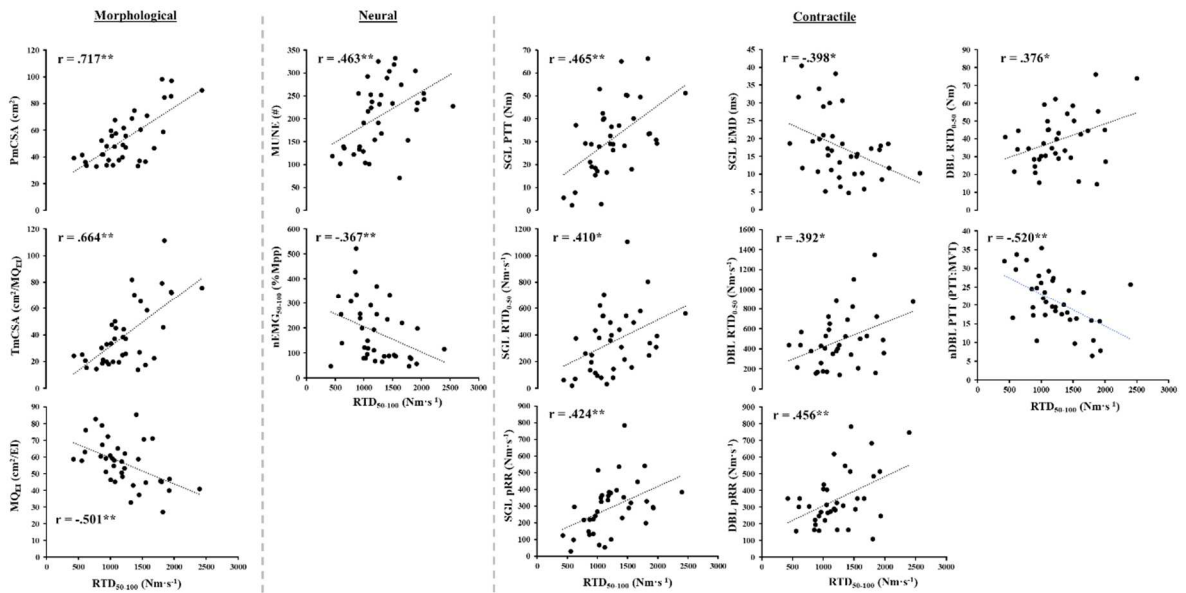
#### *4.4.1 Relationships between the determinant variables and each sequential 50 ms RTD time frame across age*

When collapsed across age, RTD<sub>0-50</sub> was positively related to PmCSA ( $p \leq 0.001$ ), TmCSA ( $p = 0.003$ ), MUNE ( $p = 0.001$ ), aEMG<sub>0-50</sub> ( $p = 0.017$ ), SGL PTT ( $p = 0.004$ ), SGL RTD<sub>0-50</sub> ( $p = 0.009$ ) and SGL pRR ( $p = 0.012$ ). RTD<sub>0-50</sub> was negatively related to muscle quality ( $p = 0.023$ ), SMUP ( $p = 0.011$ ), nDBL PTT ( $p = 0.003$ ) and age ( $p = 0.001$ ) (Figure 7). During the 50-100 ms time frame, PmCSA ( $p \leq 0.001$ ), TmCSA ( $p \leq 0.001$ ), PmCSA ( $p \leq 0.001$ ), VL PA ( $p = 0.035$ ), MUNE ( $p = 0.004$ ), SGL PTT ( $p \leq 0.001$ ), SGL RTD<sub>0-50</sub> ( $p = 0.012$ ), SGL pRR ( $p = 0.005$ ), DBL PTT ( $p = 0.022$ ), DBL RTD<sub>0-50</sub> ( $p = 0.016$ ) and DBL pRR ( $p = 0.005$ ) were positively related to RTD<sub>50-100</sub>. Further, negative relationships were observed between RTD<sub>50-100</sub> and nEMG<sub>50-100</sub> ( $p = 0.026$ ) MQ<sub>EI</sub> ( $p = 0.002$ ), nDBL PTT ( $p = 0.001$ ), age ( $p \leq 0.001$ ), and SGL EMD ( $p = 0.005$ ) (Figure 8). For the 100-150 ms frame, positive relationships were observed between PmCSA ( $p \leq 0.001$ ), TmCSA ( $p \leq 0.001$ ), MUNE ( $p = 0.001$ ), CMAP ( $p = 0.009$ ), EMG<sub>100-150</sub> ( $p = 0.019$ ), DBL PTT ( $p = 0.001$ ), DBL pRR ( $p \leq 0.001$ ), DBL RTD<sub>0-50</sub> ( $p \leq 0.001$ ), and motor nerve CV ( $p \leq 0.001$ ), and RTD<sub>100-150</sub>. Additionally, RTD<sub>100-150</sub> was negatively correlated with age ( $p \leq 0.001$ ), nDBL PTT ( $p = 0.033$ ), nDBL RTD<sub>0-50</sub> ( $p = 0.043$ ) and MQ<sub>EI</sub> ( $p \leq 0.001$ ) (Figure 9). Finally, for the 150-200 ms time frame, there were significant positive relationships between RTD<sub>150-200</sub> and PmCSA ( $p \leq 0.001$ ), TmCSA ( $p \leq 0.001$ ), VL PA ( $p = 0.009$ ), MUNE ( $p = 0.05$ ), CMAP ( $p = 0.025$ ), DBL pTT ( $p = 0.023$ ), DBL RTD<sub>0-50</sub> ( $p = 0.006$ ) and DBL pRR ( $p = 0.032$ ). Additional negative relationships were observed between RTD<sub>150-200</sub> and nEMG<sub>150-200</sub> ( $p = 0.007$ ), MQ<sub>EI</sub> ( $p = 0.002$ ), nDBL PTT ( $p = 0.003$ ), nDBL RTD<sub>0-50</sub> ( $p = 0.040$ ), and Age ( $p =$

0.009) (Figure 10). Relationships between each RTD time frame and the predictor variables are displayed in Table 3.

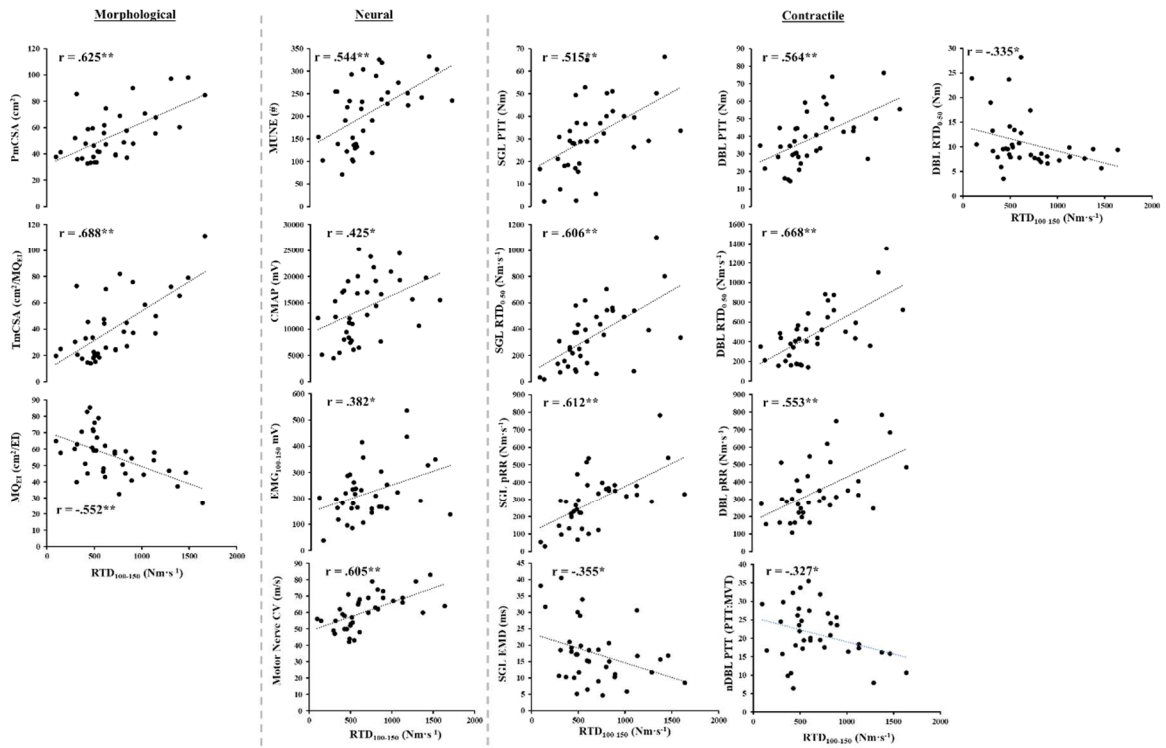


**Figure 7.** Significant relationships between predictor variables and torque produced during the first 50 ms of the explosive knee extension. \* = Significant relationships to the 0.05 level. \*\* = Significant relationships to the 0.01 level.

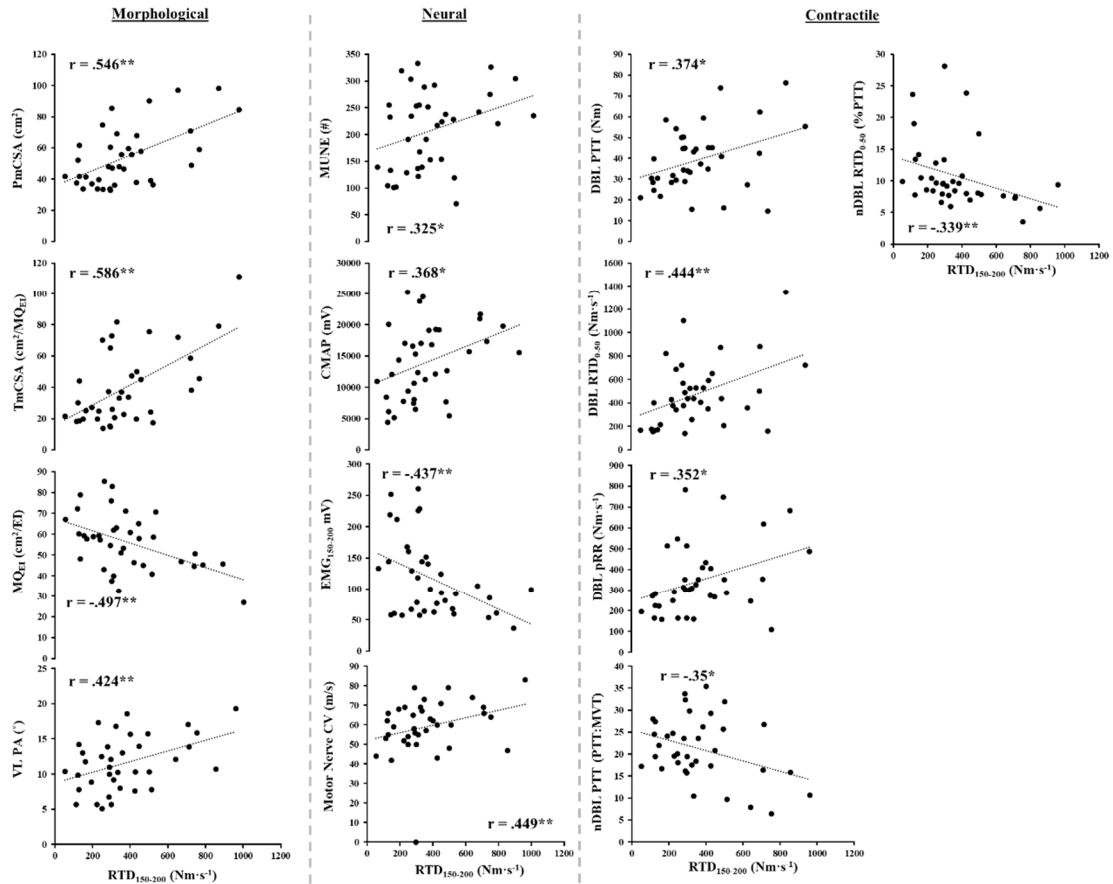


**Figure 8.** Significant relationships between predictor variables and torque produced during the 50-100 ms of the explosive knee extension. \* = Significant relationships to the 0.05 level. \*\* = Significant relationships to the 0.01 level.





**Figure 9.** Significant relationships between predictor variables and torque produced during the first 100-150 ms of the explosive knee extension. \* = Significant relationships to the 0.05 level. \*\* = Significant relationships to the 0.01 level.



**Figure 10.** Significant relationships between predictor variables and torque produced during the first 150-200 ms of the explosive knee extension. \* = Significant relationships to the 0.05 level. \*\* = Significant relationships to the 0.01 level.

**Table 3. Relationship between Predictor Variables and RTD Time Windows Across Age (collapsed across age groups)**

	<b>RTD Time Window (ms)</b>			
	<b>0-50</b>	<b>50-100</b>	<b>100-150</b>	<b>150-200</b>
<b>Age (yrs)</b>	<b>-.532**</b>	<b>-.553**</b>	<b>-.631**</b>	<b>-.351*</b>
<b>MVT (Nm)</b>	<b>.502**</b>	<b>.714**</b>	<b>.828**</b>	<b>.717**</b>
<b>Morphological</b>				
<b>PmCSA (cm<sup>2</sup>)</b>	<b>.548**</b>	<b>.717**</b>	<b>.625**</b>	<b>.546**</b>
<b>TmCSA (cm<sup>2</sup>/MQ<sub>EI</sub>)</b>	<b>.474**</b>	<b>.664**</b>	<b>.688**</b>	<b>.586**</b>
<b>MQ<sub>EI</sub> (cm<sup>2</sup>/AU)</b>	<b>-.372*</b>	<b>-.501**</b>	<b>-.552**</b>	<b>-.497**</b>
<b>PA (°)</b>	0.094	0.347	0.314	<b>.424**</b>
<b>Neural</b>				
<b>MUNE (#)</b>	<b>.541**</b>	<b>.463**</b>	<b>.544**</b>	<b>.325*</b>
<b>CMAP (mV)</b>	0.164	0.224	<b>.425*</b>	<b>.368*</b>
<b>SMUP (μV)</b>	<b>-.415*</b>	-0.229	-0.032	0.085
<b>aEMG<sub>0-50</sub> (mV)</b>	<b>.390*</b>	0.187	0.013	-
<b>nEMG<sub>0-50</sub> (%M<sub>pp</sub>)</b>	0.251	-	-	-
<b>nRER<sub>0-50</sub> (%M<sub>pp</sub>·s<sup>-1</sup>)</b>	0.292	-	-	-
<b>aEMG<sub>50-100</sub> (mV)</b>	-	0.230	-	-
<b>nEMG<sub>50-100</sub> (%M<sub>pp</sub>)</b>	-	<b>-.367*</b>	-	-
<b>aEMG<sub>100-150</sub> (mV)</b>	-	-	<b>.382*</b>	-
<b>nEMG<sub>100-150</sub> (%M<sub>pp</sub>)</b>	-	-	0.032	-
<b>aEMG<sub>150-200</sub> (mV)</b>	-	-	-	0.120
<b>nEMG<sub>150-200</sub> (%M<sub>pp</sub>)</b>	-	-	-	<b>-.437**</b>
<b>Motor CV (m/s)</b>	0.225	0.301	<b>.605**</b>	<b>.449**</b>
<b>Contractile</b>				
<b>SGL PTT (Nm/s)</b>	<b>.465**</b>	<b>.547**</b>	<b>.515**</b>	0.296
<b>SGL pRR (Nm/s)</b>	<b>.410*</b>	<b>.456**</b>	<b>.612**</b>	0.227
<b>SGL RTD<sub>0-50</sub> (Nm·s<sup>-1</sup>)</b>	<b>.424**</b>	<b>.410*</b>	<b>.606**</b>	0.243
<b>SGL EMD (ms)</b>	-0.14	<b>-.398*</b>	<b>-.355*</b>	-0.21
<b>nSGL TPT (PTT:MVT)</b>	0.058	-0.006	-0.095	-0.240
<b>nSGL pRR (%SGL PTT)</b>	0.123	0.095	-0.203	0.040
<b>nSGL RTD<sub>0-50</sub> (%SGL PTT·s<sup>-1</sup>)</b>	-0.101	-0.064	-0.281	-0.045
<b>DBL PTT (Nm)</b>	0.231	<b>.376*</b>	<b>.564**</b>	<b>.374*</b>
<b>DBL pRR (Nm·s<sup>-1</sup>)</b>	<b>.360*</b>	<b>.456**</b>	<b>.553**</b>	<b>.352*</b>
<b>DBL RTD<sub>0-50</sub> (Nm·s<sup>-1</sup>)</b>	0.311	<b>.392*</b>	<b>.668**</b>	<b>.444**</b>
<b>nDBL PTT (PTT:MVT)</b>	<b>-.469**</b>	<b>-.520**</b>	<b>-.327*</b>	<b>-.351*</b>
<b>nDBL pRR (%DBL PTT)</b>	-0.112	-0.301	-0.119	-0.281
<b>nDBL RTD<sub>0-50</sub> (%DBL PTT·s<sup>-1</sup>)</b>	-0.263	-0.271	<b>-.335*</b>	<b>-.339*</b>

\*\* Correlation is significant at the 0.01 level

\* Correlation is significant at the 0.05 level

#### *4.4.2. Relationships between the determinant variables and each sequential 50 ms RTD time frame within each age group*

In the younger men, nEMG<sub>0-50</sub> ( $p = 0.001$ ), nRER<sub>0-50</sub> ( $p = 0.05$ ) were positively related to RTD<sub>0-50</sub>. However, VL PA ( $p = 0.018$ ) and SMUP ( $p = 0.046$ ) were negatively related to RTD<sub>0-50</sub> (Table 4) (Figure 11). In the older men, MUNE ( $p = 0.023$ ), nEMG<sub>0-50</sub> ( $p = 0.003$ ), SGL PTT ( $p = 0.039$ ) were positively related to RTD<sub>0-50</sub>. However, SMUP ( $p = 0.006$ ), was negatively correlated with RTD<sub>0-50</sub> (Table 5) (Figure 15).

For the RTD<sub>50-100</sub> time frame, PmCSA ( $p \leq 0.001$ ), and TmCSA ( $p = 0.003$ ) were positively related to RTD<sub>50-100</sub> in the younger men. However, MQ<sub>EI</sub> ( $p = 0.019$ ), CMAP ( $p = 0.017$ ), SMUP ( $p = 0.017$ ), nDBL PTT ( $p = 0.025$ ) and nSGL PTT ( $p = 0.022$ ) were negatively related to RTD<sub>50-100</sub> in the younger men (Table 4) (Figure 12). Interestingly, In the older men SGL PTT ( $p = 0.037$ ), SGL pRR ( $p = 0.033$ ) were positively related to RTD<sub>50-100</sub> (Table 5) (Figure 16).

Additionally, during the 100-150 time frame, nEMG<sub>100-150</sub> ( $p = 0.01$ ), DBL RTD<sub>0-50</sub> ( $p = 0.014$ ), and TmCSA ( $p = 0.032$ ) were positively related to RTD<sub>100-150</sub> in the young men. Further, only nSGL PTT ( $p = 0.017$ ) was negatively related to RTD<sub>100-150</sub> in the younger men (Table 4) (Figure 13). Only nSGL pRR was negatively related to RTD<sub>100-150</sub>. In the older men, only nSGL RTD<sub>0-50</sub> was negatively related to RTD<sub>100-150</sub> (Table 5).

For the 150-200 ms time frame, PmCSA ( $p = 0.026$ ), TmCSA ( $p = 0.025$ ) were positively related to RTD<sub>150-200</sub> in the younger men. Additionally, both nSGL PTT ( $p = 0.007$ ) and nDBL PTT ( $p = 0.032$ ) was negatively related to RTD<sub>150-200</sub> (Table 4) (Figure

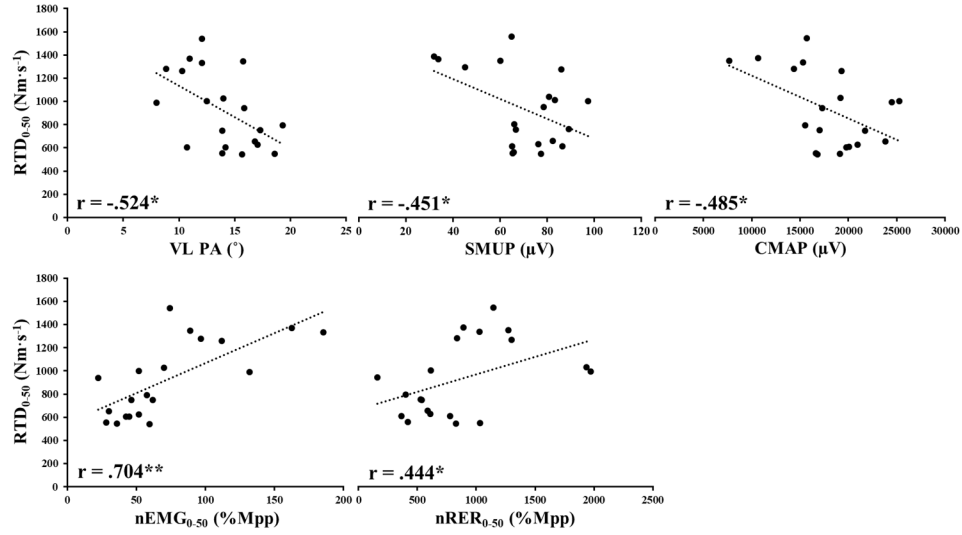
14). In the older men, motor nerve CV ( $p = 0.022$ ), DBL RTD<sub>0-50</sub> ( $p = 0.048$ ), and DBL pRR ( $p = 0.029$ ) were significantly related to RTD<sub>150-200</sub> (Table 5) (Figure 17).

**Table 4. Relationship between Predictor Variables and RTD Time Windows in the Younger Men**

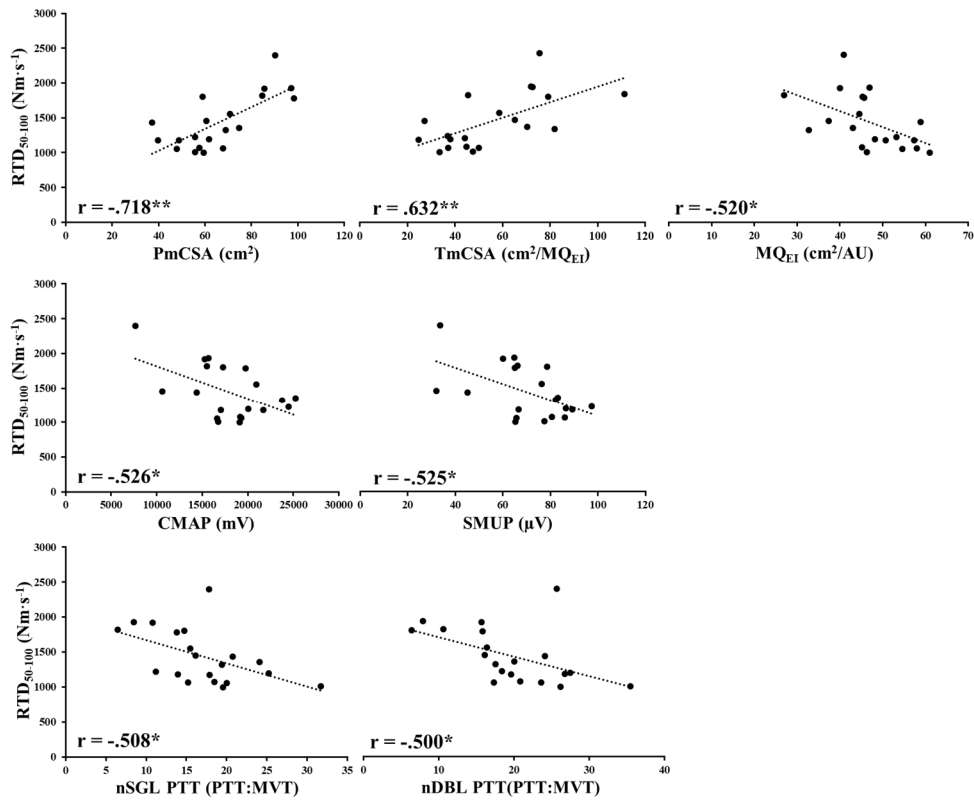
	<u>RTD Time Window (ms)</u>			
	<b>0-50</b>	<b>50-100</b>	<b>100-150</b>	<b>150-200</b>
MVT	0.253	<b>.610**</b>	<b>.764**</b>	<b>.684**</b>
<b>Morphological</b>				
PmCSA (cm <sup>2</sup> )	0.282	<b>.718**</b>	0.373	<b>.495*</b>
TmCSA (cm <sup>2</sup> /MQ <sub>EI</sub> )	0.174	<b>.632**</b>	<b>.480*</b>	<b>.498*</b>
MQ <sub>EI</sub> (cm <sup>2</sup> /AU)	-0.089	<b>-.520*</b>	-0.289	-0.372
PA (°)	<b>-.524*</b>	0.026	-0.204	0.283
<b>Neural</b>				
MUNE (#)	0.028	-0.055	0.153	-0.013
CMAP (mV)	<b>-.485*</b>	<b>-.526*</b>	-0.159	-0.026
SMUP (μV)	<b>-.451*</b>	<b>-.525*</b>	-0.217	-0.07
aEMG <sub>0-50</sub> (mV)	.371	-	-	-
nEMG <sub>0-50</sub> (mV)	<b>.704**</b>	-	-	-
nRER <sub>0-50</sub> (%M <sub>pp</sub> ·s <sup>-1</sup> )	<b>.444*</b>	-	-	-
aEMG <sub>50-100</sub> (mV)	-	-0.101	-	-
nEMG <sub>50-100</sub> (%M <sub>pp</sub> )	-	-0.112	-	-
aEMG <sub>100-150</sub> (mV)	-	-	0.376	-
nEMG <sub>100-150</sub> (%M <sub>pp</sub> )	-	-	<b>.558*</b>	-
aEMG <sub>150-200</sub> (mV)	-	-	-	-0.245
nEMG <sub>150-200</sub> (%M <sub>pp</sub> )	-	-	-	-0.053
Motor CV (m/s)	-0.213	-	0.424	0.108
<b>Contractile</b>				
SGL PTT (Nm/s)	-0.006	0.131	0.169	-0.021
SGL pRR (Nm/s)	0.063	-0.091	0.347	-0.204
SGL RTD <sub>0-50</sub> (Nm·s <sup>-1</sup> )	0.104	-0.033	0.364	-0.053
SGL EMD (ms)	0.275	-0.151	-0.041	-0.062
nSGL PTT (PTT:MVT)	-0.396	<b>-.508*</b>	<b>-.528*</b>	<b>-.582**</b>
nSGL pRR (%SGL PTT)	0.042	0.343	-0.255	0.266
nSGL RTD <sub>0-50</sub> (%SGL PTT·s <sup>-1</sup> )	0.036	-0.013	-0.044	-0.085
DBL PTT (Nm)	-0.029	0.17	0.332	0.137
DBL RTD <sub>0-50</sub> (Nm·s <sup>-1</sup> )	0.066	0.173	<b>.540*</b>	0.192
DBL pRR (%DBL PTT·s <sup>-1</sup> )	0.24	0.314	0.322	0.066
nDBL PTT (PTT:MVT)	-0.388	<b>-.500*</b>	-0.390	<b>-.479*</b>
nDBL pRR (%DBL PTT)	0.003	-0.310	0.099	-0.401
nDBL RTD <sub>0-50</sub> (%DBL PTT·s <sup>-1</sup> )	0.211	-0.072	-0.199	-0.437

\*\* Correlation is significant at the 0.01 level

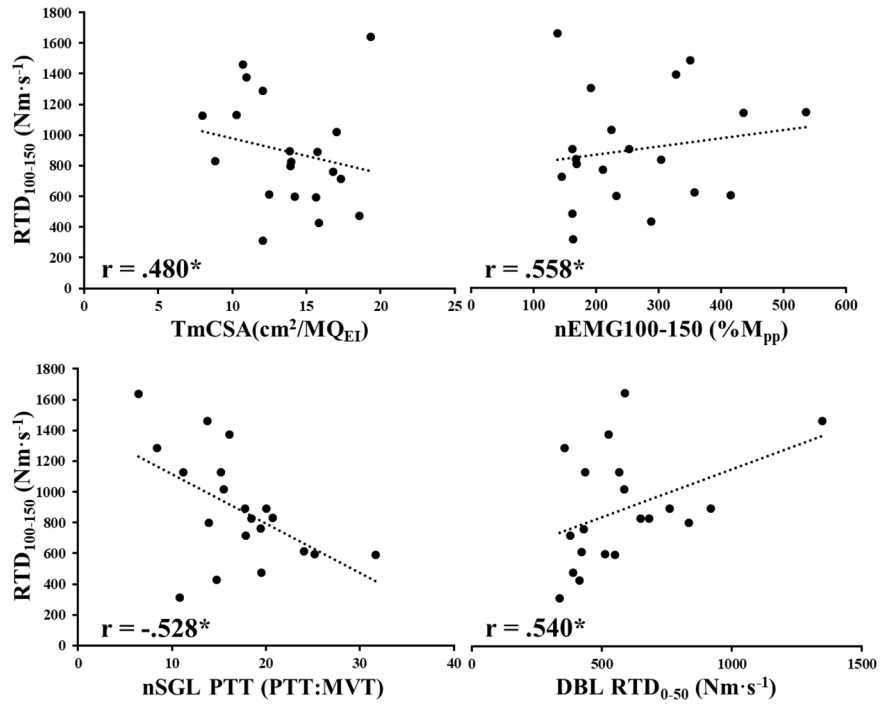
\* Correlation is significant at the 0.05 level



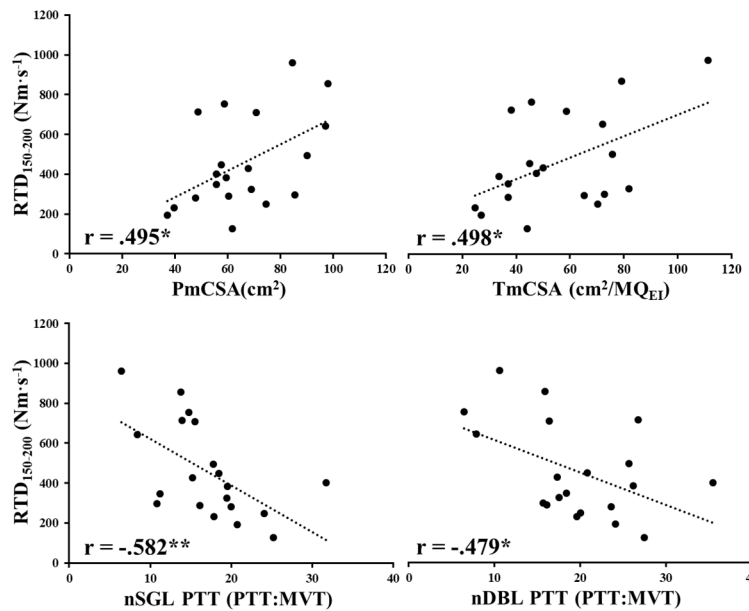
**Figure 11.** Significant relationships between the determinants and  $RTD_{0-50}$  in the younger men. \* = Significant relationship to the 0.05 level. \*\* = Significant relationship to the 0.01 level.



**Figure 12.** Significant relationships between the determinants and  $RTD_{50-100}$  in the younger men. \* = Significant relationship to the 0.05 level. \*\* = Significant relationship to the 0.01 level.



**Figure 13.** Significant relationships between the determinants and  $RTD_{100-150}$  in the younger men. \* = Significant relationship to the 0.05 level. \*\* = Significant relationship to the 0.01 level.



**Figure 14.** Significant relationships between the determinants and  $RTD_{150-200}$  in the younger men. \* = Significant relationship to the 0.05 level. \*\* = Significant relationship to the 0.01 level.

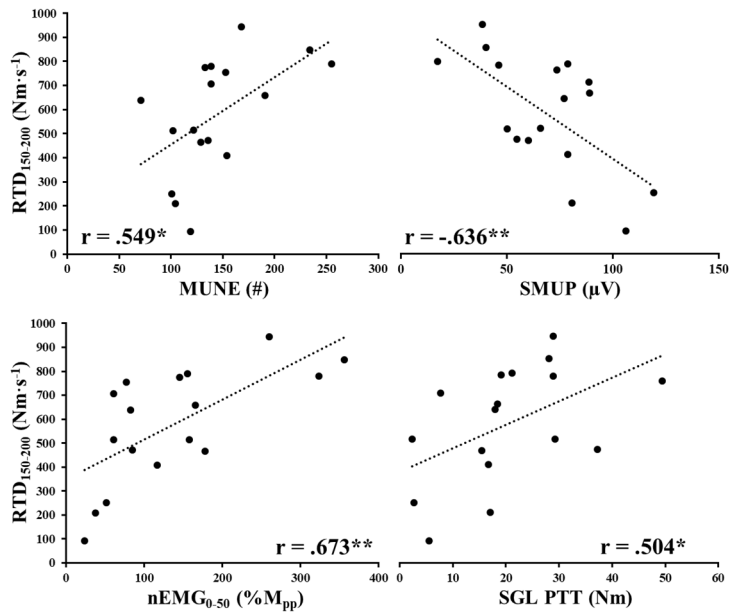
**Table 5. Relationship between Predictor Variables and RTD Time Windows in the Older Men**

	<b>RTD Time Window (ms)</b>			
	<b>0-50</b>	<b>50-100</b>	<b>100-150</b>	<b>150-200</b>
<b>MVT (Nm)</b>	0.381	<b>.746**</b>	0.153	0.391
<b>Morphological</b>				
<b>PmCSA (cm<sup>2</sup>)</b>	0.465	0.118	-0.047	-0.123
<b>TmCSA (cm<sup>2</sup>/MQ<sub>EI</sub>)</b>	0.170	-0.149	-0.096	-0.024
<b>MQ<sub>EI</sub> (cm<sup>2</sup>/AU)</b>	0.211	0.283	0.136	-0.068
<b>PA (°)</b>	-0.141	-0.128	-0.14	-0.034
<b>Neural</b>				
<b>MUNE (#)</b>	<b>.549*</b>	0.148	-0.096	-0.166
<b>CMAP (mV)</b>	-0.241	-0.036	0.099	0.284
<b>SMUP (μV)</b>	<b>-.636**</b>	-0.108	0.17	0.305
<b>aEMG<sub>0-50</sub> (mV)</b>	0.274	-	-	-
<b>nEMG<sub>0-50</sub> (%M<sub>pp</sub>)</b>	<b>.673**</b>	-	-	-
<b>nRER<sub>0-50</sub> (%M<sub>pp</sub>·s<sup>-1</sup>)</b>	0.432	-	-	-
<b>aEMG<sub>50-100</sub> (mV)</b>	-	0.327	-	-
<b>nEMG<sub>50-100</sub> (%M<sub>pp</sub>)</b>	-	-0.062	-	-
<b>aEMG<sub>100-150</sub> (mV)</b>	-	-	0.189	-
<b>nEMG<sub>100-150</sub> (%M<sub>pp</sub>)</b>	-	-	0.178	-
<b>aEMG<sub>150-200</sub> (mV)</b>	-	-	-	0.097
<b>nEMG<sub>150-200</sub> (%M<sub>pp</sub>)</b>	-	-	-	-0.411
<b>Motor CV (m/s)</b>	-0.258	-0.266	-0.19	<b>.550*</b>
<b>Contractile</b>				
<b>SGL PTT (Nm)</b>	<b>.504*</b>	<b>.510*</b>	0.237	0.065
<b>SGL pRR (Nm·s<sup>-1</sup>)</b>	0.167	<b>.518*</b>	0.324	0.14
<b>SGL RTD<sub>0-50</sub> (Nm·s<sup>-1</sup>)</b>	0.271	0.384	0.349	-0.013
<b>SGL EMD (ms)</b>	-0.047	-0.304	-0.356	-0.009
<b>nSGL PTT (PTT:MVT)</b>	0.415	0.283	0.206	-0.072
<b>nSGL pRR (%SGL PTT)</b>	0.418	0.208	-0.209	0.092
<b>nSGL RTD<sub>0-50</sub> (%SGL PTT·s<sup>-1</sup>)</b>	-0.006	0.140	<b>-.545*</b>	0.257
<b>DBL PTT (Nm)</b>	-0.307	-0.111	0.232	0.242
<b>DBL RTD<sub>0-50</sub> (Nm·s<sup>-1</sup>)</b>	-0.206	-0.097	0.084	<b>.485*</b>
<b>DBL pRR (Nm·s<sup>-1</sup>)</b>	-0.47	-0.072	0.224	<b>.528*</b>
<b>nDBL PTT (PTT:MVT)</b>	-0.478	-0.460	0.101	0.075
<b>nDBL pRR (%DBL PTT)</b>	0.044	-0.124	-0.005	0.021
<b>nDBL RTD<sub>0-50</sub> (%DBL PTT·s<sup>-1</sup>)</b>	-0.154	0.013	0.039	-0.062

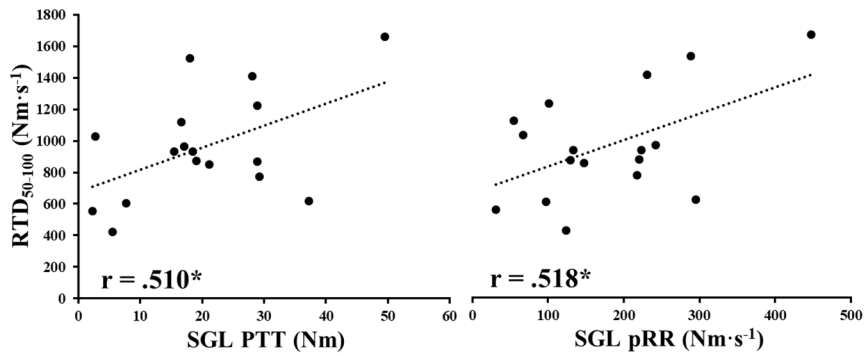
**\*\* Correlation is significant at the 0.01 level**

**\* Correlation is significant at the 0.05 level**

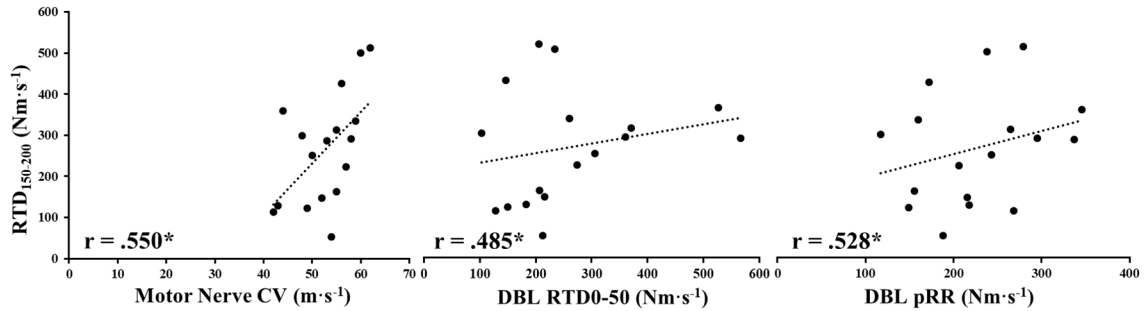




**Figure 15.** Significant relationships between the determinants and RTD<sub>0-50</sub> in the older men. \* = Significant relationship to the 0.05 level. \*\* = Significant relationship to the 0.01 level.



**Figure 16.** Significant relationships between the determinants and RTD<sub>50-100</sub> in the older men. \* = Significant relationship to the 0.05 level. \*\* = Significant relationship to the 0.01 level.

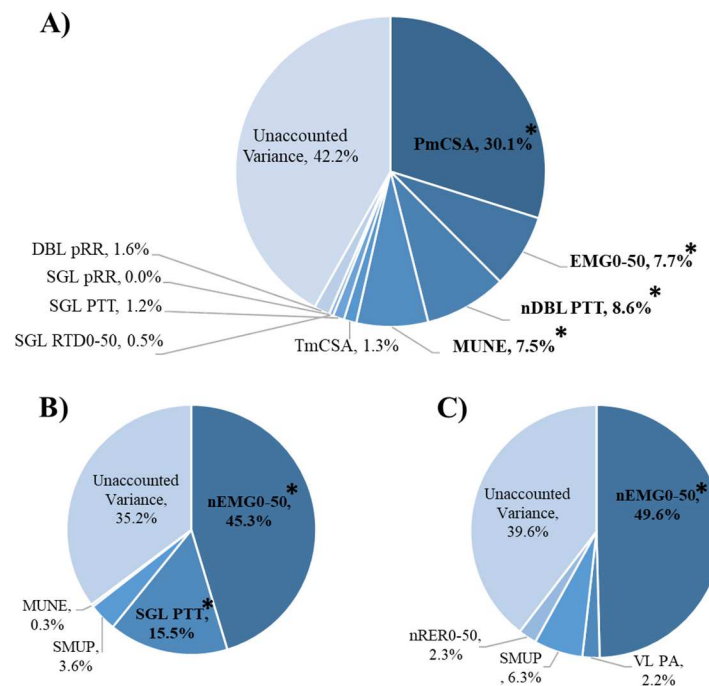


**Figure 17.** Significant relationships between the determinants and  $RTD_{150-200}$  in the older men. \* = Significant relationship to the 0.05 level. \*\* = Significant relationship to the 0.01 level.

#### ***4.5 Determinants of Rapid Torque production***

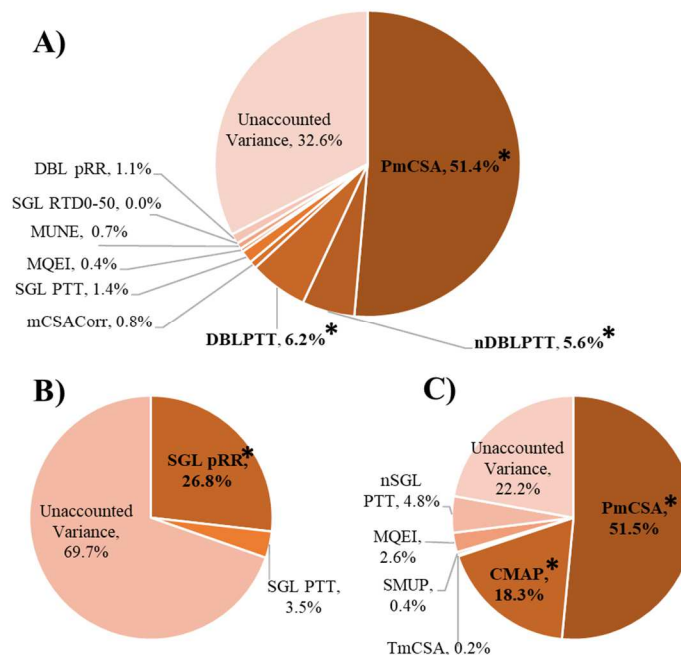
Each stepwise multiple regression only examined the physiological variables that were significantly related to each RTD time frame. The stepwise multiple regression model for  $RTD_{0-50}$  when collapsed across groups was significant ( $p \leq 0.001$ ). The primary physiological determinant for  $RTD_{0-50}$  was PmCSA, independently explaining 30.1% ( $R^2 = .301$ ,  $p \leq 0.001$ ) of the variance in  $RTD_{0-50}$ . However,  $EMG_{0-50}$  ( $p = 0.048$ ), nDBL PTT ( $p = 0.028$ ), and MUNE ( $p = 0.029$ ) further explained 7.7%, 8.6% and 7.5% of the variance in  $RTD_{0-50}$ , respectively. When the non-significant variables were entered into the regression analysis, TmCSA, SGL PTT, SGL  $RTD_{0-50}$ , SGL pRR, and DBL pRR accounted for an additional 2.96% of the variance in  $RTD_{0-50}$ . Altogether, the variables related to  $RTD_{0-50}$  accounted for a total of 58.6% of the variance in  $RTD_{0-50}$  (Figure 18, A.). In the younger men, the multiple regression model was significant ( $p = 0.001$ ) and only n $EMG_{0-50}$  uniquely explained 49.6% ( $R^2 = .496$ ,  $p = 0.001$ ) of variance in  $RTD_{0-50}$ . When the excluded physiological variables were included into the multiple regression model, VL PA, SMUP, n $RER_{0-50}$  together accounted for an additional 10.8% of the variance in  $RTD_{0-50}$ . Altogether, the significant and non-significant physiological

variables accounted for a total of 60.4% of the variance in  $RTD_{0-50}$  in the younger men (Figure 18, C.). Further, in the older men, the multiple regression model was significant ( $p = 0.001$ ) and found that  $nEMG_{0-50}$  was the primary determinant accounting for 45.3% ( $R^2 = .453$ ,  $p = 0.003$ ) of the variance in  $RTD_{0-50}$ . Additionally, SGL PTT uniquely accounted for an additional 15.5% ( $p = 0.034$ ) of the variance in  $RTD_{0-50}$ . When the excluded variables were entered into the regression model, SMUP and MUNE non-significantly ( $p > 0.05$ ) accounted for an additional 4% of the variance in  $RTD_{0-50}$ . Altogether, the significant and non-significant variables accounted for a total of 64.8% of the variance in  $RTD_{0-50}$  in the older men (Figure 18, B.).



**Figure 18.** Determinants of explosive torque production **A)** collapsed across age, in the **B)** older, and the **C)** younger men in the first 50 ms of the maximal, rapid contraction. Determinant variables that independently explained a significant proportion of the total variance in  $RTD_{0-50}$  are signified with an \*. Only determinants that were significantly correlated with  $RTD_{50-100}$  in the collapsed, younger, and older groups

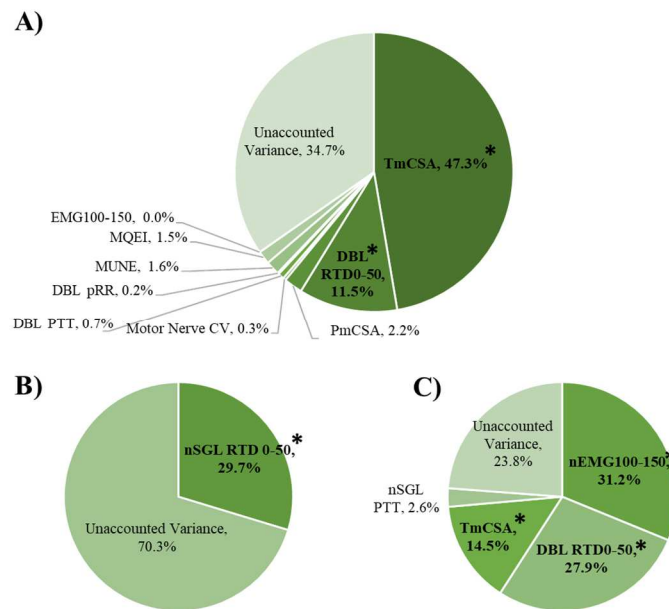
The stepwise multiple regression model for  $RTD_{50-100}$  was significant collapsed across age ( $p \leq 0.001$ ). The primary physiological determinant for  $RTD_{50-100}$  was PmCSA, independently explaining 51.4% ( $R^2 = .514$ ,  $p \leq 0.001$ ) of the variance in  $RTD_{0-50}$ . In addition, nDBL PTT ( $p = 0.044$ ) and DBL PTT ( $p = 0.025$ ) further explained 5.6% ( $p = 0.044$ ) and 6.2% ( $p = 0.025$ ) of the variance in  $RTD_{50-100}$ , respectively. When the non-significant variables were entered into the regression analysis, TmCSA, SGL PTT, SGL  $RTD_{0-50}$ , MUNE,  $MQ_{EI}$  and DBL pRR accounted for an additional 4.3% of the variance in  $RTD_{0-50}$ . Altogether, the variables related to  $RTD_{50-100}$  accounted for a total of 67.4% of the variance in  $RTD_{0-50}$  (Figure 19, A.). In the younger men, the multiple regression model was significant ( $p \leq 0.001$ ) and PmCSA was the primary determinant that uniquely explained 51.5% ( $R^2 = .515$ ,  $p \leq 0.001$ ) of variance in  $RTD_{50-100}$ . Additionally, CMAP significantly accounted for an additional 18.3% ( $p = 0.005$ ) of the variance in  $RTD_{50-100}$ . When the excluded physiological variables were included into the multiple regression model, TmCSA, SMUP,  $MQ_{EI}$ , nSGL PTT together accounted for an additional 8.0% of the variance in  $RTD_{50-100}$ . Altogether, the significant and non-significant physiological variables accounted for a total of 77.8% of the variance in  $RTD_{50-100}$  in the younger men (Figure 19, C.). Further, in the older men, the multiple regression model was significant ( $p = 0.033$ ) and found that SGL pRR was the primary determinant accounting for 26.8% ( $R^2 = .268$ ,  $p = 0.033$ ) of the variance in  $RTD_{50-100}$ . Additionally, when the excluded variables were entered into the regression model, SGL PTT non-significantly ( $p > 0.05$ ) accounted for an additional 3.5% of the variance in  $RTD_{50-100}$ . Altogether, the significant and non-significant variables accounted for a total of 69.7% of the variance in  $RTD_{50-100}$  in the older men (Figure 19, B.).



**Figure 19.** Determinants of explosive torque production **A)** collapsed across age, in the **B)** older, and the **C)** younger men in the 50-100 ms of the maximal, rapid contraction. Determinant variables that independently explained a significant proportion of the total variance in  $RTD_{50-100}$  are signified with an \*. Only determinants that were significantly correlated with  $RTD_{50-100}$  in the collapsed, younger, and older groups.

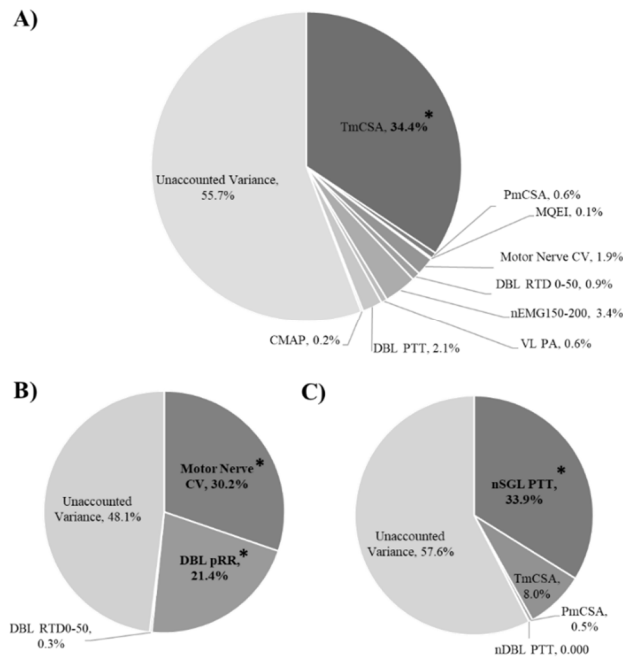
The stepwise multiple regression model for  $RTD_{100-150}$  was significant collapsed across age ( $p \leq 0.001$ ). The primary physiological determinant for  $RTD_{50-100}$  was  $TmCSA$ , independently explaining 47.3% ( $R^2 = .473$ ,  $p \leq 0.001$ ) of the variance in  $RTD_{100-150}$ . In addition,  $DBL\ RTD_{0-50}$  ( $p = 0.004$ ) further explained 11.5% ( $p = 0.044$ ) of the variance in  $RTD_{50-100}$ . When the non-significant variables were entered into the regression analysis,  $PmCSA$ , Motor Nerve CV,  $DBL\ PTT$ ,  $DBL\ pRR$ ,  $MUNE$ ,  $MQ_{EI}$  and  $EMG_{100-150}$  accounted for an additional 6.5% of the variance in  $RTD_{100-150}$ . Altogether, the variables related to  $RTD_{100-150}$  accounted for a total of 65.3% of the variance in  $RTD_{100-150}$  (Figure 20, A.). In the younger men, the multiple regression model was

significant ( $p = 0.001$ ) and  $nEMG_{100-150}$  was the primary determinant that uniquely explained 31.2% ( $R^2 = .312$ ,  $p = 0.01$ ) of variance in  $RTD_{100-150}$ . Additionally, DBL  $RTD_{0-50}$  and TmCSA significantly accounted for an additional 27.9% ( $p = 0.003$ ) and 14.5% of the variance in  $RTD_{100-150}$ , respectively. When the only excluded physiological variable, nSGL PTT, was included into the multiple regression model, an additional 2.6% of the variance was in  $RTD_{100-150}$  was explained. Altogether, the significant and non-significant physiological variables accounted for a total of 76.2% of the variance in  $RTD_{100-150}$  in the younger men (Figure 20, C.). Further, in the older men, the multiple regression model was significant ( $p = 0.033$ ) and found that nSGL  $RTD_{0-50}$  was the only primary determinant accounting for 29.7% ( $R^2 = .297$ ,  $p = 0.024$ ) of the variance in  $RTD_{100-150}$  (Figure 20, B.).



**Figure 20.** Determinants of explosive torque production **A)** collapsed across age, in the **B)** older, and the **C)** younger men in the first 100-150 ms of the maximal, rapid contraction. Determinant variables that independently explained a significant proportion of the total variance in  $RTD_{100-150}$  are signified with an \*. Only determinants that were significantly correlated with  $RTD_{100-150}$  in the collapsed, younger, and older groups.

The stepwise multiple regression model for  $RTD_{150-200}$  was significant collapsed across age ( $p \leq 0.001$ ). The primary physiological determinant for  $RTD_{150-200}$  was TmCSA, independently explaining 34.4% ( $R^2 = .344$ ,  $p \leq 0.001$ ) of the variance in  $RTD_{150-200}$ . When the non-significant variables were entered into the regression analysis, PmCSA, MQEI, Motor Nerve CV, DBL  $RTD_{0-50}$ , nEMG $_{150-200}$ , VL PA, DBL PTT, and MUNE accounted for an additional 9.9% of the variance in  $RTD_{150-200}$ . Altogether, the variables related to  $RTD_{150-200}$  accounted for a total of 44.3% of the variance in  $RTD_{150-200}$  (Figure 21, A). In the younger men, the multiple regression model was significant ( $p = 0.007$ ) and nSGL PTT was the primary determinant that uniquely explained 33.9% ( $R^2 = .339$ ,  $p = 0.007$ ) of variance in  $RTD_{150-200}$ . When the excluded physiological variables, TmCSA, PmCSA, and nDBL PTT, were included into the multiple regression model, an additional 8.5% of the variance was in  $RTD_{150-200}$  was explained. Altogether, the significant and non-significant physiological variables accounted for a total of 42.4% of the variance in  $RTD_{150-200}$  in the younger men (Figure 21, C.). Further, in the older men, the multiple regression model was significant ( $p = 0.006$ ) and found that Motor Nerve CV was the primary determinant accounting for 30.2% ( $R^2 = .302$ ,  $p = 0.024$ ) of the variance in  $RTD_{150-200}$ . Additionally, DBL pRR uniquely accounted for an additional 21.4% ( $p = 0.009$ ) of the variance in  $RTD_{150-200}$ . When the non-significant physiological variable, DBL  $RTD_{0-50}$ , was entered into the regression equation, an additional 0.3% of the variance in  $RTD_{150-200}$  was explained. Altogether, the significant and non-significant physiological variables accounted for a total of 51.9% of the variance in  $RTD_{150-200}$  (Figure 21, B.).

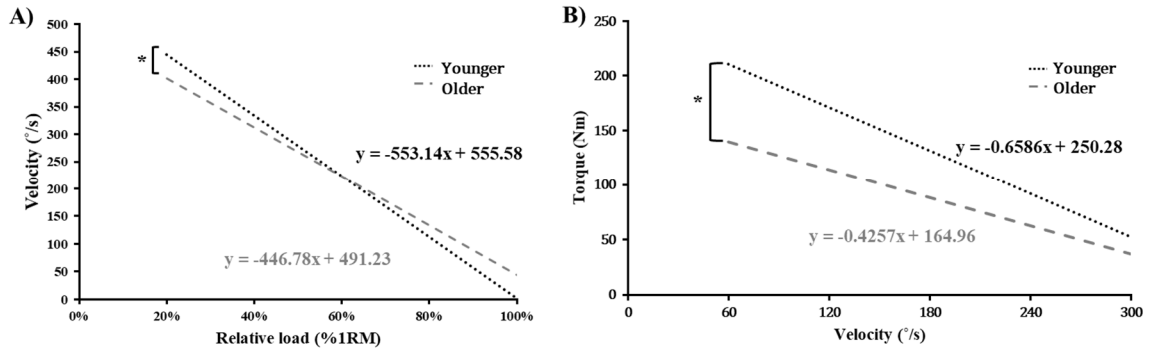


**Figure 21.** Determinants of explosive torque production **A)** collapsed across age, in the **B)** older, and the **C)** younger men during the 150-200 ms of the maximal, rapid contraction. Determinant variables that independently explained a significant proportion of the total variance in  $RTD_{150-200}$  are signified with an \*. Only determinants that were significantly correlated with  $RTD_{150-200}$  in the collapsed, younger, and older groups.

#### ***4.6 Age related adaptations to the torque-velocity curves and relationship with the physiological variables***

Out of the 37 participants, only 35 participants were examined. Two older men were excluded from the analysis because these participants were unable to produce torque at  $300^\circ/s$ . The linear regression analysis revealed that the slopes for the load-controlled and velocity-controlled torque-velocity curves were best fit with a linear fit. Therefore, the statistical analysis revealed that the velocity controlled slope was significantly more negative in the younger men ( $F_{(1,34)} = 25.349$ ,  $p \leq 0.001$ ) when compared to the older men (Figure 22, B.). Similarly, for the load controlled condition, the younger men had a significantly more negative slope ( $F_{(1,34)} = 13.805$ ,  $p = 0.001$ ) (Figure 22, A.).





**Figure 22.** Age differences in **A)** relative load-velocity and **B)** torque-velocity curve. \* = Significant difference between slopes to the 0.05 level.

The Pearson correlation coefficient revealed significant positive relationships between SLOPE-ISK and MQEI ( $p \leq 0.001$ ), nDBL PTT ( $p \leq 0.001$ ), nDBL RTD<sub>0-50</sub> ( $p = 0.004$ ) across age (Figure 23). Additionally, significant negative relationships between the morphological, neural, and contractile variables across age. Data is presented in table 6 and Figures 24-26. For the load-controlled condition, significant positive and negative relationships were found between Slope-ISOT and neural, contractile and morphological variables (Table 6) (Figure 27).

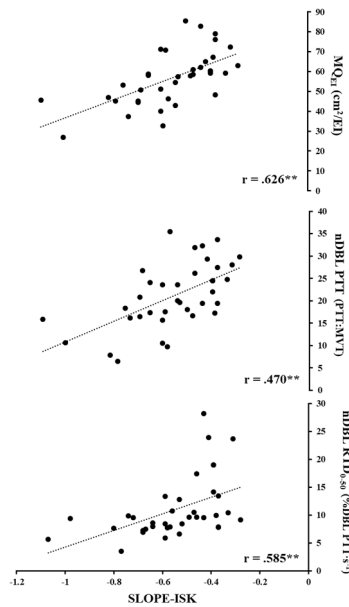
**Table 6. Relationships between the velocity and load controlled torque-velocity curve across age.**

	SLOPE-ISK	SLOPE-ISOT
<b>Morphological</b>		
PmCSA (cm <sup>2</sup> )	-.734**	-.646**
MQEI (cm <sup>2</sup> /EI)	.626**	.436**
TmCSA (cm <sup>2</sup> /MQEI)	-.747**	-.449**
VL PA (°)	-.415*	-.397*
<b>Neural</b>		
MUNE (#)	-.582**	-.369*
<b>Contractile</b>		
SGL PTT (Nm)	-.544**	-0.223
SGL RTD <sub>0-50</sub> (Nm·s <sup>-1</sup> )	-.495**	-0.118
SGL pRR(Nm·s <sup>-1</sup> )	-.529**	-0.120

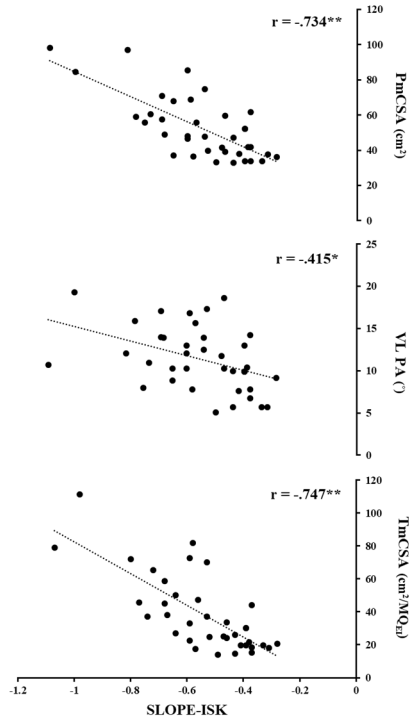
DBL PTT (Nm)	<b>-.492**</b>	-0.204
DBL RTD <sub>0-50</sub> (Nm·s <sup>-1</sup> )	<b>-.623**</b>	-0.180
DBL pRR (Nm·s <sup>-1</sup> )	<b>-.501**</b>	-0.108
nDBL PTT (PTT:MVT)	<b>.585**</b>	<b>.420*</b>
nDBL RTD <sub>0-50</sub> (%DBL PTT)	<b>.470**</b>	0.300

\*\* = Singificant relationship to the 0.01 level

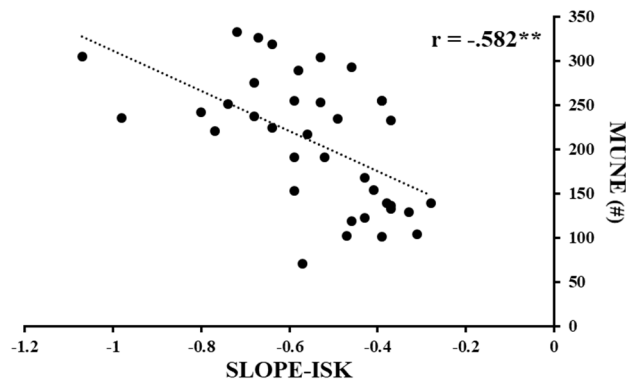
\* = Singificant relationship to the 0.05 level



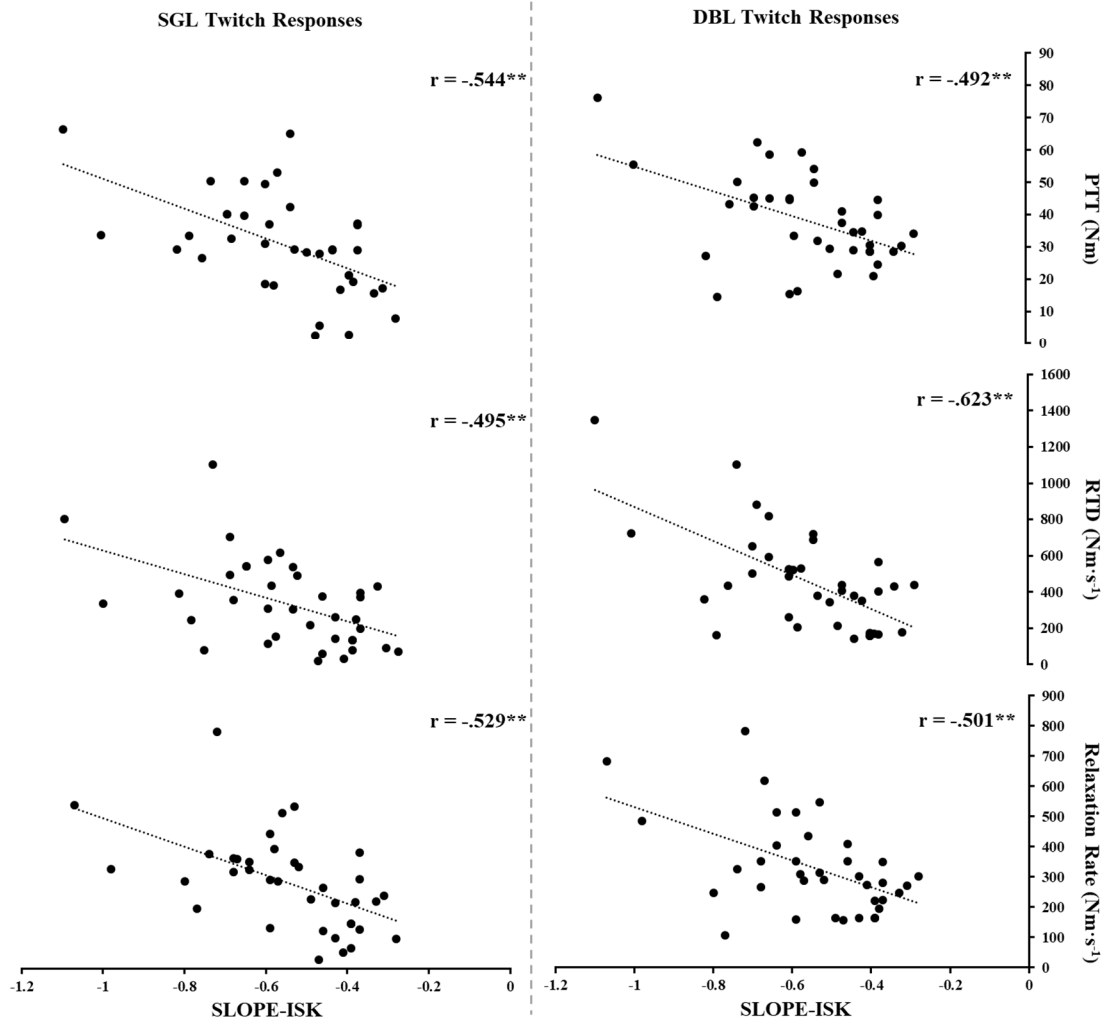
**Figure 23.** Significant positive relationships between the determinant variables and SLOPE-ISK across age. \*\* = Significant relationship to the 0.01 level.



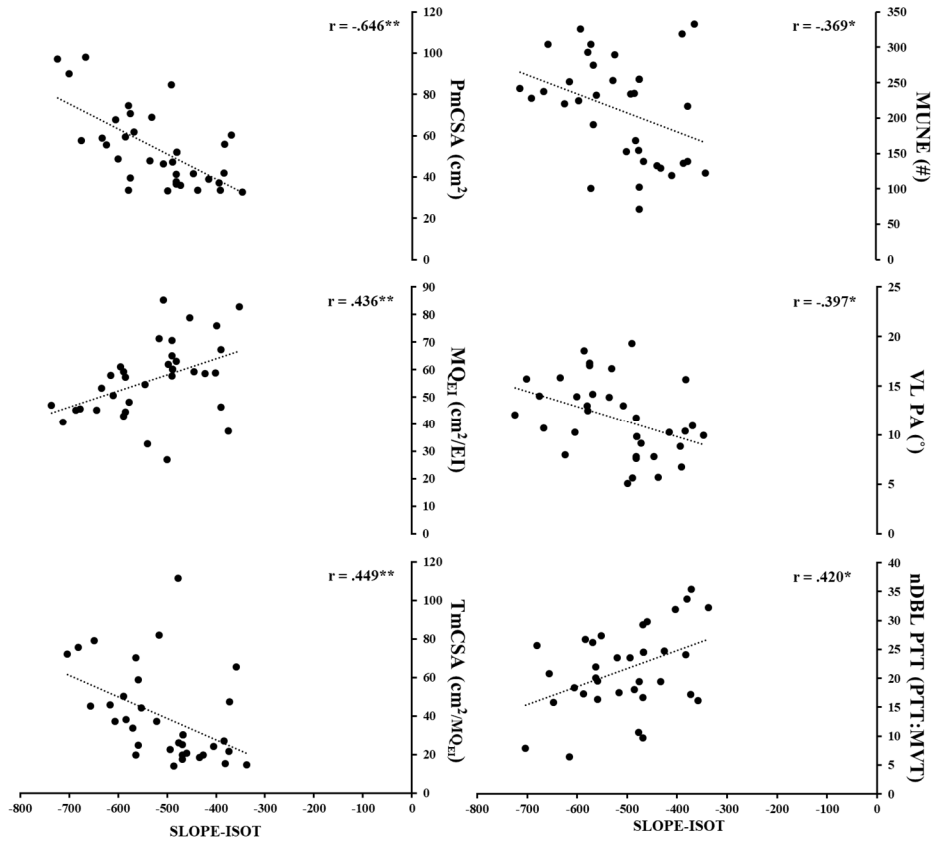
**Figure 24.** Significant negative relationships between SLOPE-ISK and the morphological variables. \* = Significant to the 0.05 level. \*\* = Significant to the 0.01 level.



**Figure 25.** Significant negative relationship between MUNE and SLOPE-ISK across age. \*\* = Significant to the 0.01 level.



**Figure 26.** Significant negative relationship between Twitch responses and SLOPE-ISK across age. \*\* = Significant to the 0.01 level.



**Figure 27.** Significant negative relationship between Twitch responses and SLOPE-ISOT across age. \* = Significant to the 0.05 level. \*\* = Significant to the 0.01 level.

## CHAPTER V

### DISCUSSION

The purpose of this investigation was three-fold: 1) to examine the effect of age on the neural, contractile and morphological determinants of rapid torque production; 2) to investigate how the determinants of RTD may change as a result of the aging process; and 3) to examine the effect of age on the torque-velocity curves. The results of this study suggest that the older men expressed reduced RTD throughout the explosive contraction, as well as, possessed altered neural, contractile and morphological variables compared to the younger men. A blend of physiological variables influenced RTD throughout the explosive contraction across age. Additionally, the primary physiological variables influencing RTD were different between the younger and older men throughout the explosive contraction. Finally, the older men possessed a significantly less negative torque-velocity slope in each condition compared to the younger men.

The data collected in this study could provide information about the importance of certain physiological variables required to express high levels of torque quickly in rapid movements (i.e., fall recovery, balance perturbations, and quick athletic movements) (Aagaard et al. 2007; Aagaard et al. 2002; Bento et al. 2010; Clark et al. 2013; Thompson et al. 2014; Thompson et al. 2013).

The results of the study are in accordance with those of Mau-Moeller et al. (2013) where older adults produced significantly less torque during each 50 ms time frame. Additionally, the results from the current study corresponds well with Folland et al. (2014) in that different physiological variables influence voluntary RTD at different time frames.

However, the current study built on these prior studies and included measures of motor unit number estimates, additional evoked twitch responses, and morphological data to provide a more comprehensive examination of the physiological determinants necessary for high voluntary RTD across age. The data from the current study show that different physiological variables influence different phases of RTD during an explosive contraction across age, as well as, in the younger and older men. Additionally, these data reveal significant age differences in the slope of the torque-velocity curves and what physiological variables are related to the slope of the curve. The data collected in this study provides additional knowledge into the complex interplay between the neural, contractile and morphological variables that contribute to voluntary RTD. Further, these data suggest that the determinants of RTD are a blend of neural, contractile and morphological variables across age and in younger and older men.

### *5.1. Neural Determinants of the Rate of Torque Development*

Previous research has shown that muscle activation during the initial phase of a rapid contraction is extremely important for producing high levels of torque quickly (Aagaard et al. 2002; Hakkinen et al. 1998; Van Cutsem and Duchateau 2005; Van Cutsem et al. 1998) and has been shown to be highly related to the early production of

torque (i.e.  $\leq 80 - 100$  ms) (Klass et al. 2008; Mau-Moeller et al. 2013). The results of the current study provide additional evidence that a reduction in early phase RTD (0-50 ms) could be highly dependent on peripheral muscle function and neural activation (Haikkinen et al. 1996, Aaggard et al. 2002). In accordance with previous research (Gerstner et al. 2017a; Hakkinen et al. 1996; Hakkinen et al. 1995), absolute muscle activation was lower in the older compared to the younger men and normalized muscle activation (%Mwave peak-to-peak) was also significantly related to RTD (Folland et al. 2014). However, muscle activation amplitude was only a significant determinant of the early phase of RTD across age and in the younger and older men accounting for 7.7%, 45.3% and 49.6% of the variance in RTD<sub>0-50</sub>, respectively. This result is similar to previous research suggesting that muscle activation is a key physiological variable for early RTD (Andersen and Aagaard 2006; De Ruitter et al. 2004; de Ruitter et al. 2007; Folland et al. 2014). Additionally, Mau-Moeller et al. 2013 suggested that a reduction in EMG amplitude may be an indicator of reduced neural drive to the muscle. The older men in the current study had a lower CMAP and aEMG<sub>0-50</sub> amplitude than the younger men. In addition, nEMG<sub>0-50</sub> was a significant determinant of early RTD suggesting that neural drive could be a limiting factor leading to a reduced RTD<sub>0-50</sub> (Mau-Moeller et al. 2013). Although muscle activation is a primary determinant in RTD, the age-related reduction in viable motor units may be another limiting factor for RTD.

This is highlighted by the significant reduction in motor unit number in the older men. Surprisingly, MUNE was associated with each consecutive 50 ms RTD time frame across age, suggesting that possessing more viable motor units is associated with increased RTD throughout each 50 ms time frame during the the first 200 ms of an



explosive voluntary contraction. However, since MUNE is the ratio of the CMAP and SMUP, the reduced MUNE observed in the older men was most likely due to a lower CMAP because the SMUP was not different between age. Although not a significant predictor, SMUP was negatively related to the torque produced during the first 50 ms of the explosive contraction across age. After further examination, SMUP was negatively related to  $RTD_{0-50}$  in the older men suggesting that the increase in SMUP is linked to a reduced  $RTD_{0-50}$ . Previous research has suggested that an elevated SMUP may be an indication of skeletal muscle remodeling (McNeil et al. 2005) or a shift in skeletal muscle fiber composition. The remodeling process is thought to be a survival method to compensate for the reduction of functional motor units to maintain muscle strength (Power et al. 2016a). An elevated SMUP has been attributed with lower threshold motor units reinnervating larger, more powerful muscle fibers leading to an increased SMUP (Power et al. 2016a; Scaglioni et al. 2003). Although the SMUP was not significantly elevated in the older men, the CMAP was significantly lower compared to the younger men. Because high threshold motor units are preferentially lost and lead to fiber atrophy, a smaller CMAP or elevated SMUP could be related to a higher predominance of Type I muscle fibers, which in turn, can lead to a reduction in muscle strength, power, and RTD (Fling et al. 2009; Ling et al. 2009; Power et al. 2010). This result may provide evidence of a reduced ability to maintain viable, high threshold motor units or an inability to reinnervate neighboring, recently vacated type II muscle fibers (Piasecki et al. 2018). Although MUNE was not a significant determinant of RTD, a reduced MUNE could lead to a reduction in RTD (Power et al. 2016b). Therefore, the data from the current study

suggests that possessing and maintaining a high number of viable motor units could lead to a maintained RTD through the aging process.

Motor nerve function is another piece of the neural puzzle that is associated with significant age-related alterations in neuromuscular function. Age-related alterations to motor nerve function has been observed to increase with advancing age (Bouche et al. 1993; Gregg et al. 2004; Palve and Palve 2018; Resnick et al. 2001; Resnick et al. 2000; Taylor 1984). Previous research has shown a decline in motor nerve conduction velocity in older adults (Rivner et al. 2001; Saeed and Akram 2008; Strotmeyer et al. 2009; Thakur et al. 2010; Tong et al. 2004; Ward et al. 2015; Werner et al. 2012) could play a significant role in rapid force production. Similar to previous research (Ward et al. 2015; Ward et al. 2014a), the results of the current study suggests that a reduction in motor nerve conduction velocity was associated with a reduced strength and RTD in the later phase (100-200 ms) of the explosive contraction. This result is somewhat surprising in that it was not associated with the early phase RTD. Nevertheless, a reduced motor nerve conduction velocity may be an integral part of the reduction in RTD across age.

## *5.2. Contractile Determinants of the Rate of Torque Development*

Previous research has suggested that the intrinsic contractile properties of the muscle can significantly influence RTD across the age span (Gerstner et al. 2017a; Hakkinen et al. 1996; McPhee et al. 2018). The results from the current examination are similar to previous research in that the older men possessed degraded contractile properties compared to the younger men (Petrella et al. 1984, Roos et al. 1999, Klass et al. 2008, Aagaard et al. 2007, Mau-Moeller et al. 2013). Specifically, the older men in the

current study possessed reduced peak twitch torques, slower evoked RTD and slower peak rate of relaxation in response to a single and doublet stimulus.

The older men were able to produce significantly less evoked peak twitch torque in response to a single and doublet stimulus when compared to the younger men. Additionally, the SGL PTT was significantly related to voluntary RTD in each 50 ms time frame from the beginning of the contraction to 150 ms. Additionally, the DBL PTT was significantly related to voluntary RTD in each 50 ms time frame from 50 ms to 200 ms. Along with muscle activation, SGL PTT was a significant determinant of voluntary  $RTD_{0-50}$  in the old, but was not a significant determinant of voluntary RTD at any time point in the younger men. Coupled with the neural determinants, this result suggests that the older men may rely on muscle activation amplitude and contractile capacity of the muscle in the early phase RTD. The results of the current study are similar to those of Mau-Moeller et al. 2013 who also found that contractile properties were altered in the older adults and were related to RTD suggesting that changes in contractile properties play a significant role in rapid torque production. Further, Dalton et al. 2010 found that older adults possessed significantly reduced peak twitch torques in the leg muscles when compared to younger adults. Therefore, in combination with the altered neural physiological variables and smaller muscle size, the reduction in PTT observed in the older men could be a result of altered contractile properties of the muscle.

The normalization of the peak twitch torque to the maximal strength could provide additional evidence about neural contribution to RTD. Previous research has suggested that the nDBL PTT provides unique information about the contribution of the central nervous system to muscular strength (Jenkins et al. 2017). The absolute DBL PTT

provides peripheral information without the influence of the central nervous system, therefore when DBL PTT is normalized to maximal strength, the ratio could provide information about neural and contractile contribution to muscle strength (Jenkins et al. 2017). Therefore, in theory, an increased ratio (e.g., lower PTT relative to MVT) indicates an increased neural contribution to muscular strength (Cannon et al. 2008; Jenkins et al. 2017). Interestingly, when collapsed across age, nDBL PTT was a significant determinant of the early phase RTD. The older men had a larger nDBL PTT compared to the younger men and nDBL PTT was a significant determinant of early phase RTD across age. This result provides additional evidence that the early phase of RTD is highly dependent on neural contribution across age (Jenkins et al. 2017).

Although absolute and normalized PTT provides valuable intrinsic contractile information, the evoked rate of torque development may provide additional unique information about the age related reduction in voluntary RTD. The results from the current study are in accordance with previous studies (Dalton et al. 2012; McNeil et al. 2007) in that older men produced significantly lower twitch RTD in response to a single and doublet stimulus. The two different stimuli provide different contractile information. For instance, the DBL stimulus provides two stimuli that, in theory, acts to fully activate the motor unit pool, drive the motor units to a high/maximal firing rate, removing the muscle slack leading to a better examination of force transfer (Herda et al. 2013). In contrast, the SGL stimulus examines the contractile capability of the resting muscle including overcoming the muscle slack (Herda et al. 2013). When collapsed across age, the SGL RTD<sub>0-50</sub> was related to voluntary RTD during the first three voluntary RTD time frames (i.e., 0-50, 50-100, 100-150 ms), whereas the DBL RTD<sub>0-50</sub> became increasingly

related to the voluntary RTD from 50 ms and on. These results suggests that the increased relationship between the SGL RTD<sub>0-50</sub> and voluntary RTD in the earlier time frames could be increasingly dependent on the slack that is taken up. Although not statistically significantly different between ages, SGL EMD was negatively related to the 50-150 ms time frame suggesting that the take up of slack may influence the voluntary RTD after the first 50 ms of an explosive contraction.

It is interesting to note that DBL RTD<sub>0-50</sub> was a significant determinant of voluntary RTD during the 100-150 ms time frame across age, as well as in the younger men. However, when age was separated, only the SGL PTT was was a significant determinant of voluntary RTD in the first 50 ms in the older men, not in the younger men. This result is similar to those of Folland et al. 2014 and Andersen et al. 2006, where the maximal contractile capacity of the muscle is significantly related to and a determinant of the later phase of voluntary RTD in the young. The reduced evoked RTD observed in the older men indicates a slower contractile speed when compared to the younger men (D'Antona et al. 2003; Hakkinen et al. 1995). There is a significant relationship between the muscle fiber size, fiber type and the rate of torque development in response from an electrical stimulus (Harridge et al. 1996). Additionally, Type II muscle fibers have been shown to have a faster shortening velocity and higher force production compared to the Type I muscle fibers (Harridge et al. 1996). The slowing of the contractile properties in the older adults in the current study could be an indication of the age-related loss of type II muscle fibers and atrophy of remaining, viable type II muscle fibers (Larsson et al. 1979; Wilder and Cannon 2009). Therefore, a reduction in

fast-twitch contractile properties could have a significant influence on muscle performance and RTD across age (Hvid et al. 2010; Korhonen et al. 2006).

Similar to the results of previous research (Dalton et al. 2012; Wilder and Cannon 2009), the older adults in the current study had a significantly slower relaxation rates when compared to the younger men. Additionally, the SGL and DBL pRR were related to each 50 ms time frame of the voluntary RTD contraction across age. When examined further, SGL pRR was significantly related and was a significant determinant of RTD during the 50-100 ms time frame in the older, not the younger men. Additionally, DBL pRR was a determinant of RTD<sub>150-200</sub> in the older, not the younger men. The reduced peak relaxation rates in response to an electrical stimulus in older men has been associated to the age-related alterations in skeletal muscle function (Wilder and Cannon 2009). One explanation for the reduced peak relaxation rate in the older men in the current study could be due to the alteration in Ca<sup>2+</sup> sensitivity and handling (Baylor and Hollingworth 2003). A study by Lamboley et al. (2015) found that physically active older adults possessed significantly lower proportion of type II muscle fibers and both type I and type II muscle fibers had a significantly lower amount of stored Ca<sup>2+</sup> compared to the younger adults. Further, the viable type II muscle fibers in the older adults had a significantly altered Ca<sup>2+</sup> sensitivity and a reduced specific tension (fCSA/Force) compared to the younger men (Lamboley et al. 2015). In another recent study, Straight et al. (2018) observed that older adults had a significantly reduced Ca<sup>2+</sup> response in both type I and type II muscle fibers, and this reduction in Ca<sup>2+</sup> sensitivity was significantly related to a reduction in muscle strength and power in the older adults.

The results of the current study suggests that the contractile properties significantly influence RTD across age. In the combination with the previous studies highlighted, the results from the current study suggest that the age related reduction motor unit number, lower muscle activation amplitude, lower PTT, slower evoked RTD and a slower evoked pRR could provide indirect evidence of altered contractile properties and function in the older men. Although the neural and contractile determinants provide important information related to voluntary RTD across age, morphological variables may provide additional insight into the age-related reduction in RTD.

### *5.3. Morphological Determinants of the Rate of Torque Development*

Both neural activation, and intrinsic contractile properties of skeletal muscle play a significant role in RTD contractions, however, the morphological and architectural structure of the muscle also plays a part in the development of torque (Gerstner et al. 2017a; Roos et al. 1999; Strasser et al. 2013; Thom et al. 2007; Thompson et al. 2013; Wu et al. 2016). Muscle size and quality have been shown to be related to strength and RFD capabilities in older adults (Fukumoto et al. 2012; Hakkinen and Hakkinen 1991; Kent-Braun et al. 2000; Kubo et al. 2003; Nishihara et al. 2014; Stenroth et al. 2012; Watanabe et al. 2013; Wilhelm et al. 2014).

Specifically, older adults have been shown to have a lower amount of muscle mass and worse muscle quality, which is undoubtedly due to the remodeling process associated with advancing age (Goodpaster et al. 2006; Rech et al. 2014). The results of the current study are similar to previous research showing that muscle size, quality and VL pennation angle were significantly different between the younger and older men

(Fukumoto et al. 2015; Magrini et al. 2018; Rech et al. 2014; Wilhelm et al. 2014).

Additionally, the absolute muscle size (PmCSA) was significantly smaller in the older men compared to the younger men. Muscle quality, assessed as the weighted total EI, was significantly higher in the older men suggesting a lower muscle quality compared to the younger men. When mCSA was corrected for EI, the age differences were increased between younger and older men. Interestingly, muscle size and muscle quality were significant determinants in each of the 50 ms time frames when collapsed across age. However, when examined further, bigger muscle size and better muscle quality were a significant predictor of RTD from 50 ms and on in the younger men, but not in the older men. This result is different from previous research that observed muscle size was significantly related to the later phase RTD and a determinant of maximal strength in older adults (Gerstner et al. 2017, McPhee et al. 2018). Nevertheless, the data collected from the current study suggests that a greater muscle size is related to higher RTD in the early time frames. The reduction in muscle size is primarily due to atrophy of muscle fibers (Type I and Type II), but older adults have been shown to have smaller muscle fiber areas and lower number of Type II muscle fibers (McPhee et al. 2018), which could lead to smaller muscles and lower RTD (Callahan et al. 2015; McPhee et al. 2018).

Additionally, the lower MUNE observed in the older men could be linked to the reduction in the total number of muscle fibers existing in the older men, and could also lead to reductions in muscle strength and RTD (McPhee et al., 2018, Piasecki et al., 2016). Further, the EI corrected muscle size (PmCSA/EI for each muscle) was a significant predictor for later phase RTD across age suggesting larger, better quality muscles are associated with a higher voluntary RTD across age. However, the lack of



relationship between muscle size and quality in the older men may suggest that altered neural activation and intrinsic contractile properties may influence RTD to a greater extent than muscle size and quality (Callahan and Kent-Braun 2011). Nevertheless, our data suggests that possessing a greater muscle size and better quality muscle is important for maintenance of RTD through the aging process.

Additionally, previous research has observed a smaller pennation angle in the older population and was significantly related to RFD capabilities (Morse et al. 2005; Narici et al. 2003; Stenroth et al. 2012). The results of the current study revealed that the older men had a significantly smaller pennation angle when compared to the younger men. Additionally, the VL pennation angle was significantly related to RTD in the last 50 ms time frame across age. These data suggest that the increased VL pennation angle is associated with an increased torque produced during the 150-200 ms time frame of an explosive contraction. The later RTD time frame is close in time to the maximal torque production, therefore a larger VL pennation angle is associated with higher torque production later in the contraction (Gerstner et al. 2017b). This is in agreement with previous research in that a wider VL pennation angle is associated with higher torque production (Gerstner et al. 2017b).

#### *5.4. Age-related changes to and the Relationships between the Physiological variables and the Torque-Velocity curves*

As previously discussed, aging is associated with significant alterations in the neural contractile and morphological systems leading to a reduction in RTD, however, these physiological variables may play a significant role in the torque and velocity

production (Harries and Bassey 1990). Because of these physiological changes observed during the aging process, previous research has shown an alteration in the force-velocity relationship in older adults (Alcazar et al. 2017; Alcazar et al. 2018; Callahan and Kent-Braun 2011; Jenkins et al. 2015a; Lanza et al. 2003; Petrella et al. 2007; Pojednic et al. 2012; Thom et al. 2007; Yamauchi et al. 2010). The inability to produce torque or high velocities or relative loads could be an important non-invasive indicator of age-related changes in neuromuscular function (Jenkins et al. 2015a; Reid et al. 2014). The results from the current study reveal that the older men had a significantly less negative slope compared to the younger men in the SLOPE-ISK and SLOPE-ISOT torque-velocity conditions.

In accordance with previous research (Lanza et al., 2003, Thom et al., 2007), the older men in the current study produced a SLOPE-ISK that was shifted down and to the left suggesting that older men produced less average torque at the same absolute velocities as the younger men. As previously discussed, older adults suffer from age-related reduction in type II muscle fiber number and smaller muscle fibers which could contribute to the less negative slope observed in the older men (Doherty et al. 1993; Gür et al. 2003; McPhee et al. 2018). Several negative relationships between SLOPE-ISK and the physiological variables indicate that the age-related changes in neuromuscular and morphological variables could lead to the less negative slope observed in the older men (Gerstner et al. 2017a; Wilhelm et al. 2014). Similar to research by Callahan and Kent-Braun (2011), the SLOPE-ISK was significantly related to contractile properties, specifically the SGL and DBL pRR across age in the current study. This result suggests that calcium handling (discussed previously) could play a significant role in the torque

velocity slope. This result is in accordance with those of Straight et al. (2018), who found that absolute and relative knee extension performance was significantly lower in the older adults compared to the younger adults and discovered a significant relationship between reduced knee extension performance and reduced muscle fiber  $\text{Ca}^{2+}$  sensitivity in the older adults (Straight et al. 2018). Further, SGL and DBL  $\text{RTD}_{0-50}$  were significantly lower in the older men and were related to the less negative SLOPE-ISK across age, which may be an indicator of an age-related altered contractile function at the muscle fiber level leading to reduced performance at the whole muscle level (Callahan and Kent-Braun 2011; Callahan et al. 2015; Straight et al. 2018). The age-related alteration in muscle fiber function could explain the reduction in torque produced at each isokinetic velocity (Valour et al. 2003). As previously discussed, muscle fiber atrophy and preferential loss of Type II muscle fibers account for the age-related muscle atrophy (McPhee et al. 2018), potentially leading to a slower movement velocity observed in the older men (Gür et al. 2003; Korhonen et al. 2006). Additionally, the negative relationship between MUNE, PmCSA, and TmCSA could provide more evidence of a reduction in muscle size, muscle function, or composition could lead to a less negative SLOPE-ISK across age (Gerstner et al. 2017a; Gür et al. 2003).

Previous research has suggested that assessment of the torque-velocity curve in an isotonic mode may be more advantageous to examine physical function across age (Alcazar et al. 2017). For the SLOPE-ISOT condition, the less negative slope suggests that the older men were unable to achieve the velocity that the younger men were able to at a low relative loads. However, the isotonic torque-velocity condition was normalized to maximal knee extension strength, as a result, the older men were able to move at a

faster velocity at a heavier relative load compared to younger men. Interestingly, only the morphological variables and the number of motor units were significantly related to the SLOPE-ISOT. This result suggests that muscle size, muscle quality, and the number of viable motor units in the knee extensors are essential to achieving a more negative slope in the isotonic condition (Gerstner et al. 2017a; Gür et al. 2003; Wilhelm et al. 2014).

### *5.5 Limitations*

One of the largest limitations to the current study was the low number of participants used for the stepwise multiple regression analysis. Traditionally, significantly more participants are needed for the study to have adequate power. However, due to the time commitment as well as the variables assessed, the number of participants were similar to other research within the kinesiology subject area.

Another limitation to this study was the use of all non-invasive variables, therefore external factors may have influenced the data. Using surface EMG and other equipment limits the results of the study to a point. Because of this, the results provide evidence that are indirect evidence of physiological mechanisms. Therefore, the study utilizes the term determinants because this allows the reader to understand that the results displayed in this study are in no way definitive.

Another limitation would be the motivation level of each participant. Differences in motivation levels between participants may produce varying levels of effort during the voluntary contractions. Although this is inevitable, participants were verbally encouraged to give their best effort for the full duration of the study.

### *5.6 Future Research and Recommendations*

This study provided important information about the determinants of RTD across the age span, as well as, within the age groups. This study revealed that the determinants of RTD were different between the age groups. A future study should examine these variables in different age groups from children to the very old adults. This could provide evidence of which physiological variables are most important to RTD at different ages.

Because this study has provided a more comprehensive insight into the physiological determinants of RTD across age and between age groups, it would be interesting to examine the effect of different exercise training programs on these physiological determinants and RTD. The rate of torque development and many of these physiological determinants have been linked to functional ability in the older adults, therefore, designing an exercise training program aimed at maintaining or improving these physiological determinants could lead to improved functional ability, longer independence, and increased quality of life in older adults. Due to the age of these individuals, it is essential to determine the most efficient and effective exercise training program that can lead to maintained physical function and overall successful aging.

The current study only examined age differences in the torque-velocity curves and the relationships of the curves with different neuromuscular variables. However, it is unknown if the power produced by older adults are either torque or velocity deficient. This could provide information to improve exercise training methodology in hopes of maintaining muscle power throughout the aging process. Additionally, the current study simply examined the relationships between the slopes from the isokinetic and isotonic

torque-velocity curves in younger and older men, therefore examining what physiological variables contribute to the torque produced at each isokinetic and isotonic velocity may lead to improved exercise training programs.

Only the torque-velocity slopes were examined in the current study, however it would be interesting if the % decline in torque produced at each isokinetic movement speed was correlated with any of the physiological variables assessed in the current study. This data could provide further information about changes in neuromuscular function across the age span. Additionally, these data could provide additional knowledge about how these variables relate to torque production at different movement speeds.

### *5.7 Conclusions*

This study has provided a more comprehensive and improved insight into the determinants of RTD across the age span, as well as, between age groups. In agreement to the results of Folland et al. (2014), the results suggest that high levels of RTD are determined by different physiological variables across the age span. However, the ability to achieve high muscle activation amplitudes, maintain a higher number of viable motor units, possess more powerful muscle fibers, and larger/better quality muscles could lead to maintaining a high level of RTD across the age span. Although functional ability was not directly assessed in the current study, possessing an improved RTD may lead to better maintenance of functional ability during the aging process (Thompson et al. 2013).

The determinants are different between the younger and older men throughout the first 200 ms of a maximal voluntary RTD contraction. First, neural activation is an extremely important variable for producing a higher early phase RTD. Secondly, older

men have compromised intrinsic contractile properties when compared to younger men highlighted by the reduced contractile twitch performance. The altered intrinsic contractile properties were significantly related in the later time frames (100-200 ms) in the young and throughout the contraction in the older men. The morphological variables were significant determinants of RTD throughout the explosive contraction across age and the younger men.

The older men had a drastically less negative slope for both the isokinetic and the isotonic maximal knee extension torque-velocity curves. Different physiological variables were related to the less negative slope in the isotonic and isokinetic torque velocity curves across age. These data suggests that the age-related changes in neural, contractile and morphological function could be a significant factor for the more positive torque-velocity slope in the older men.

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## APPENDIX A: IRB APPROVAL LETTER



### Oklahoma State University Institutional Review Board

Date: 07/17/2018  
Application Number: ED-18-75  
Proposal Title: The Physiological Determinants of Rate of Force Production Across the Life Span

Principal Investigator: Mitchel Magrini  
Co-Investigator(s):  
Faculty Adviser: Jason Defreitas  
Project Coordinator:  
Research Assistant(s):

Processed as: Expedited

Status Recommended by Reviewer(s): Approved

Approval Date: 07/17/2018

Expiration Date: 07/16/2019

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The IRB application referenced above has been approved. It is the judgment of the reviewers that the rights and welfare of individuals who may be asked to participate in this study will be respected, and that the research will be conducted in a manner consistent with the IRB requirements as outlined in section 45 CFR 46.

The final versions of any recruitment, consent and assent documents bearing the IRB approval stamp are available for download from IRBManager. These are the versions that must be used during the study.

As Principal Investigator, it is your responsibility to do the following:

1. Conduct this study exactly as it has been approved. Any modifications to the research protocol must be approved by the IRB. Protocol modifications requiring approval may include changes to the title, PI, adviser, other research personnel, funding status or sponsor, subject population composition or size, recruitment, inclusion/exclusion criteria, research site, research procedures and consent/assent process or forms.
2. Submit a request for continuation if the study extends beyond the approval period. This continuation must receive IRB review and approval before the research can continue.
3. Report any unanticipated and/or adverse events to the IRB Office promptly.
4. Notify the IRB office when your research project is complete or when you are no longer affiliated with Oklahoma State University.

Please note that approved protocols are subject to monitoring by the IRB and that the IRB office has the authority to inspect research records associated with this protocol at any time. If you have questions about the IRB procedures or need any assistance from the Board, please contact the IRB Office at 223 Scott Hall (phone: 405-744-3377, [irb@okstate.edu](mailto:irb@okstate.edu)).

Sincerely,

A handwritten signature in black ink, appearing to read 'Hugh Crethar'.

Hugh Crethar, Chair Institutional  
Review Board

VITA

Mitchel A. Magrini

Candidate for the Degree of

Doctor of Philosophy

Dissertation: THE PHYSIOLOGICAL DETERMINANTS OF RATE OF TORQUE  
PRODUCTION ACROSS THE LIFE SPAN

Major Field: Health, Leisure, and Human Performance

Biographical:

Education:

Completed the requirements for the Doctor of Philosophy in Health, Leisure,  
and Human Performance at Oklahoma State University, Stillwater, Oklahoma in  
May, 2019.

Completed the requirements for the Master of Science in Sports Medicine at  
University of Colorado Colorado Springs, Colorado Springs, Colorado in 2015.

Completed the requirements for the Bachelor of Science in Physical Education  
at Doane University, Crete, Nebraska in 2013.

Experience:

Graduate teaching associate Aug '15 – Present  
Department of Health and Human Performance  
Oklahoma State University

Professional Memberships:

American College of Sports Medicine; 2015 – Present  
National Strength and Conditioning Association; 2015 – Present  
Central States Region, American College of Sports Medicine; 2015 – Present