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## Effect of ankle joint position on triceps surae contractile properties and motor unit discharge rates

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A thesis submitted in partial fulfillment of the requirements for the Master of Science degree in Kinesiology

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## Abstract

The length-tension relationship of the triceps surae (TS) can be altered by changing the knee joint position, ankle joint position or both. However, studies exploring the effect of muscle length on triceps surae (TS) neuromuscular properties have focused only on changes in knee joint position, affecting only two of the three muscle components of the TS. Thus, the purpose of this study is to compare the neuromuscular properties of the three TS muscles during plantar flexion contractions at two ankle joint positions, 20° dorsiflexed (DF) and 20° plantar flexed (PF). Maximal isometric voluntary strength (MVC), voluntary activation, and evoked contractile properties of the ankle plantar flexors were compared between both ankle joint positions. Additionally, motor unit discharge rates (MUDRs) of the soleus, medial (MG) and lateral (LG) gastrocnemii were sampled during plantar flexion contractions at 25, 50, 75 and 100% MVC using indwelling tungsten electrodes. Peak twitch torque and MVC were lower by ~70% and 61%, respectively, whereas maximal rate of torque relaxation was 39% faster in the PF compared with the DF position. Voluntary activation (~95%) was unaffected by changes in ankle joint position. LG MUDRs showed no differences between ankle joint positions, regardless of contraction intensity. Submaximal MG and soleus MUDRs showed no differences between the two ankle joint positions, however at 100% MVC both muscles had 9% and 20% higher rates in the DF position, respectively.

## Key words

gastrocnemius, soleus, muscle length, EMG, motor unit

## **Lay summary**

The muscles of the calf region of the leg serve a major role in the successful completion of daily tasks, such as standing, walking and running. During walking, these muscles undergo constant changes in length with rotations of the knee and ankle joints. These length changes are associated with different nerve signaling rates, which can increase or decrease muscle activity, affecting how much force the muscles produce and ultimately the successful completion of these daily tasks. This thesis explores how muscle length changes affect muscle contractile properties and nerve signaling rates to the calf muscles in young adults (~24 years of age). The findings in this thesis indicate that the rate of nerve signaling was faster in two of the three muscles of the calf when they were at a longer compared with a shorter length. In the other muscle, there was no difference in the rate of nerve signaling between the two different muscle lengths. This work provides further information regarding the underlying mechanisms of the interaction between nervous system control and muscle function during contractions at different joint configurations, which mimic everyday movements.

## Co-Authorship statement

Experimental data were collected by Kalter Hali, Alexander M. Zero and Jacob Fanous. Surface electromyography data were analyzed by Alexander Zero. All other data were analyzed by Kalter Hali. Alexander M. Zero and Charles L. Rice participated in the interpretation of the experimental data.

## Acknowledgments

There are many people that have supported me throughout my graduate studies here at Western, all of which deserve my gratitude. However, here I will mention only a few.

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Eric, Kevin, Dave, Colin and Jacob, thank you for welcoming me into the lab with your support and continuous guidance with whatever I needed. Nothing I did would have been possible without your patience and mentorship and for that, I will always be thankful. Zero and Paish, it has been a pleasure working with you two over the past year. Zero has played an integral role in the completion of my thesis project, and despite his poor choices when it comes to soccer teams, I have been lucky to have such a dedicated friend by my side. You have all contributed to making my graduate experience as unique as it was.

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## List of abbreviations

ANOVA – analysis of variance

CD – contraction duration

CoV – coefficient of variation

DF – dorsiflexed position

EC – excitation-contraction

EMG – electromyography

HRT – half-relaxation time

ISI – interspike interval

LG – lateral gastrocnemius

MG – medial gastrocnemius

MU – motor unit

MUDR – motor unit discharge rate

MVC – maximal voluntary contraction

MyHC – myosin heavy chain

NMRR – normalized maximal rate of torque relaxation

NMRTD – normalized maximal rate of torque development

PCSA – physiological cross-sectional area

PF – plantar flexed position

Pt – peak twitch torque

RMS – root mean square

sEMG – surface electromyography

TPT – time to peak torque

TS – triceps surae

VA – voluntary activation

# Chapter 1

## 1 Literature Review

### 1.1 Skeletal muscle properties and architecture

Skeletal muscle is composed of up to thousands of muscle fibres. Each muscle fibre is an elongated, multinucleated cell comprised of a number of myofibrils arranged in parallel. Within each myofibril are sarcomeres, the basic functional unit of muscle contraction, arranged in-series. Mammalian skeletal muscle fibres are commonly classified into three main types based on the myosin heavy chain (MyHC) isoform present in the fiber (I, IIA and IIX) with MyHC I being the slowest and MyHC IIX the fastest. Examination of fibre type proportions of each muscle has revealed that muscles with a predominantly postural function such as the soleus and tibialis anterior have a high percentage of Type I fibres, whereas muscles with predominantly phasic activity such as the orbicularis oculi and triceps brachii have a high percentage of Type II fibres (Johnson et al., 1973). However, more recent work has found that muscle fibers can express combinations of these isoforms and as such muscle fiber types are not so discrete, but rather are on a continuum (Heckman & Enoka, 2012).

Skeletal muscle architecture has been defined as the arrangement of muscle fibres within a muscle relative to the axis of force generation (Lieber, 1992). Different muscles within an individual demonstrate variability in architecture which strongly affects the function of the respective muscle. The main architectural features described in the literature are pennation angle, muscle fibre length and physiological cross-sectional area (PCSA). Pennation angle is defined as the fibre angle relative to the force-generating axis of the muscle (Lieber & Jan Friden, 2000). Cadaveric studies have shown that most muscles fall into the multi-pennate category meaning that their fibres are oriented at different pennation angles. Fascicle length, which is an estimate of muscle fibre length, is defined as the length of a line coincident with the fascicle between the deep and superficial aponeurosis of a muscle (Lieber & Jan Friden, 2000). The pennation angle and muscle fibre length measurements can be used to estimate the PCSA, which theoretically represents the sum of the cross-sectional areas of all the muscle fibres within a muscle (Lieber & Jan Friden, 2000). The PCSA is the only architectural parameter directly proportional to the

maximum tetanic tension generated by a muscle – the greater the PCSA, the greater the tension a muscle can produce.

## 1.2 Voluntary limb movement

In humans, voluntary limb movement is initiated in the pre-motor cortices of the brain ~100 ms prior to muscle activation (Chen et al., 1998). Electro-chemical signals, referred to as action potentials, travel from the brain through the corticospinal tract, ultimately acting upon an alpha motor neuron in the spinal cord (Liddell & Sherrington, 1925). The spinal motor neuron is composed of dendrites, a cell body, an axon and the axon terminal branches. The dendrites of an alpha motor neuron receive signals from the central nervous system and sensory neurons from the peripheral nervous system. If the net excitatory inputs are higher than the overall inhibitory inputs, the resting membrane potential of the cell body (-70 mV) will depolarize. If this depolarization reaches a certain threshold (-55 mV), an all-or-none action potential is generated from the axon hillock of the motor neuron (Enoka, 2006). The action potential travels to the axon terminals where it opens calcium channels leading to an influx of the ion into the neuron. This causes stored packets of acetylcholine to be released into the neuromuscular junction identified as the space between the neuron and the muscle fibres it innervates. The acetylcholine attaches to its receptors on the muscle fibre membrane, thus increasing the muscle fibre's permeability of sodium and potassium (Enoka, 2006). With sufficient activation of these post-synaptic receptors the muscle fibre is depolarized which initiates the excitation-contraction (EC) coupling cycle. Electrical impulses travel along the muscle plasma membrane into the T-tubules. Stored calcium is then released from the sarcoplasmic reticulum and binds to troponin, which then slides off the tropomyosin allowing the actin and myosin contractile filaments to bind. Once the myosin releases the adenosine diphosphate and inorganic phosphate bound to it, a jerk is created causing the myosin head to pull on the actin thus shortening the sarcomere by bringing the Z-lines together. The cross-bridge cycling of the actin-myosin complex results in the sarcomere shortening. The additive effect of many sarcomeres being shortened acts to shorten the muscle which transfers the force onto bone through the musculotendinous junction producing angular joint rotation (Enoka, 2006).

## 1.3 The motor unit

The motor unit is the smallest functional component of the neuromuscular system. It consists of the motor neuron and all the muscle fibres it innervates. Each muscle is comprised of a population of motor units that vary in number (from a few tens to several hundred) and innervation ratio (number of muscle fibres innervated by one motor neuron) (McNeil et al., 2005; Boe et al., 2006; Stevens et al., 2013). The cell bodies of motor neurons that innervate a single muscle are arranged in a longitudinal cluster in the spinal cord or brainstem known as a motor neuron pool. The muscle fibres that make up a given motor unit are uniform in their histochemical and biochemical properties, although these vary considerably among motor units (Bigland-Ritchie et al., 1998). Motor units are usually classified into three different types based on their contractile speed and sensitivity to fatigue: slow, fatigue resistant, fast but fatigue resistant and fast fatigable (Bigland-Ritchie et al., 1998).

Voluntary action is achieved through the regulation of multiple motor units within each muscle's motor neuron pool in coordination with other muscles. There are two mechanisms through which motor units grade force: 1) temporal regulation and 2) spatial regulation (Adrian & Bronk, 1928). Temporal regulation, referred to as rate coding, involves modulating the rate at which the motor neuron transmits action potentials to the muscle. The discharge rates required to elicit a given force from each unit depend critically on the contractile speed of the motor unit in question: slow units generate more relative force at low excitation rates than do fast ones (Bigland-Ritchie et al., 1998). When first recruited during voluntary contractions, human motor units fire at 6 – 8 Hz (Bigland-Ritchie et al., 1998). The upper limit of motor unit discharge rates is different in human muscles, with maximal discharge rates of 16 Hz in the soleus (Dalton et al., 2009), 22 Hz in the gastrocnemii (Graham et al., 2016; Kirk et al., 2016), 23 Hz in the hamstrings (Kirk & Rice, 2017), 25 Hz in the quadriceps (Kamen & Knight, 2004) 47 Hz in the superior trapezius (Kirk et al., 2019). Maximal motor unit discharge rates within a muscle differ under different conditions such as fatigue length and adapted states such as training, aging and disease (Bigland-Ritchie et al., 1998; Kirk & Rice, 2017). Spatial regulation, referred to as motor unit recruitment, involves increasing or decreasing the number of active motor units within a muscle. According to the Henneman's size principle, the order in which motor units are recruited is determined by the motor unit's size: smaller motor units are recruited before larger motor units. (Henneman et al.,

1964). Low threshold, slow type motor units have lower innervation ratios and longer contraction times as compared with higher threshold, fast type motor units. This finding is supported by reports from the first dorsal interosseous (Moritz et al., 2005), biceps brachii (Gydikov & Kosarov, 1974), soleus (Oya et al., 2009), gastrocnemii (Hali et al., 2019) and elbow extensors (Harwood et al., 2013), in which low threshold motor units showed lower motor unit discharge rates than the later recorded higher threshold motor units. The relative contribution of rate coding and recruitment in muscles is known to vary depending on the muscle and its function. For example, the upper limit of recruitment for hand muscles is ~50–75% of MVC (Kukulka & Clamann, 1981; Thomas et al., 1986; Moritz et al., 2005), whereas the biceps brachii, tibialis anterior, soleus and gastrocnemii have motor units that are recruited at ~75% MVC or above (Kukulka & Clamann, 1981; Van Cusem et al., 1997; Oya et al. 2009; Hali et al. 2019). In theory, to achieve maximal voluntary force within a muscle, complete recruitment of all motor units with each being activated at its highest absolute discharge rate would occur.

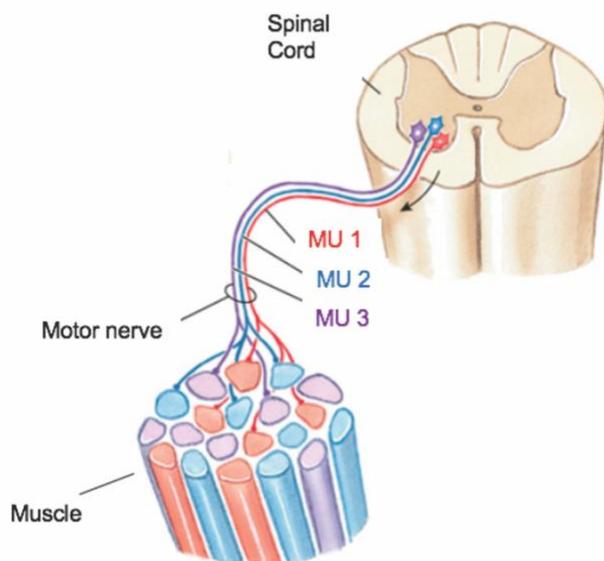


Figure 1. Diagram of three motor units (MU). (Adapted from <http://www.saptstrength.com/blog/2014/10/27/rate-of-force-development-what-it-is-and-why-you-should-care>)

## 1.4 Proprioception

Proprioception is the sense of position and movement of body parts relative to one another (Macefield & Knellwolf, 2018). This awareness is achieved through sensory input provided by various sources in the peripheral nervous system. Joint receptors contribute to proprioception mostly at the extreme ends of the normal range of motion (Burgess & Clark 1969; Clark & Burgess 1975). The sense of muscle tension is largely attributed to Golgi tendon organs which respond to the force a muscle produces (Houk & Henneman, 1967). Muscle spindles, which are stretch-sensitive mechanoreceptors found in all limb skeletal muscle, provide a significant contribution to proprioception (Macefield & Knellwolf, 2018). The spindle's function as a length detector comes from its anatomical relationship with the muscle it belongs to. Spindles consist of a bundle of intrafusal muscle fibres that lie parallel to the extrafusal muscle fibers. As such, when the length of the muscle fibre is altered, so is the length of the spindle intrafusal fibres and this change is detected by the sensory receptors in the spindle. This stretch is then transduced into action potentials from the muscle spindle (Bewick & Banks, 2015). The central nervous system provides motor innervation to muscle spindles via gamma motor neurons which actively modulate the spindle's stretch sensitivity. This contraction does not make a significant contribution to the overall force the muscle produces due to the small cross-sectional area of the intrafusal fibres, yet it is sufficient to deform the sensory terminals of the spindle which provide sensory information regarding muscle length (Kuffler et al., 1951). Despite the lack of contribution to force, feedback from the contracting intrafusal spindle fibers provides a significant contribution to the contracting motor neuron pool as demonstrated in the literature. These studies report that discharge rates of motor axons with deprived spindle feedback reach ~2/3 of those with intact sensory feedback (Gandevia et al., 1990; Gandevia et al., 1993).

## 1.5 Electromyography

Surface electromyography (EMG) is a non-invasive technique used to assess global muscle activity over the surface of the skin. This technique is affected by multiple factors such as thickness of subcutaneous tissue and inter-electrode distance among other factors (Farina, 2006). For this reason, more invasive techniques have been developed to record individual motor unit properties. The fine-wire technique is used to record single motor unit activity by insertion of

electrodes into the muscle. Each electrode contains two stainless steel wires threaded and hooked at the tip of a hypodermic needle which is inserted into the muscle and slowly withdrawn leaving the wire electrodes in the muscle. When the signal-to-noise ratio is high, this technique can follow motor units throughout the full range of contraction intensities. However, it often has a very low yield, because once the wires have been hooked on to the muscle, the experimenter cannot adjust their position to increase the number of motor units recorded. The monopolar tungsten needle electrode can also be used to record motor unit activity in the muscle. This technique allows the experimenter to continuously move the electrode in the muscle during a contraction in order to sample a larger range of motor units. The inherent limitation of this technique is not being able to follow recruitment and derecruitment of individual motor units. For the purpose of this thesis, we used a monopolar tungsten needle to record motor unit trains. This allowed us to create a motor unit discharge rate profile for each subject at all contraction intensities including maximal voluntary contraction. Despite small electrode movements, offline analysis has shown that active motor unit trains can be identified for short contraction durations.

## **1.6 The effect of muscle length on force production and motor unit properties**

In order for a maximally activated muscle to generate the greatest active isometric force, its sarcomeres must be at a length which allows for optimal overlap of myofilaments (Blix, 1984). This can be explained by the sliding filament and cross-bridge theories which state that active force of an isometric contraction depends on the number of myosin heads that can bind with actin and contribute to force generation (Huxley, 1957). Thus, active force decreases when a contraction is performed at lengths shorter or longer than that which allows for optimal actin-myosin overlap. In addition, studies report that the time course of a muscle twitch is lower when the muscle is in a shortened compared with a lengthened position (Marsh et al. 1981; Bigland-Ritchie et al., 1992). Furthermore, when stimulating human muscles such as the tibialis anterior, abductor digiti minimi and hamstrings, higher rates of stimulation are needed to reach tetanic fusion in a shortened compared with a lengthened position (Gandevia & McKenzie, 1988; Marsh et al., 1981; Kirk et al., 2017). Theoretically, this suggests that motor unit discharge rates in a short muscle should be higher compared with a lengthened muscle in order for torque fusion to

occur. Several studies have explored the changes in muscle activity with alterations in muscle length and have reached conflicting conclusions.

Using surface EMG, both increases (Heckathorne et al., 1981; Lunne et al., 1981) and decreases (Fugl-Meyer et al., 1979; Cresswell et al., 1995) in the level of EMG have been reported in response to muscle length changes. More invasive techniques have also been used to assess the effect of muscle length on motor unit properties. In the tibialis anterior, low threshold (<10% maximal voluntary contraction) motor unit discharge rates are higher in a shortened compared with a lengthened position (Vander Linden et al., 1991; Pasquet et al., 2005) whereas maximal motor unit discharge rates (100% maximal voluntary contraction) show no change (Bigland-Ritchie et al., 1992), in a shortened compared with a lengthened muscle. Motor unit discharge rates have been reported to be higher in the shortened position in the biceps brachii (Christova et al., 1988) and hamstrings (Kirk et al., 2017), whereas no change has been reported in the triceps brachii (Del Valle et al., 2004). The reasons for these discrepancies remain unclear, however they can include the different EMG recording techniques used, the relative amount of shortening experienced by each muscle and task specificity likely varies among the different muscles.

## **1.7 The triceps surae**

The triceps surae muscle group is comprised of the soleus and the medial (MG) and lateral (LG) gastrocnemii which contribute ~ 60, 25, and 15% of the total physiological cross-sectional area of the triceps surae, respectively (Morse et al., 2005). The soleus crosses the ankle joint contributing only to plantar flexion. It is composed of ~85% type I muscle fibres (Johnson et al. 1973) and is engaged chronically during any postural adjustments (Héroux et al., 2014). The gastrocnemii cross both the knee and ankle joints, thus contributing to plantar flexion and knee flexion. The MG and LG are composed of ~50% type I muscle fibres (Johnson et al., 1973) and are predominantly active during fast, explosive movements (Herzog et al., 1993). The soleus has a muscle spindle density ~2.5 fold greater than that of the gastrocnemii (Voss, 1971; Banks, 2006) and receives greater spindle feedback (Tucker & Türker, 2004). The soleus, MG and LG account for ~70, 20, and 10% of the plantar flexion torque produced by the triceps surae, respectively (Fukunaga et al., 1992). Furthermore, these muscles display differences in muscle fibre length and pennation angle regardless of knee or ankle joint position (Kawakami et al., 1996).

The gastrocnemii display higher maximal steady-state motor unit discharge rates (~23 Hz) compared with the soleus (~16 Hz) (Bellemare et al., 1983; Dalton et al., 2009; Graham et al., 2016; Kirk et al., 2016). The soleus, MG and LG recruit motor units up to ~ 100%, ~90% and ~90% MVC during voluntary contractions, respectively (Oya et al., 2009; Hali et al., 2019). It has been reported that the heads of the gastrocnemii demonstrate different activation patterns when participants perform a balancing task, with motor unit recruitment thresholds of the LG being up to 20 times higher than that of the MG (H eroux et al., 2014). This recruitment strategy remains the same during voluntary plantar flexion contractions (Hali et al., 2019). These studies suggest that the triceps surae demonstrates a preferential activation of motor units from muscles contributing most to plantar flexion torque, with the soleus being recruited first followed by the MG and then the LG.

Interestingly, the gastrocnemii are the only muscles that demonstrate decreased motor unit discharge rates when placed in a shortened position by flexing the knee joint (Kennedy & Cresswell, 2001; Hali et al. 2019). Additionally, other work has proposed a reciprocal activation of the gastrocnemii and the soleus where a flexed knee joint position decreases gastrocnemii activation but increases soleus activation to compensate for the compromised torque producing capability of the gastrocnemii compared with an extended knee joint position (Kennedy & Cresswell, 2001; Lauber et al., 2014). However, work from our lab has shown that there is no change in soleus motor unit discharge rates during plantar flexion contractions with the knee joint in a flexed compared with an extended position (Hali et al., 2019). It remains unknown how the motor unit discharge rates of the triceps surae muscle group are affected by a change in ankle joint position, which would affect the length of the soleus and the gastrocnemii.

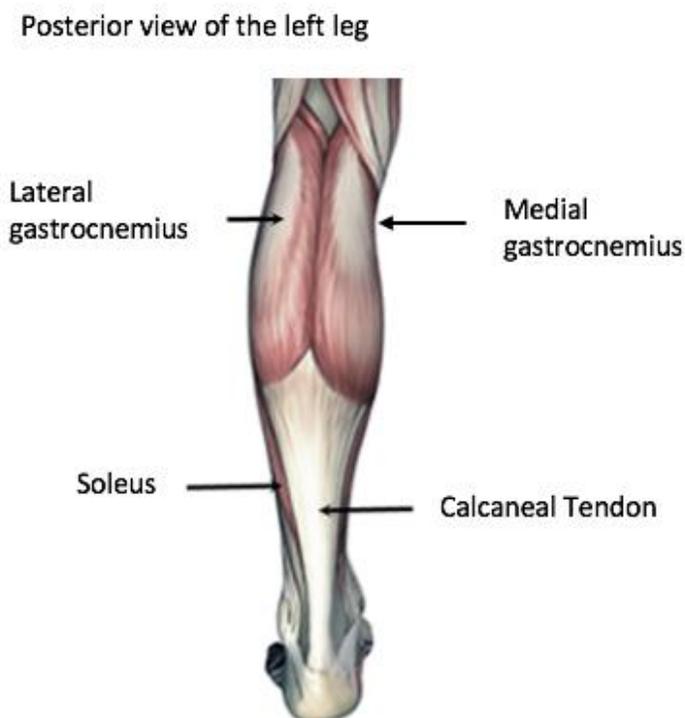


Figure 2. Anatomical view of the triceps surae (Adapted from <https://westcoastsci.com/general-blog/2018/6/4/soleus>)

## 1.8 Purpose and hypothesis

The purpose of this study was to compare neuromuscular properties of the MG, LG and soleus at two ankle joint positions during the common task of plantar flexion throughout a range of submaximal and maximal contraction intensities. For this, maximal voluntary strength, contractile properties, voluntary activation and submaximal and maximal motor unit discharge rates of the triceps surae muscles were recorded at two ankle joint positions: 20° dorsiflexed (lengthened) and 20° plantar flexed (shortened). Given the faster contractile properties of the shortened triceps surae (Sale et al., 1982), it was hypothesized that MG, LG and soleus motor unit discharge rates would be higher in the PF compared with the DF position. The interpolated twitch technique was used to assess maximal voluntary activation at both joint positions. Tungsten microelectrodes were used to record motor unit discharge rates from each muscle during separate steady state 3-10 s isometric plantar flexion contractions at 25, 50, 75, and 100% maximal voluntary contraction at each ankle joint position. Participants visited the lab multiple times to repeat the intervention in order to sample from many motor units.

## Chapter 2

### 2 Effect of ankle joint position on triceps surae motor unit discharge rates

#### 2.1 Introduction

The length-tension relationship indicates that the maximal voluntary isometric force produced by a muscle depends on the length of the muscle (Gordon et al. 1966). This can be explained by the sliding filament and cross-bridge theories which state that the force produced during an isometric contraction depends on the number of myosin heads that bind to actin and contribute to force generation (Huxley, 1957). Thus, force decreases when a contraction is performed at lengths shorter or longer than that which allows for optimal actin-myosin overlap. Studies exploring muscle length changes in humans report that the time course of a muscle twitch is longer when the muscle is in a shortened compared with a lengthened position (Marsh et al. 1981; Bigland-Ritchie et al., 1992). When electrically stimulating human muscles, higher rates of stimulation are required to reach tetanic fusion in a shortened compared with a lengthened muscle (March et al. 1981; Gandevia & McKenzie, 1988; Kirk & Rice, 2017). Thus, in principle, motor unit discharge rates (MUDRs) should be higher in a shortened compared with a lengthened muscle in order for optimal torque fusion to occur. However, studies exploring MUDRs across different muscle lengths have reported conflicting results. Submaximal MUDRs have been reported to be higher in the shortened biceps brachii (Christova et al., 1998) whereas no change has been found when comparing submaximal MUDRs between two different muscle lengths in the triceps brachii (Del Valle & Thomas, 2004). In the tibialis anterior, submaximal MUDRs were higher when the muscle was shortened (Vander Linden 1991; Pasquet et al., 2005) whereas maximal MUDRs at maximal voluntary contraction forces showed no difference between muscle lengths (Bigland-Ritchie et al., 1992). In the hamstrings, both submaximal and maximal MUDRs were higher in the shortened compared with a lengthened position (Kirk & Rice, 2017). The

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gastrocnemii are the only muscles that demonstrated decreased MUDRs when placed in a shortened position by flexing the knee joint (Hali et al., 2019; Kennedy & Cresswell, 2001)

The bi-articular medial (MG) and lateral (LG) gastrocnemii together with the mono-articular soleus form the triceps surae muscle group. The length-tension relationship of the triceps surae can be altered by changes in the angle of the knee joint, ankle joint, or both. Flexion of the knee joint leads to shortened gastrocnemii with no length changes in the soleus (Lauber et al., 2014). It has been proposed from surface electromyography (sEMG) recordings that when the knee joint is flexed, there is an increase in soleus activity and a decrease in gastrocnemii activity (Kennedy & Cresswell, 2001). Studies exploring individual motor unit properties demonstrated a decrease in submaximal gastrocnemii MUDRs and increased motor unit recruitment thresholds in the shortened compared with the lengthened gastrocnemii (Hali et al., 2019; Kennedy & Cresswell, 2001; Lauber et al., 2014). However, no change in soleus MUDRs was found during plantar flexion contractions in a flexed compared to an extended knee joint position (Hali et al., 2019). It remains unclear how a change in ankle joint position, which affects the length of all components of the triceps surae (MG, LG and soleus) affects the neuromuscular properties of this muscle group.

Thus, the purpose of this study is to compare neuromuscular properties of the MG, LG and soleus at two ankle joint positions during the common task of plantar flexion throughout a range of submaximal and maximal contraction intensities. For this, we recorded maximal voluntary strength, contractile properties, voluntary activation and submaximal and maximal MUDRs of the triceps surae muscles at two ankle joint positions: 20° dorsiflexed (lengthened) and 20° plantar flexed (shortened). Given the faster contractile properties of the shortened triceps surae (Sale et al., 1982), we hypothesized that MG, LG and soleus MUDRs will be higher in the PF compared with the DF position. The interpolated twitch technique was used to assess maximal voluntary activation at both joint positions. Tungsten microelectrodes were used to record MUDRs from each muscle during separate steady state 3-10 s isometric plantar flexion contractions at 25, 50, 75, and 100% maximal voluntary contraction at each ankle joint position. Participants visited the lab multiple times to repeat the intervention in order to sample from many motor units.

## 2.2 METHODS

### *Participants*

Ten males ( $24 \pm 3$  years old,  $81 \pm 7$  kg,  $181 \pm 5$  cm) volunteered for the study. All participants were considered healthy, recreationally active, and free of neuromuscular disease. All participants gave oral and written consent prior to the testing. The study was approved by the local University's Review Board for Health Sciences Research Involving Human Participants.

### *Experimental arrangement*

Participants were seated upright in an isometric dynamometer used to record plantar flexion torque (Marsh et al 1981). All tests were conducted on the non-dominant (left) leg with the hip and knee joint angles positioned at  $90^\circ$ . The ankle joint angles tested were  $20^\circ$  dorsiflexion (DF; lengthened triceps surae muscles) and  $20^\circ$  plantar flexion (PF; shortened triceps surae muscles). The foot was secured to the dynamometer using two inelastic straps across the toes and dorsum of the foot and one at the ankle. A metal C-shaped bar pressing firmly against the distal aspect of the thigh minimized extraneous leg and hip movement during the contractions. Plantar flexion torques were transmitted through a rigid footplate and strain gauge mounted at the joint axis of rotation. Torque was recorded from the dynamometer, analog-to-digitally converted (Power 1401, Cambridge Electronic Design), and sampled at 500 Hz (Spike2, Cambridge Electronic Design, Cambridge, UK). Real-time torque production was displayed on a computer screen  $\sim 1$  m away from the participant for visual feedback.

All electrically stimulated properties were evoked via stimulation of the tibial nerve at the distal popliteal fossa using a stimulator (Model DS7AH; Digitimer, Welwyn Garden City, UK) with a 200 microsecond square wave pulse delivered at 400 V. Current intensity was adjusted until there were no further increases in twitch amplitude, and then increased 20% to ensure supramaximal stimulation (60 – 120 mA).

### *Electromyography*

Surface EMG (sEMG) from the triceps surae and tibialis anterior were recorded through self-adhering (GE Healthcare, resting ECG electrodes) electrodes arranged in a monopolar setup. For a global triceps surae sEMG measure, the active electrode was placed on the border separating

the MG, LG and soleus with the reference electrode placed over the calcaneal tendon. For antagonist coactivation measures, the active electrode was placed over the muscle belly of the tibialis anterior and the reference electrode over its tendon at the ankle. All sEMG signals were pre-amplified (100x), filtered between 10 Hz and 10 kHz (Neurolog, NL844, Digitimer, Welwyn Garden City, UK), and sampled at 2 kHz (Spike2, Cambridge Electronic Design).

Intramuscular EMG recordings were obtained with custom-made insulated tungsten microelectrodes (123 micrometers in diameter and 45 mm length; Frederick Haer Company Inc, Bowdoin, ME, USA). The insertion sites were cleansed with 70% isopropyl-alcohol by swabbing the skin surface over the muscle bellies. Two sterile microelectrodes (connected to separate channels) were individually inserted by two operators. The microelectrode EMG signals were pre-amplified (100x), filtered between 10 Hz and 10 kHz (Neurolog; NL844, Digitimer, Welwyn Garden City, UK) and each channel sampled at 20 kHz (Spike2, Cambridge Electronic Design). Reference surface electrodes for the tungsten intramuscular electrodes were placed on the medial and lateral malleoli. A common ground electrode for both sEMG and intramuscular EMG was positioned over the patella. Audio and visual feedback were provided to each operator independently.

### *Experimental procedure*

The starting ankle joint position was randomly chosen prior to initiation of the testing session. Participants performed two ~3 s isometric dorsiflexion maximal voluntary contractions (MVCs) to record maximal tibialis anterior activity for the coactivation sEMG normalization (details below). This was followed by two ~3 s isometric plantar flexion MVCs in order to establish the baseline maximal plantar flexion torque. If the difference between the first two dorsiflexion or plantar flexion MVC attempts was greater than 5%, participants performed a third MVC. All maximal efforts were separated by at least 3 min to avoid fatigue. All participants were provided with strong verbal encouragement and visual feedback during the MVC attempts. In order to assess plantar flexion voluntary activation, a supramaximal electrical square pulse was delivered 1s prior to, at the plateau region and 1s following the plantar flexion MVC. Once baseline MVC values were determined, participants performed 3 – 10 s steady state contractions at four different contraction intensities (25, 50, 75 and 100% MVC) in a pseudo-randomized order with 30 s (after 25% MVC contractions) to 180 s (after 100% MVC contractions) rest periods

between contractions to minimize fatigue. The ankle joint was placed in a neutral position ( $0^\circ$ ) during the rest periods to avoid the effects of prolonged stretch or shortening on the muscles of the leg (Guissard et al., 1988; Trajano et al., 2014). Prior to the subsequent contraction, the ankle joint was returned to the testing position and the contraction was performed  $\sim 5$  s after the change in ankle joint position. Motor units (MU) were sampled during the plateau region of the contractions. To ensure collection of as many MU as possible, each microelectrode was manipulated and advanced slowly during the contraction (Dalton et al. 2009; Kirk & Rice, 2017). During one session, MU were recorded from each muscle during all contraction intensities. Several attempts were made at each contraction intensity until an MVC contraction was reduced to 95% of the baseline MVC, likely indicating fatigue and the session ended. Participants returned to the lab a minimum of 4 times in order to acquire a representative number of motor units from all three triceps surae muscles creating an adequate profile of MUDRs of their MU pools

#### *Data acquisition and analyses.*

Analysis was performed offline using Spike2 (Cambridge Electronic Design). For contractile properties of the evoked plantar flexion twitch, the following measurements were made: peak twitch amplitude, twitch time-to-peak tension, one-half relaxation time, contraction duration and peak rates of torque development and relaxation. Voluntary activation was calculated using the interpolated twitch technique as previously described (Todd et al., 2004). To measure maximal tibialis anterior neuromuscular activation, sEMG root-mean-squared (RMS) amplitude was calculated for a 1 s epoch at the plateau phase of a dorsiflexion MVC. This value was used to normalize equivalent epochs of tibialis anterior RMS sEMG for all other plantar flexion contraction intensities in order to assess coactivation. Submaximal (25, 50, 75% MVC) triceps surae sEMG RMS was calculated for a 1 s epoch at the plateau phase of the plantar flexion contractions and normalized to a 1 s epoch at the plateau phase of a plantar flexion MVC in the same ankle joint position.

A template shape algorithm facilitated the process for the MU analysis, but visual inspection by an experienced operator was required to confirm spike allocation to each specific MU train. Inclusion criteria for MUs included: consistent shape as viewed in a sequential overlay of MU potentials, and a minimum of five contiguous action potentials per MU train with an interspike

interval coefficient of variation equal or less than 30% (Fuglevand et al. 1993). For statistical comparisons, the MU trains were grouped into four bins based on torque level: 25% bin containing torque levels 12.5 - 37.5 MVC; 50% bin containing torque levels 37.5 - 62.5% MVC; 75% MVC bin containing torque values between 62.5 – 87.5 % MVC; 100% MVC bin containing torque levels between 87.5 - 100% of MVC.

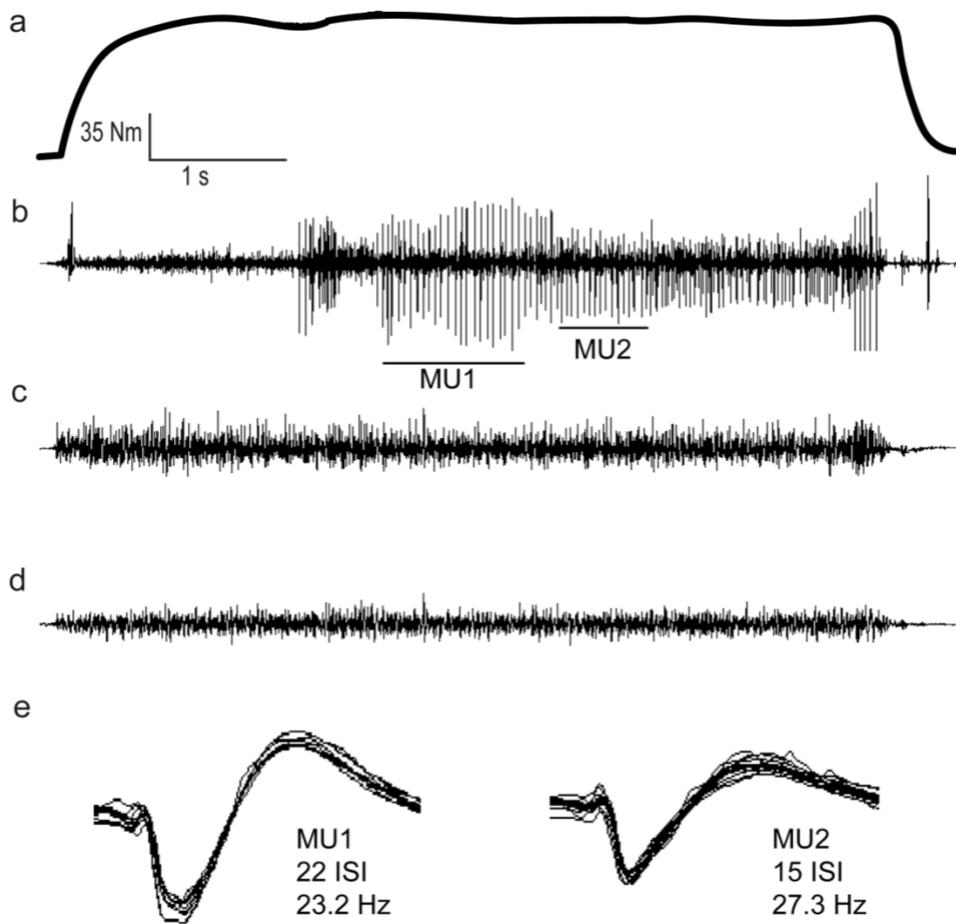


Figure 3. Example of motor unit (MU) action potential trains recorded at 100% maximal voluntary contraction with the ankle joint in the plantar flexed position. a: voluntary isometric torque. b: intramuscular electromyography recorded using a tungsten intramuscular electrode into the medial gastrocnemius. c: surface electromyography recorded from the triceps surae. d: surface electromyography recorded from the tibialis anterior muscle for coactivation . e: overlay

of motor unit 1 (MU1; 22 interspike intervals; motor unit discharge rate 23.2 Hz) and motor unit 2 (MU2; 15 interspike intervals; motor unit discharge rate 27.3 Hz) action potentials.

### *Statistical analysis*

Analysis was performed in R (version 3.4.3). A paired two-tailed t-test was used to compare voluntary activation, MVC torque and twitch characteristics between the PF and DF ankle joint positions. A three-way Analysis of Variance (ANOVA) was used to compare the normalized sEMG for the triceps surae and tibialis anterior (coactivation) across all plantar flexion contraction intensities between the two ankle joint positions. A Tukey Post Hoc significance test was used to assess where the differences in coactivation exist. These data are reported as mean  $\pm$  standard deviation.

For MUDR comparisons, a mixed linear model was constructed using the *lme4* package (Bates, Maechler & Bolker, 2012). In this model, we included MUDRs as the dependent variable with ankle joint position (DF and PF) and contraction intensity (25, 50, 75, 100% MVC) as fixed effects. We accounted for the inter-subject and day-to-day variability in MUDRs by including participants, MVC and day of testing as random effects. The statistical significance of the fixed effects (ankle joint position and contraction intensity) was tested by fitting the model with restricted maximum likelihood (REML) and deriving degrees of freedom via Satterthwaite approximation using the *lmerTest* package (Kuznetsova et al., 2017). When significance was found, we contrasted the estimated marginal means of the levels of significant effects with Tukey adjustments for multiple comparisons using the *emmeans* package (updated version of *lsmeans* in Lenth, 2016). The MUDRs recorded from each muscle (MG, LG and soleus) were analyzed separately. These data are reported in the text and displayed as least square means (95% confidence intervals). Alpha was set at 0.05.

## 2.3 Results

### *Strength, voluntary activation, and contractile properties.*

Despite no difference in voluntary activation between the DF and PF ankle joint positions ( $p = 0.33$ ), plantar flexion MVC torque was 61% lower in the PF compared with the DF position ( $p < 0.001$ ). Similarly, peak twitch torque was 70% lower in the PF compared to the DF position ( $p < 0.001$ ). Half relaxation times (HRT) were ~37% slower in the DF compared with the PF ankle joint positions ( $p < 0.001$ ), whereas time-to-peak torque (TPT) was ~5% slower in the DF compared with the PF position ( $p = 0.16$ ). Thus, overall contraction duration (TPT + HRT) was significantly lower in the PF compared with the DF position ( $p < 0.001$ ). Normalized maximal rate of torque development and maximal rate of torque relaxation ( $s^{-1}$ ) were calculated by dividing the peak rate of torque development and peak rate of torque relaxation (Nm/s) by the twitch peak torque (Nm), respectively. Normalized maximal rate of torque development was not statistically different between the two positions ( $p = 0.34$ ), whereas normalized maximal rate of torque relaxation was significantly faster in the PF compared to the DF position ( $p < 0.001$ ) (Table 1).

Parameter	DF	PF
MVC (Nm)	284.8 ± 65	112.7 ± 31.1*
VA (%)	94.5 ± 5.1	95.6 ± 6.4
Pt (Nm)	39.5 ± 12.5	11.9 ± 4.8*
TPT (ms)	109.2 ± 10.7	103.5 ± 11.0
HRT (ms)	100.9 ± 7.2	64.2 ± 7.7*
CD (ms)	210.1 ± 12.5	167.7 ± 10.3*
NMRTD ( $s^{-1}$ )	16.2 ± 1.0	16.9 ± 2.1
NMRR ( $s^{-1}$ )	-12.2 ± 1.3	-7.5 ± 0.4*

Table 1. Mean plantar flexion maximal voluntary contraction (MVC) torque, voluntary activation (VA) and twitch contractile properties (Pt = peak twitch torque; HRT = half relaxation time; TPT = time to peak torque; CD = contraction duration (TPT + HRT); NMRTD = normalized maximal rate of torque development; NMRR =

normalized maximal rate of torque relaxation) at two different ankle joint positions. PF refers to a plantar flexed ankle joint at 20°. DF refers to a dorsiflexed ankle joint 20°. Values are reported as mean  $\pm$  standard deviation. \* signifies the value is significantly different between positions ( $p < 0.05$ ).

### *Electromyography*

A significant interaction was detected between muscle  $\times$  contraction intensity  $\times$  joint position for the normalized sEMG values. No differences were detected for triceps surae normalized sEMG at 25 ( $p = 0.98$ ), 50 ( $p = 0.37$ ) and 75% MVC ( $p = 0.75$ ) between the two ankle joint positions. Tibialis anterior coactivation normalized sEMG showed no significant differences during 25% MVC plantar flexion contractions in the DF ( $10.0 \pm 3.6\%$ ) compared to the PF ( $18.1 \pm 8.1\%$ ) position ( $p = 0.72$ ), however it was significantly lower at 50 ( $p = 0.03$ ), 75 ( $p < 0.001$ ) and 100 ( $p < 0.001$ ) % MVC plantar flexion contractions in the DF ( $18.0 \pm 6.0\%$ ;  $27.8 \pm 8.9\%$  and  $47.3 \pm 18.2\%$  respectively) compared with the PF ( $34.3 \pm 15.3\%$ ,  $52.8 \pm 20.2\%$  and  $82.0 \pm 28.0\%$  respectively) ankle joint position.

A total of 2273 motor units were recorded from the three muscles of the triceps surae combined including both ankle joint positions (1144 in DF and 1129 in PF). The numbers of MG, LG and soleus motor units identified from each muscle across all four contraction intensities is given in Table 2. The MUDRs mixed linear models identified a significant interaction between contraction intensity and ankle joint position in the MG ( $p = 0.007$ ) and soleus ( $p < 0.001$ ), but not in the LG ( $p = 0.21$ ). In the MG, MUDRs showed no differences between the ankle joint positions at 25 ( $p = 0.74$ ), 50 ( $p = 0.12$ ) and 75% MVC ( $p = 0.64$ ), but at 100% MVC were ~9% higher in the DF compared with the PF position ( $p = 0.001$ ). In the soleus, MUDRs showed no significant differences between the ankle joint positions at 25 ( $p = 0.36$ ), 50 ( $p = 0.63$ ) and 75% MVC ( $p = 0.73$ ), but at 100% MVC were ~20% higher in the DF compared with the PF position ( $p < 0.001$ ). All three muscles showed a significant increase in MUDRs with contraction intensity ( $p < 0.001$ ) in both ankle joint positions (Figure 4).

Parameter	Muscle	Contraction intensity bins							
		25% MVC		50% MVC		75% MVC		100% MVC	
		DF	PF	DF	PF	DF	PF	DF	PF
MG									
# of MU		149	129	129	118	91	85	44	63
MU/person		6.1 ± 2.8	5.6 ± 2.5	5.5 ± 2.9	5.7 ± 2.8	5.1 ± 2.7	6.2 ± 2.7	6.5 ± 2.3	6.1 ± 2.8
# of ISI		8.2 ± 4.6	8.2 ± 4.7	7.2 ± 4.4	7.5 ± 4.1	6.9 ± 4.2	6.7 ± 3	6 ± 1.9	6.3 ± 4
CoV		9.3 ± 4.2	10.2 ± 4.6	10.2 ± 5	10.8 ± 4.8	10.7 ± 4.8	12.3 ± 5.1	13.8 ± 5.5	14 ± 5.8
MVC%		23.4 ± 2.6	24.0 ± 1.9	47.7 ± 2.9	47.7 ± 2.2	72.9 ± 3.8	72.7 ± 3.4	97.6 ± 2.8	98.4 ± 4.5
LG									
# of MU		134	118	89	96	51	60	28	43
MU/person		5.8 ± 2.7	6.1 ± 2.7	5.9 ± 2.6	6.4 ± 3.1	5.9 ± 2.8	6.0 ± 2.7	6.6 ± 2.7	6.2 ± 2.9
# of ISI		8.6 ± 5.1	7.8 ± 5.2	7.5 ± 4.6	8.8 ± 5.2	5.9 ± 2.4	6.3 ± 3	5.8 ± 2.2	6.3 ± 3
CoV		10.3 ± 5.8	10.1 ± 5	11.7 ± 5.8	12.1 ± 4.3	11 ± 5.4	13.1 ± 5.6	12.1 ± 4.9	13.3 ± 6.3
MVC%		24.1 ± 1.8	24.2 ± 1.9	48.6 ± 1.5	48.3 ± 2.1	72.3 ± 3.1	73.8 ± 3.1	97.5 ± 3.2	99.5 ± 5.4
Soleus									
# of MU		191	178	126	106	58	64	54	45
MU/person		5.8 ± 2.9	6.4 ± 2.6	5.6 ± 3.3	6.3 ± 2.8	6 ± 2.9	6.1 ± 2.6	5.3 ± 2.9	6.3 ± 2.4
# of ISI		7 ± 3.3	7.9 ± 4.9	7.4 ± 5.3	7 ± 3.5	7.1 ± 6	6.4 ± 3	5.7 ± 3.0	6.6 ± 3
CoV		8.6 ± 4.1	9 ± 4.7	9.7 ± 5.1	10.2 ± 4.6	10.2 ± 4.7	11.8 ± 5.2	12.1 ± 5	11.8 ± 5.7
MVC%		24.2 ± 3.3	23.9 ± 2.1	48.3 ± 3.2	47.8 ± 2.1	72.0 ± 3.9	73.1 ± 3.5	97.1 ± 3.3	98.7 ± 5.0

Table 2. Parameters of motor unit trains identified from the medial gastrocnemius (MG), lateral gastrocnemius (LG) and soleus at the two ankle joint positions for each contraction intensity binned as a percentage of the maximal voluntary contraction (MVC) plantar flexion torque. DF refers to a dorsiflexed ankle joint. PF refers to a plantar flexed ankle joint. The 25% MVC bin contains torque levels 12.5 - 37.5 MVC. The 50% MVC bin contains torque levels 37.5 - 62.5% MVC. The 75% MVC bin contains torque values between 62.5 – 87.5 % MVC. The 100% MVC bin contains torque levels between 87.5 - 100% of MVC. # of MU refers to the total number of motor units collected. MU/person refers to the mean number of motor units identified from each individual. # of ISI refers to the mean number of interspike intervals used to assess the discharge rate of a motor unit train. CoV refers to the coefficient of variation in the interspike intervals used to assess the discharge rate of a motor unit train. MVC% refers to the plateau torque at which the motor units were collected. Values are reported as mean ± standard deviation.

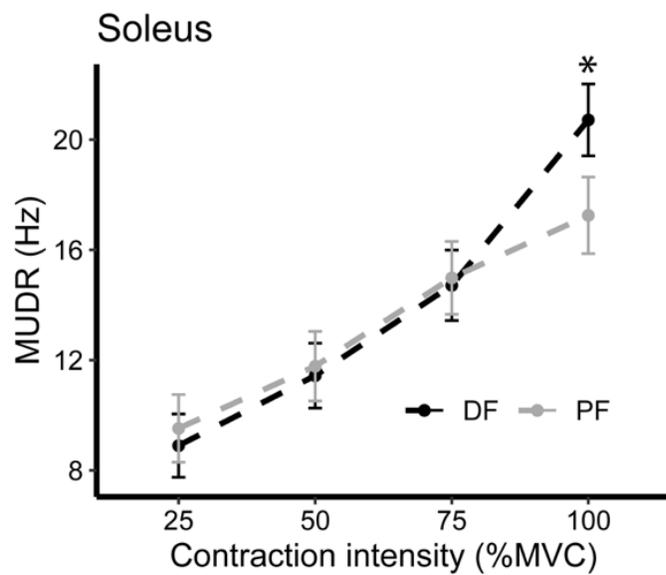
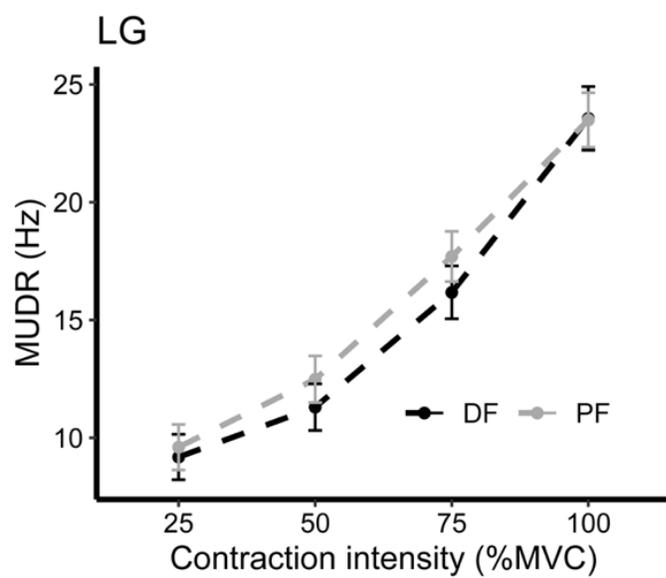
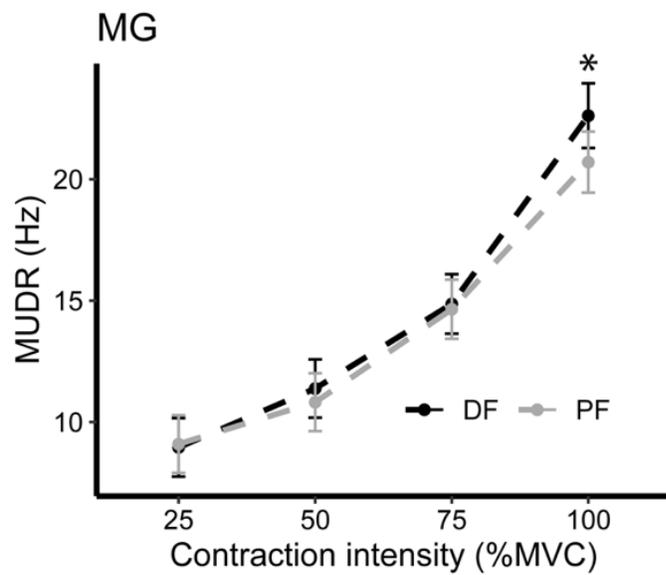


Figure 4. Motor unit discharge rates from the medial gastrocnemius (MG), lateral gastrocnemius (LG) and soleus across two ankle joint positions for each contraction intensity set based on plantar flexion maximal voluntary contraction (MVC) torque. DF refers to a dorsiflexed ankle joint. PF refers to a plantar flexed ankle joint. The 25% MVC bin contains torque levels 12.5 - 37.5 MVC. The 50% MVC bin contains torque levels 37.5 - 62.5% MVC. The 75% MVC bin contains torque values between 62.5 – 87.5 % MVC. The 100% MVC bin contains torque levels between 87.5 - 100% of MVC. Data are reported as means (95% confidence interval). \* signifies the value is significantly different between positions ( $p < 0.05$ ).

## Chapter 3

### 3 Discussion and summary

#### 3.1 Discussion

The purpose of this study was to compare the neuromuscular properties of the three components of the triceps surae between two ankle joint positions: 20 degrees PF (shortened triceps surae muscles) and 20 degrees DF (lengthened triceps surae muscles). Plantar flexion maximal voluntary torque was lower in the PF position, despite no changes in voluntary activation of the plantar flexors between the two ankle joint positions. Additionally, peak twitch torque was lower and half-relaxation time, contraction duration and normalized maximal rate of torque relaxation were faster in the PF position. Normalized sEMG showed significantly higher tibialis anterior coactivation during plantar flexion contractions in the PF compared with the DF position, whereas no changes were detected in triceps surae normalized sEMG between the two ankle joint positions. Finally, MG and soleus MUDRs were higher in the DF compared with the PF position only at 100% MVC, whereas there were no differences in LG MUDRs between the two ankle joint positions. In all three muscles, mean MUDRs increased with contraction intensity.

Maximal plantar flexion torque was 61% lower in the PF compared with the DF position, despite plantar flexion voluntary activation showing no differences between the two ankle joint positions. Previous reports looking at the voluntary activation of plantar flexors (Kluka et al., 2016), abductor digiti minimi, elbow flexors and tibialis anterior (Gandevia & McKenzie, 1988) across different muscle lengths have also reported maximal voluntary activation levels independent of muscle length and a lower maximal torque in the shortened position. Peak twitch torque was also lower when the triceps surae muscles were shortened as has been previously reported in the literature (Sale et al., 1982; Landin et al., 2015; Kluka et al. 2016). Our findings provide further evidence that the central nervous system is capable of fully activating the ankle plantar flexors maximally regardless of ankle joint position. The differences in strength between the two positions can be explained by the suboptimal overlap of actin and myosin due to the shortening of the triceps surae components in the PF compared with the DF position, as indicated by the cross-bridge theory of contraction (Huxley, 1957). In this study we did not make direct measurements of muscle fiber lengths, but have assumed muscle length changes due to

alterations of the ankle joint position. In support of this assumption, previous work exploring muscle length changes has reported shorter MG, LG and soleus muscle fiber lengths when the ankle joint is placed in a PF compared with a DF position with the knee joint flexed at 90° (Kawakami et al., 1998). In addition to a decrease in twitch torque, plantar flexion contractile properties were faster when the muscles were in the shortened (PF) position. Similar findings have been previously reported in single isolated frog muscle fibers (Edman & Flitney, 1982), isolated cat muscle (Rack & Westbury, 1969) and in human muscles such as the tibialis anterior (Bigland-Ritchie et al., 1992), abductor digiti minimi, elbow flexors (Gandevia & McKenzie, 1988), hamstrings (Kirk & Rice, 2017) and ankle plantar flexors (Marsh et al. 1981; Sale et al., 1982). The slowing of supramaximal twitch contractile properties and higher electrical stimulation rates required to reach tetanic torque fusion at shorter muscle lengths (Gandevia & McKenzie; 1988; Marsh et al. 1981; Kirk & Rice, 2017) suggest that higher maximal MUDRs may be required to generate a maximal voluntary contraction at a shorter muscle length.

In agreement with other studies (Bigland-Ritchie et al., 1992; Del Valle & Thomas, 2004; Kirk et al. 2017), mean MUDRs were higher at greater levels of contraction intensity in the MG, LG and soleus during plantar flexion contractions at both ankle joint positions (Figure 4). Therefore, rate coding appears to be a contributing mechanism throughout the range of isometric contractile intensity. For contraction intensities up to 75% MVC no differences in MUDRs were detected between the two joint positions, but at 100% MVC MUDRs in the MG and soleus were greater in the DF position. Previous work reports either no differences in maximal MUDRs between the lengthened and shortened tibialis anterior (Bigland-Ritchie et al., 1992) or higher maximal MUDRs in the shortened compared with the lengthened hamstrings (Kirk & Rice, 2017). In these studies, the muscles tested remained in the stretched or shortened position throughout the entire experimental procedure. It has been previously reported that static stretch of the muscle causes an inhibition of the motor neuron pool (Guissard, Duchateau, & Hainaut, 1988) and a decrease in maximal neural drive (Trajano et al., 2014). As such, recorded MUDRs could have been inhibited due to the prolonged stretch demonstrating no change (Bigland-Ritchie et al., 1992) or a decrease (Kirk & Rice, 2017) in the lengthened compared with the shortened muscle. In order to mitigate the effects of prolonged passive stretching of the triceps surae muscles in this study, the ankle joint was placed in a neutral position (0°) during the rest periods between subsequent contractions. Our data show that MG and soleus maximal MUDRs are higher when the muscles

are at a lengthened compared with a shortened position. It has been previously reported that the persistent inward current amplitude, which serves to amplify the synaptic input received at the motor neuron dendrites, was higher when the ankle was in a flexed compared with an extended position in the triceps surae motor neurons of the adult cat (Hyngstrom et al., 2007). When the antagonist (tibialis anterior and extensor digitorum longus) tendons were cut, the persistent inward current amplitude showed no difference between the different ankle joint positions. This provides evidence that Ia reciprocal inhibition from the antagonist muscle group has a fundamental role in modulating persistent inward current, thus affecting motor neuron excitability across different ankle joint positions (Hyngstrom et al. 2007). In accordance with these findings, our data show that tibialis anterior coactivation was higher during plantar flexion contractions in the PF position, which leads to increased Ia inhibitory input from the antagonist to the triceps surae motor neuron pool, thus decreasing MUDRs in the shortened triceps surae muscles. This increased inhibition may serve an important role in modulating the motor neuron excitability of the triceps surae during the swing phase of gait, which begins with the ankle in the PF position, where these muscles are shortened. It is worth noting that there is a wide range of afferent feedback affecting a motor neuron pool. Muscle spindles are composed of neurons that are sensitive to both dynamic and static stretch, with the latter exerting an effect on both the primary (type Ia) and secondary (type II) afferents (Matthews 1962). Furthermore, muscle tension is detected through Golgi tendon organ feedback (Houk and Henneman 1967). Finally, joint receptors also contribute to the sense of joint positions (Mountcastle and Power 1959). This study is unable to differentiate between the different sources of afferent feedback regulating the changes in MUDRs between the two ankle joint positions. It is most reasonable to assume that these changes are a result of an interplay of all afferent feedback sources affecting the triceps surae motor neuron pool.

The higher maximal MUDRs in the lengthened MG and soleus may serve as a compensatory mechanism for the higher susceptibility of muscles to fatigue, as demonstrated by a greater decrease in muscle torque, when placed in a lengthened compared with a shortened position (Fitch & McComas, 1985; McKenzie & Gandevia, 1987). As such, given the previously reported decrease in MUDRs during a sustained 100% MVC task (Bigland-Ritchie et al., 1983; Dalton et al., 2010) and the higher susceptibility to fatigue at a longer muscle length (Fitch & McComas, 1985; McKenzie and Gandevia, 1987), higher MUDRs in the DF position may serve

to counteract the muscle's susceptibility to fatigue in this position compared with a PF position. This may also explain why the differences in MG and soleus MUDRs between the two ankle joint positions were only evident during 100% MVC contractions and triceps surae normalized submaximal sEMG showed no differences between the two ankle joint positions. During sustained submaximal contractions, muscle EMG increases which can be explained by the recruitment of additional motor units to compensate for the fatigue in those initially activated (Fitch & McComas, 1985; Fuglevand et al., 1993; Weir et al., 2000; Griffin et al., 2001; Davidson et al., 2010). Previous studies have shown that the soleus, MG and LG are able to recruit motor units up to 100, 90 and 90% MVC, respectively (Hali et al., 2020; Oya, Riek, & Cresswell, 2009). For this reason, it may not be necessary to compensate for the increased fatiguability of the muscles in the lengthened position during submaximal (<100% MVC) contractions, as this can be done through recruitment of additional motor units.

Surprisingly, we found no differences in LG maximal MUDRs between the DF and PF positions. Previous work has shown that the LG demonstrates higher motor unit recruitment thresholds compared with the MG and soleus when participants perform a balancing task (H eroux et al. 2014) and during voluntary plantar flexion contractions (Hali et al. 2020), suggesting that the LG is comprised of higher threshold motor units compared to the other muscles of the triceps surae. An inverse relationship exists between Ia afferent feedback and the size of a motor neuron, meaning that lower threshold, small type motor neurons receive stronger Ia feedback compared with higher threshold, larger motor neurons (Windhorst & Kokkoroyiannis, 1991). Given the lack of a muscle length effect on LG MUDRs, our findings provide further support for the speculation that higher threshold motor neurons innervate this muscle. Another factor to consider is that all contractions in this study were performed in a flexed knee joint position. This has been suggested to lead to functionally insufficient gastrocnemii muscle fiber lengths compared with an extended knee joint position, which then results in the inhibition of the MG and LG motor neuron pools, as demonstrated by lower MUDRs and higher motor unit recruitment thresholds (Kennedy & Cresswell, 2001; Lauber et al. 2014; Hali et al. 2019). It is possible that the LG muscle fiber length in the DF position remains insufficient, leading to increased inhibition of its motor neuron pool at both ankle joint positions.

## 3.2 Conclusions

This study compared the effect of the ankle joint position on the neuromuscular properties of the triceps surae muscle group. Consistent with previous results, we report a decreased strength, twitch torque and faster contractile properties when the triceps surae muscles were shortened. Our results demonstrate that maximal MUDRs are higher in the MG and soleus at a lengthened compared with a shortened muscle length. This may be a result of the increased Ia inhibitory inputs from the antagonist muscles and may serve as a compensatory mechanism for the greater susceptibility to neuromuscular fatigue of muscles in a lengthened position. Lastly, our findings indicate that LG MUDRs are similar at both ankle joint positions, providing further support for a differential activation between gastrocnemii heads.

## 3.3 Limitations

A benefit of the tungsten microelectrode technique is the ability to record from a large sample of motor units during high intensity contractions. However, this technique does not allow the investigator to record from the same motor unit throughout multiple different contractions and therefore did not provide direct information about recruitment and derecruitment thresholds. Furthermore, recording from the same motor unit during contractions at two different ankle joint positions may have provided more concrete evidence of how motor unit discharge rates are modulated with changes in ankle joint position. This is challenging due to the difficulty of following the same motor unit during multiple contractions at two different muscle lengths using indwelling fine wire.

In this study, muscle fibre length or pennation angle were not measured at the two ankle joint positions. The relative change in these architectural properties may affect how MUDRs are modulated in each individual muscle. Additionally, there were no direct measures of afferent feedback to the motor neuron pool. For this reason, the underlying mechanism behind the differences in MUDRs when compared between the two ankle joint positions may not be attributed solely to one source of afferent feedback.

The wide range of neuromuscular strategies used to perform plantar flexion contractions was evident during our experimental sessions. An example is the relatively low medial and lateral gastrocnemii involvement in some participants during low intensity (<50% MVC) plantar flexion

contractions, especially at the plantar flexed (shortened muscles) position. Furthermore, we only tested young, healthy males in this study as an initial look into how the triceps surae component MUDRs are affected by a change in ankle joint position. This homogenous sample was chosen to minimize the potential confounding effect of sex or age in this modest sample size. For these reasons, findings should not be generalized to other populations.

### **3.4 Future directions**

The triceps surae is a unique muscle group owing to the fact that it is composed of the biarticular gastrocnemii and the mono-articular soleus. As such, the length-tension relationship of this muscle group is affected by both changes in knee and ankle joint positions. Previous work has reported that the greatest changes in MG and LG length are found when comparing a fully extended knee joint and dorsiflexed ankle joint combination to a flexed knee joint and plantar flexed ankle joint combination (Kawakami et al., 1998). Therefore, it would be interesting to compare maximal MG and LG discharge rates between the two different length extremes.

Using intramuscular fine-wire electromyography, the same motor unit can be recorded during plantar flexion ramp contractions in both ankle joint positions. Although the motor unit yield may be low, multiple testing sessions may allow for a reasonably-sized data set. This subset of motor units recorded from each muscle at both ankle joint positions will provide more direct evidence of how the motor neuron pool excitability of these three muscles is affected by the ankle joint position through measures of motor unit recruitment and derecruitment thresholds, and MUDRs at recruitment and during plateau contractions.

It appears that there are many discrepancies in the literature regarding the effect of muscle length on MUDRs, with increases, decreases and no changes reported when comparing lengthened with shortened muscles (Christova et al., 1988; Vander Linden et al., 1991; Bigland-Ritchie et al., 1992; Kennedy & Cresswell, 2001; Del Valle et al. 2004; Pasquet et al., 2005; Lauber et al. 2014; Kirk et al., 2017; Hali et al., 2019). As such, a study recording MUDRs during contractions at different muscle lengths in multiple muscles from the same individuals may be necessary in order to get a better understanding of how muscle length affects motor unit discharge rates.

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## Appendix

### Appendix A. Ethical Approval



**Date:** 25 February 2020

**To:** Charles Rice

**Project ID:** 107505

**Study Title:** Motor neuron and muscle fiber resilience in humans

**Application Type:** Continuing Ethics Review (CER) Form

**Review Type:** Delegated

**REB Meeting Date:** 10/Mar/2020

**Date Approval Issued:** 25/Feb/2020

**REB Approval Expiry Date:** 07/Mar/2021

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Dear Charles Rice,

The Western University Research Ethics Board has reviewed the application. This study, including all currently approved documents, has been re-approved until the expiry date noted above.

REB members involved in the research project do not participate in the review, discussion or decision.

Western University REB operates in compliance with, and is constituted in accordance with, the requirements of the TriCouncil Policy Statement: Ethical Conduct for Research Involving Humans (TCPS 2); the International Conference on Harmonisation Good Clinical Practice Consolidated Guideline (ICH GCP); Part C, Division 5 of the Food and Drug Regulations; Part 4 of the Natural Health Products Regulations; Part 3 of the Medical Devices Regulations and the provisions of the Ontario Personal Health Information Protection Act (PHIPA 2004) and its applicable regulations. The REB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000940.

Please do not hesitate to contact us if you have any questions.

Sincerely,

Daniel Wyzynski, Research Ethics Coordinator, on behalf of Dr. Joseph Gilbert, HSREB Chair

*Note: This correspondence includes an electronic signature (validation and approval via an online system that is compliant with all regulations).*

## Curriculum vitae for Kalter Hali

2014/9 - 2018/6 BSc, Honour Specialization in Kinesiology

University of Western Ontario

Degree Status: Completed

Awards and scholarships: Ontario Graduate Scholarship (2018, 2019)

NSERC Summer Undergraduate Student Award (2018)

Dean's Honour List (2015, 2016, 2017, 2018)

Ontario University Athletics Student Athlete award (2015, 2016)

Western Entrance Scholarship (2014)

### Teaching Assistant

2018/9 – 2018/12 Kinesiology 3336 – Physiology of Fitness Appraisal

2019/1 – 2019/4 Kinesiology 2236B – Introduction to athletic injuries

2019/9 – 2019/12 Kinesiology 4430 – Neuromuscular physiology

### Publications

**Hali, K.**, Kirk, E.A. & Rice, C.L. (2019) Effect of knee joint position on triceps surae motor unit recruitment and firing rates. *Exp Brain Res* 237: 2345. DOI: 10.1007/s00221-019-05570-7

**Hali, K.**, Dalton, B.D, Harwood, B., Fessler, A.F., Power, G.A. & Rice, C.L. (2020) Differential Modulation of Motor Unit Properties from the Separate Components of the Triceps Surae in Humans. *Neuroscience* 428: 192-198 DOI: 10.1016/j.neuroscience.2019.12.023

**Hali, K.**, Zero, A.M. & Rice, C.L. (2020) Effect of ankle joint position on triceps surae contractile properties and motor unit discharge rates. (submitted to *Experimental Brain Research*)

### Conference presentations

**Hali, K.**, Kirk E.A., Rice C.L. (2018). Effect of knee joint angle on neural activity of leg muscles in humans. *Applied Physiology Nutrition & Metabolism*, Volume 23, 2018. Canadian Society of Exercise Physiology 2018 (S61) (poster presentation)

**Hali, K.**, (2019) Frequency-dependent conduction block in chronic inflammatory demyelinating polyneuropathy. Exercise Neuroscience Group (oral presentation)

**Hali, K.**, Zero, A.M., Fanous, J., Rice, C.L. (2020). Effect of ankle joint position on triceps surae motor unit firing rates. Federation of American Societies for Experimental Biology (FASEB), Volume 34, 2020. *Experimental Biology* (S1) (poster presentation)

### Undergraduate course guest lecture

**Hali, K.**, Hip joint injuries and nerve disease – A brief overview (2019), Kinesiology 2236B