The potential for potentiation in the unconditioned quadriceps

by

Gerard Michael James Power

A thesis submitted to the

School of Graduate Studies

In partial fulfillment of the requirements for the degree of

Master of Kinesiology

School of Human Kinetics and Recreation

Memorial University of Newfoundland

June 2020

St. John’s, Newfoundland and Labrador

ABSTRACT

Post-activation potentiation has been studied in muscles since the 1930s. The phenomenon is related to an increase in force and rate of force production of the muscle following a conditioning stimulus. Studies have evolved over the years, starting with electrical stimuli and testing in muscles of small animals, and progressing to volitional stimuli and testing in trained humans. Phosphorylation of myosin regulatory light chains has been the only well-established mechanism contributing to post-activation potentiation. Research has also found that post-activation potentiation coexists with fatigue in the muscle. Fatigue has been shown to elicit effects in unconditioned muscles. Therefore, the primary objective of this thesis was to investigate the possibility for a unilateral conditioning activity to cause enhancements in performance to an unconditioned, contralateral, homologous muscle group. The results of the study did not give any evidence at this time for post-activation potentiation effects in an unconditioned muscle. However, the results did demonstrate the complexity of the interaction between potentiation and fatigue, and how participant characteristics and timing can affect this.

ACKNOWLEDGEMENTS

I would first like to thank my supervisor, Dr. David Behm for his patience, help in designing protocols and tremendous writing support throughout my master’s degree. Your work ethic is second to none, it motivated me during my master’s and will continue to motivate throughout my life.

I would also like to thank Dr. Duane Button, who was another constant support during my degree. Your thoughtfulness and support meant a lot to me, and I appreciate your role in shaping my future plans.

Finally, I would like to thank all of my fellow graduate students for making the experience during my master’s an exciting and memorable one. Particularly Emily and Leah, who were constantly there for me. Without you, finishing my degree would not have been possible.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

ANOVA	Analysis of Variance
BF	Biceps Femoris
CMJ	Countermovement Jump
D-ND	Dominant to Non-Dominant Crossover Group
DJ	Drop Jump
EMG	Electromyography
F100	Force in the First 100 milliseconds
H-Reflex	Hoffman Reflex
MEP	Motor Evoked Potential
MVC	Maximum Voluntary Contraction
MVIC	Maximum Voluntary Isometric Contraction
ND-D	Non-Dominant to Dominant Crossover Group
PAP	Post-Activation Potentiation
PAPE	Post-Activation Performance Enhancement
PIC	Persistent Inward Current
PTP	Post-Tetanic Potentiation
RM	Repetition Maximum
RSI	Reactive Strength Index
VL	Vastus Lateralis

Chapter 1: Review of Literature

1.1 Introduction

Post-activation potentiation (PAP) is a phenomenon in the muscle, which causes increases in force, rate of force development, or both due to a conditioning stimulus (Hodgson et al., 2005). PAP investigations have evolved over the years of research, starting out with an electrical conditioning stimulus, and electrical test stimulus (Brown & Von Euler, 1938; Lloyd, 1949; Rosenblueth & Morison, 1937). The process then moved onto a volitional conditioning stimulus and electrical test stimulus (Belanger & Quinlan, 1982; Vandervoort et al., 1983), and finally to volitional conditioning and test stimulus (Gullich & Schmidtbleicher, 1996; Young et al., 1998). Through these studies, identifying contributing mechanisms was often challenging, particularly in entirely volitional studies. The primary identified mechanism so far has been the phosphorylation of myosin regulatory light chains (Sweeney et al., 1993).

A coexistence of PAP and fatigue has also been established in the literature (Rassier & MacIntosh, 2000), with both phenomena playing a role in the performance of targeted muscles. The coexistence seems to indicate that different mechanisms are at play for PAP and fatigue, and the overall effect on muscle performance depends on the magnitude of the PAP mechanisms compared to the magnitude of the fatigue mechanisms. Contrary to PAP, muscle fatigue studies have successfully identified many contributing mechanisms (Bellemare & Garzaniti, 1988; Bergstrom & Hultman, 1988; Bigland-Ritchie et al., 1986; Bigland-Ritchie et al., 1982; Dietz, 1978; Jami et al., 1983; Maton & Gamet, 1989; Sjogaard et al., 1986; Stephens & Taylor, 1972). Researchers have used non-local studies of muscle fatigue in order to help identify fatigue mechanisms beyond the muscle itself (Halperin et al., 2015; Matsuura & Ogata, 2015; Takahashi et al., 2011).

The goal of this review is to introduce PAP, its effects and postulated mechanisms. Additionally, this review will look into fatigue literature with a focus on its relationship to PAP, and how crossover or non-local studies were able to identify additional mechanisms contributing to fatigue. The review will identify the lack of literature into PAP mechanisms superior to the muscle and help rationalize how studies similar to the non-local muscle fatigue studies, could help contribute to better understanding PAP mechanisms. Better understanding PAP mechanisms and investigating non-local effects is important in multiple fields. First of all, in strength and conditioning and athletic performance, non-local performance enhancement could increase performance of a targeted limb by conditioning another limb prior to the activity on the target limb. Also, in a rehabilitation setting, a stronger or healthy limb could be conditioned first, increasing performance and potentially recovery rate in the weak or injured limb.

1.2 Post-Tetanic Potentiation

PAP has been studied for the better part of a century. It was first observed in animal models, such as the gastrocnemius of an anesthetized cat (Brown & Von Euler, 1938; Lloyd, 1949; Rosenblueth & Morison, 1937). In each of these studies, the popliteal nerve was stimulated with tetanus of various frequencies (57 – 555 Hz) and durations (2 seconds – 5 minutes) and twitch tension of the gastrocnemius after the tetanic stimulation was compared to pre-tetanus values (Brown & Von Euler, 1938; Lloyd, 1949; Rosenblueth & Morison, 1937). Similar results were found in each of the three studies; immediately following tetanus, twitch tensions were the highest, they then decreased but remained above pre-tetanus values for up to 5 minutes (Brown & Von Euler, 1938; Lloyd, 1949; Rosenblueth & Morison, 1937). This first type of PAP using tetanus as the conditioning stimulus was termed post-tetanic potentiation (PTP) (Lloyd, 1949).

PTP was first explored in humans during the 1950s. The first study observed changes in the twitch tension of the adductor pollicis brevis muscle following 1 second of tetanus at 30 Hz to the ulnar nerve (Botelho & Cander, 1953). The twitch response was very similar to the cat studies, with potentiation peaking at 3 seconds but remaining elevated up to 10 minutes post-tetanus (Botelho & Cander, 1953). Several other studies have elicited tetanus in various human muscles such as the adductor pollicis (Hughes & Morrell, 1957), platysma (Krarup, 1977), elbow flexors (Krarup & Horowitz, 1979), dorsiflexors (O'Leary et al., 1997), and quadriceps (Binder-Macleod et al., 2002). Each of the studies had similar findings, with initial peaks in twitch tension, followed by a slow decline to pre-tetanus levels. In terms of duration of tetanus, it was found that the magnitude of potentiation increased as duration of tetanus increased from one second to three seconds, but then decreased from four seconds to six seconds of tetanus, demonstrating an inverted 'U' relationship between duration of tetanus and level of potentiation (Hughes & Morrell, 1957). In terms of frequency of tetanus, higher frequencies of tetanus (100 Hz and 300 Hz), had higher initial levels of potentiation, but the potentiation did not last as long as the lower frequencies (10 Hz and 30 Hz) of tetanus (Hughes & Morrell, 1957). These studies highlight that, albeit through external stimulation, muscles can undergo acute physiological changes to enhance force producing capabilities.

1.3 Voluntary Post-Activation Potentiation

Eventually, researchers began to explore if it was possible to elicit PAP through voluntary activity instead of evoked electrical stimulation. Two studies in the early 1980s measured pre- and post-twitch tensions following plantar flexion and dorsiflexion isometric maximum voluntary contractions (MVC) (Belanger, & Quinlan, 1982; Vandervoort, Quinlan, & McComas, 1983). In one of the studies, the volume of the MVC was altered. Changes in the magnitude of potentiation of the twitch torques were observed. Similar to the tetanic stimulation studies, as the volume increased from 1 s to 60 s, the magnitude of potentiation immediately following the MVC followed an inverted 'U' shape, with the highest magnitude of potentiation being after the 10-second MVC (Vandervoort et al., 1983). In terms of decay, potentiation was still evident at 6-minutes post-MVC and was even seen as long as 10-minutes post-MVC (Vandervoort et al., 1983). Both studies also found that twitch potentiation was greater in the dorsiflexor muscles, specifically tibialis anterior, compared to the plantar flexors (Belanger, & Quinlan, 1982; Vandervoort, Quinlan, & McComas, 1983). It is believed that the dorsiflexor muscle group has a higher portion of fast-twitch muscle fibres, which have been shown to have increased potentiation effects (Vandervoort et al., 1983). Several other studies have also observed potentiation in twitch tension following MVCs to various muscle groups, including the knee extensors (Green & Jones, 1989; Houston et al., 1985; Houston & Grange, 1990; Stuart et al., 1988), plantar flexors (Alway et al., 1987; Belanger et al., 1983; Hamada et al., 1997; Petrella et al., 1989), dorsiflexors (Belanger et al., 1983), and triceps brachii (Hamada et al., 1997). These voluntary studies gave evidence that the PAP changes occurring within muscles were attainable without electrical stimulation, and that fast-twitch muscle fibres appeared to be more susceptible to the change.

1.4 Mechanism of Twitch Potentiation

The post-conditioning changes to twitch tension, which has been termed ‘twitch potentiation’ in the literature (Hodgson et al., 2005), has been mainly attributed to one specific adaptation within the muscle. The adaptation is the phosphorylation of myosin regulatory light chains. The process begins with a stimulus to the muscle (electrical or volitional), which causes a release of Ca^{2+} into the myoplasm (Sweeney et al., 1993). Ca^{2+} in the myoplasm binds to a messenger protein, calmodulin, and this formed complex binds to and activates the enzyme, myosin light chain kinase (Sweeney et al., 1993). The activated kinase then phosphorylates the myosin regulatory light chain, which is located at the base of the moving portion of the myosin protein, acting as a hinge (Sweeney et al., 1993). This phosphorylation causes a conformational change to the regulatory light chain, which renders the myosin closer to a force producing state (Sweeney et al., 1993). As a result, the myosin can attach to the actin-binding site quicker, and more often, resulting in an increased rate of cross-bridging and more overall cross-bridges. This phosphorylation effect has been thought to be demonstrated by the potentiation of twitches that occur in the research following a high-intensity conditioning stimulus to the muscle (Hodgson et al., 2005). While the effect of the phosphorylation of myosin regulatory light chains has been established in the literature through the potentiation of muscle twitches, the significance of this twitch potentiation to human performance is not well known (Hodgson et al., 2005). There have been studies over the past 30 years which have aimed to measure potentiation through actual functional performance measures rather than through evoked twitch potentiation (Gullich & Schmidtbleicher, 1996; Young et al., 1998).

1.5 Functional Measures of Post-Activation Potentiation

In the late 1990s, a research study was completed in Germany on speed-strength athletes (Gullich & Schmidtbleicher, 1996). The upper body and lower body were conditioned using bench presses and single-leg, isometric leg presses, respectively (Gullich & Schmidtbleicher, 1996). Performance changes were assessed in the upper body by comparing force-time curves of explosive bench presses before and following various bench press conditioning protocols and in the lower body by comparing jump height of countermovement jumps and jump height and contact time of drop jumps before and following three, five-second leg presses (Gullich &

Schmidtbleicher, 1996). The findings in the upper body were that 1-5 maximal load [1 repetition maximum (RM)] bench presses with adequate rest resulted in an enhanced rate of force development of explosive bench presses compared to pre-conditioning tests (Gullich & Schmidtbleicher, 1996). While all volumes improved the rate of force development, performing three or greater bench presses resulted in a decreased maximum force post-conditioning, a potential sign of fatiguing effects (Gullich & Schmidtbleicher, 1996). In the lower body, the countermovement jump heights were significantly higher following the set of leg presses, as for the drop jumps, contact time remained relatively the same, while jump height significantly increased (Gullich & Schmidtbleicher, 1996). This was the first study to give evidence that volitional conditioning activities could potentiate volitional performance measures in humans.

Another study, completed shortly after, also used resistance exercises to assess if they can affect performance measures. This study used one set of five half-squats (a ballistic intent squat with a reduced range of motion) at a 5-RM load and measured the jump height of loaded countermovement jumps before and 4 minutes after the conditioning exercise (Young et al., 1998). There was a significant increase in jump height following the half-squats (Young et al., 1998). There were several other studies which used volitional conditioning activities to test if potentiation was present in performance measures. While there were more examples of potentiation in both the upper body (Baker, 2003), and lower body (Chiu et al., 2003; Duthie et al., 2002; French et al., 2003; Gourgoulis et al., 2003), there were also many examples where potentiation did not occur (Gossen & Sale, 2000; Hrysomallis & Kidgell, 2001; Jensen & Ebben, 2003; Jones & Lees, 2003; Scott & Docherty, 2004).

There were differences between the studies, which may have explained the lack of potentiation. Firstly, in several of the studies which elicited potentiation, it was found that the effect was higher or only present in stronger (Duthie et al., 2002; Gourgoulis et al., 2003) and more athletic (Chiu et al., 2003) populations. The populations of many of the studies which did not have evidence of potentiation included recreational, resistance-trained populations (Gossen & Sale, 2000; Hrysomallis & Kidgell, 2001; Jones & Lees, 2003; Scott & Docherty, 2004). Therefore, it could be possible that the population was not strong or athletically trained to a high enough degree in order for PAP to be elicited. However, some studies used seemingly similar populations and did show evidence for potentiation (Duthie et al., 2002; Young et al., 1998), so this is not a definitive reason for the lack of potentiation.

Also, the timing of the post-tests could have affected the ability of the researchers to identify when potentiation was occurring. Most of the potentiation studies had tests around 5 minutes post-conditioning, and it was at this time that potentiation was often found (Baker, 2003; Chiu et al., 2003; Gullich & Schmidtbleicher, 1996; Young et al., 1998). Other studies may have had potentiation occurring, but their post-tests occurred before and after this 5-minute mark, which could have been outside the window of potentiation (Hrysomallis & Kidgell, 2001; Jensen & Ebben, 2003; Jones & Lees, 2003).

A third and more notable difference in the non-potentiating studies is related to the volume of the conditioning activity. The conditioning activity in four of the five studies was one set of five squats (Jensen & Ebben, 2003; Jones & Lees, 2003; Scott & Docherty, 2004) or bench presses (Hrysomallis & Kidgell, 2001) at the individual’s 5RM, while the other study used a 10-second MVC of the knee extensors (Gossen & Sale, 2000). As for the potentiating studies, many used less repetitions, at higher relative intensities, often with an explosive intent (Chiu et al., 2003; Duthie et al., 2002; French et al., 2003; Gourgoulis et al., 2003; Gullich & Schmidtbleicher, 1996; Young et al., 1998). The higher volume of the non-potentiating studies may have induced fatigue and could have masked the potentiating effects that were present at the time that the tests were performed (Gossen & Sale, 2000). The aforementioned studies give evidence that the PAP and PTP measured by changes to twitch tension also cause changes to external muscle performance. However, when exploring more than just muscle twitch properties, results become much more variable and demonstrate that there are many factors simultaneously at play.

1.6 Coexistence of Potentiation and Fatigue

The coexistence of potentiation and fatigue has been established in the literature. It has been found that potentiating and fatiguing effects can be present at the same time, and the resultant performance is often the net effect of fatigue and potentiation (Behm, 2004; Rassier & MacIntosh, 2000; Sale, 2002). When considering internal or evoked measures of potentiation at the muscle, such as twitch potentiation, fatigue effects may reduce the concentration of myoplasmic Ca^{2+}, and affect the resultant peak twitch (Rassier & MacIntosh, 2000). However, the short-duration tetanic stimulations, which were used to induce potentiation, did not cause much fatigue, since evidence of PAP was evident in these studies (Botelho & Cander, 1953; Hughes & Morrell, 1957; Krarup & Horowitz, 1979). Contrastingly, when considering the functional performance measures used in the studies mentioned above, the brain, spinal cord, peripheral nerves and muscle all play a part in performing the activity. Fatigue effects at each of these areas could diminish the presence of the potentiating effects occurring due to myosin light chain phosphorylation or any other mechanisms when solely observing functional performance outcomes (Rassier & MacIntosh, 2000). Since this coexistence exists, no change, or a decrease in performance, does not necessarily mean no potentiation is present. In order to have the best chance of observing any PAP that is present, researchers should measure performance throughout a period of time (i.e. every minute from 0 to 10 minutes) (Rassier & MacIntosh, 2000). This way, they will have an increased chance at finding windows of time where the PAP effects are higher than the fatigue effects, which will result in increased performance.

1.7 Mechanism of H-reflex Potentiation

In addition to phosphorylation of the myosin regulatory light chains, there is one other mechanism that is mentioned as a possible contributor to PAP. Similar to the twitch potentiation studies, there have been numerous studies over the years which have used stimulation techniques to elicit and measure potentiation of the Hoffman (H)-reflex (Blom et al., 1964; Corrie & Hardin, 1964; Hagbarth, 1962; Kitago et al., 2004; Lagerquist & Collins, 2010; Lance et al., 1966; Van Boxtel, 1986). H-reflexes are elicited by stimulating the nerve at relatively low amplitudes and activating Ia afferent neurons, which synapse with alpha-motoneurons and elicit a relatively slower twitch response in the muscle compared to a standard twitch (Trimble & Enoka, 1991). Changes to H-reflex can be an indication of changes to the afferent excitability of the alpha-motoneuron pool, changes to presynaptic inhibition, or both (Anthi et al., 2014). The general procedures of H-reflex potentiation studies were similar to the twitch potentiation studies. However, there are several differences worth mentioning. Firstly, the conditioning tetanus frequencies, which elicited the most significant potentiation were typically higher (greater than 200Hz) than the frequencies that elicited the most significant twitch potentiation (Blom et al., 1964; Corrie & Hardin, 1964; Hagbarth, 1962; Kitago et al., 2004; Lance et al., 1966; Van Boxtel, 1986). The duration of the tetanus was also usually longer, typically between 10 and 20 seconds (Corrie & Hardin, 1964; Hagbarth, 1962; Lance et al., 1966; Van Boxtel, 1986). However, since the Ia afferent neurons, the targets for H-reflex, are a larger diameter than the efferent alpha-motor neurons, the targets for muscle twitches, and as a result, can be activated at lower stimulation intensities, the intensity of the tetanus was often at a reduced intensity compared to the twitch potentiation studies (Hagbarth, 1962; Kitago et al., 2004; Lagerquist & Collins, 2010; Lance et al., 1966; Van Boxtel, 1986).

When analyzing the changes in H-reflex following the conditioning stimulation, there are also a couple of differences compared to twitch potentiation. Firstly, the peak H-reflex amplitude, post-conditioning, was typically reached at 10-20s post-conditioning (Blom et al., 1964; Corrie & Hardin, 1964; Hagbarth, 1962) and even later in one study, peaking at 4 minutes post-conditioning (Kitago et al., 2004). This is unlike the twitch potentiation studies, where peak amplitude was often reached immediately post-conditioning. However, it is similar to the voluntary performance potentiation studies, where potentiation was often measured around 5 minutes. Secondly, in many of the H-reflex studies, immediately post-conditioning, there was a depression of H-reflex, below pre-conditioning values (Enoka et al., 1980; Gollhofer et al., 1998; Hagbarth, 1962; Moore & Kukulka, 1991; Trimble & Harp, 1998). Following a depression of the H-reflex, the amplitudes would then increase, and as previously mentioned, reach a maximum amplitude near 5 minutes. Once again, these findings conflict with the typical findings of the twitch potentiation studies but are similar to the voluntary performance studies, where there was often an initial decrease in performance if measured immediately after conditioning.

There have been a few potential explanations for why H-reflex is often depressed immediately following conditioning, and why it takes some time before the amplitude reaches potentiated levels. Immediately following conditioning, the activation of the motor units can cause recurrent inhibition to occur, thereby inhibiting previously activated motor units, and decreasing the excitability of the motoneuron pool (Moore & Kukulka, 1991). Additionally, the previous activity could cause muscle fatigue, which in turn decreases the excitability of the motoneuron pool and depresses the H-reflex (Trimble & Harp, 1998). Changes to presynaptic inhibition, leading to H-reflex depression can occur due to a depletion of neurotransmitters at the axon terminal of the Ia afferents, causing decreased activation of the motoneuron pools (Trimble & Harp, 1998; Van Boxtel, 1986). They can also occur due to a decrease in reflex responsiveness caused by increased activation and communication between Ia afferent neurons from the muscle activity, which occurred immediately prior (Moore & Kukulka, 1991). Because of the similarities in time-course of H-reflex and muscle performance potentiation studies, these mechanisms contributing to decreases in H-reflex post-conditioning may also be contributors to the decreases in muscle performance following conditioning, which in the literature have been broadly described as fatigue (Gossen & Sale, 2000; Jensen & Ebben, 2003; Scott & Docherty, 2004).

The studies which gave evidence of H-reflex potentiation highlight a couple of mechanisms that may have contributed to the increased H-reflex amplitude. At the presynaptic terminal (axon terminal of Ia afferent neuron), it was suggested that the prior activity can cause increased release of neurotransmitters (Gullich & Schmidtbleicher, 1996; Lagerquist & Collins, 2010; Van Boxtel, 1986), which may contribute to an increased availability of calcium in the presynaptic terminal, an important element to neurotransmitter release (Gullich & Schmidtbleicher, 1996). At the motoneuron pool, previous muscle activity can activate a phenomenon, termed persistent inward currents (PICs) (Lagerquist & Collins, 2010). PICs cause motoneurons to fire without any stimuli (self-sustained firing), these PICs could contribute to an increased number of active motoneurons, leading to an increased H-reflex (Lagerquist & Collins, 2010). These mechanisms contributing to H-reflex potentiation, have also been suggested to be potential mechanisms contributing to PAP (Rassier & MacIntosh, 2000).

However, there has been little consistent success in the literature at confirming that any mechanisms other than phosphorylation of myosin regulatory light chains are an important contributor to PAP. Once observations are made beyond the muscle twitch, such as H-reflex and performance measures, results become much more variable between studies, and within studies. This makes it difficult to come to conclusions about mechanisms beyond the muscle, which contribute to PAP.

1.8 Post Activation Performance Enhancement

While phosphorylation of the myosin regulatory light chains has been the main mechanisms attributed to PAP, in recent years, a new term, post-activation performance enhancement (PAPE), has been used by researchers. PAPE has been used to describe improvements in voluntary performance measures following a conditioning activity, particularly in research settings that do not use any electrical stimulation techniques (Blazevich & Babault, 2019; Prieske et al., 2020). Potentiation refers to the increases in electrically evoked twitch potentiation following a conditioning activity, as such, if twitches are not measured in a study, performance changes cannot be associated with the potentiation (Sweeney et al., 1993). Alternatively, factors including muscle temperature change, metabolism changes, altered muscle activation, motor learning, and changes to the psychological state of the subject could contribute to the increases in performance (Blazevich & Babault, 2019; Prieske et al., 2020). Therefore, studies that focus on voluntary changes to performance and do not directly measure muscle twitch changes should avoid using the phrase PAP, and should instead use PAPE (Blazevich & Babault, 2019; Prieske et al., 2020).

1.9 Muscle Fatigue

Muscle fatigue, defined as a decrease in muscle force-producing capabilities following prior activity (Gandevia, 2001), is a phenomenon that has received much greater attention than PAP in the literature. As previously stated, fatigue effects can coexist with and oppose PAP effects (Rassier & MacIntosh, 2000). Mechanisms of muscle fatigue can be divided into two subgroups of fatigue, central fatigue, related to an inability to voluntarily drive maximal muscle activity, and peripheral fatigue, related to any factors distal to the neuromuscular junction (Gandevia, 2001). Many fatigue studies have been conducted, and fatigue-related changes have been found at the level of the muscle (Jami et al., 1983; Sjogaard et al., 1986), motoneuron(Bellemare & Garzaniti, 1988; Stephens & Taylor, 1972), spinal cord (Bigland-Ritchie et al., 1986; Maton & Gamet, 1989), and brain (Bergstrom & Hultman, 1988; Bigland-Ritchie et al., 1982; Dietz, 1978), among other regions. To better understand if mechanisms located beyond the muscle itself play a significant part in muscle fatigue, researchers have studied if there are fatigue effects in non-working muscles, located contralateral, ipsilateral, superior, or inferior, to the muscle group being worked (Halperin et al., 2015). The findings of these studies have given indications to several muscle fatigue mechanisms in locations proximal to the muscle.

1.10 Non-Local Fatigue Effects

A few studies analyzed changes to the corticospinal tract projecting to non-exercised muscle groups during and following fatiguing protocols. The first study found that during a bilateral fatiguing protocol targeting the quadriceps, there was an increase in motor evoked potential (MEP) amplitude, measured at the right first dorsal interosseous muscle and biceps brachii, and a decrease in MEP amplitude following the protocol at these two arm muscles (Takahashi et al., 2011). Another study found that following a fatiguing contraction to the plantar flexors, compared to the pre-test value, there was a 28% and 47% increase in the MEP amplitude of the contralateral first dorsal interosseous muscle immediately after and ten minutes after, respectively (Matsuura & Ogata, 2015). While these studies do not make it clear what the exact mechanisms are that cause the changes to the corticospinal tract, they do indicate that fatiguing protocols do cause changes to corticospinal excitability projecting to non-exercised muscles. Another study also looked at neurological changes, this time, voluntary activation. It was found that following a sustained fatiguing contraction of the dominant knee extensors, there was reduced voluntary activation in the contralateral knee extensors, particularly in men (Martin & Rattey, 2007). It is suggested that this reduction in voluntary activation of the contralateral limb is due to interhemispheric communication between the fatigued motor cortex and the contralateral motor cortex projecting to the non-exercised muscle (Martin & Rattey, 2007). This communication results in inhibitory signals being received by the unfatigued motor cortex resulting in a reduced activation (Martin & Rattey, 2007). Other studies give a possible physiological based alternative explanation for a reduction in the central drive to unexercised muscle groups. One study found that fatiguing exercise resulted in a decrease in the oxygenation level of the brain (Rasmussen et al., 2010), while another study found decreases in blood glucose levels (Nybo, 2003). In both studies, there was an associated reduction in central drive (Nybo, 2003; Rasumussen et al., 2010). It is suggested that these reductions may play a part in central fatigue, which may affect previously exercised muscle groups as well as rested muscle groups (Rasmussen et al., 2010).

In contrast, there were several studies which once again showed evidence of changes to corticospinal excitability in non-exercised muscles following a fatigue protocol, however there were not changes to MVC force, EMG activity or voluntary activation (Aboodarda et al., 2015a;

Aboodarda et al., 2015b; Sambaher et al., 2016). These studies demonstrate that non-local changes to corticospinal excitability do not always indicate that fatigue is occurring in these muscles. More studies need to be conducted to better understand the relationship between corticospinal excitability changes and muscle performance. More specifically, non-local studies which implement a conditioning protocol that promotes PAP could provide more insight into how corticospinal changes alter muscle performance.

1.11 Biochemical Mechanisms of Fatigue

In addition to neurological changes, there have also been suggested biochemical, biomechanical and psychological changes that could have contributed to non-local fatigue effects. Multiple studies have found evidence of increased metabolites in the blood surrounding non-working muscles. This includes potassium ions (Bangsbo et al., 1996; Nordsborg et al., 2003), hydrogen ions (Bangsbo et al., 1996; Johnson et al., 2014), and plasma lactate concentrations (Halperin et al., 2014; Johnson et al., 2014). The increased concentration of potassium and hydrogen ions from previous activity are all suggested to contribute to an increased level of fatigue in non-working muscles, compared to when no previous activity is performed (Bangsbo et al., 1996; Johnson et al., 2014; Nordsborg et al., 2003).

1.12 Biomechanical Mechanisms of Fatigue

Another study showed that lower body peak power is significantly reduced when the performance is preceded by arm exercise compared to when it is not (Grant et al., 2014). It was suggested that there were biomechanical reasons for this decrease in peak power. More specifically, the grip strength of the participants was reduced following the arm exercise, and it was suggested that the reduced handgrip decreased the ability to stabilize the upper body which did not allow the participants to produce as much cycling power in the lower body (Grant et al., 2014). Additionally, upper body (Tarnanen et al., 2008) and lower body (Danneels et al., 2003) exercise have both been shown to cause fatigue in the trunk muscles, measured by changes to EMG activity. This is suggested to play a part in increasing the level of fatigue in unworked muscle groups of the lower body when preceded by upper body exercise, or vice versa (Halperin et al., 2015).

1.13 Psychological Effects of Fatigue

Finally, there have also been some suggested psychological changes that could cause non-local fatiguing effects. Studies have shown that prior mentally fatiguing tasks (Marcora et al., 2009; Pageaux et al., 2014), and physically fatiguing tasks (Amann et al., 2013) cause an increased perceived level of effort in muscle performance tasks compared to when there is no prior fatigue, and also a decreased time to failure.

1.14 Other Non-Local Effects

In addition to muscle fatigue, there have also been other studies that have used study designs to measure changes in non-worked muscles in order to help determine if the phenomenon has mechanisms central to the muscle that contribute to its effect. This includes non-local increases in range of motion due to stretching (Behm et al., 2016; Chaouachi et al., 2015) and foam rolling (Kelly & Beardsley, 2016) and non-local changes to pain perception from foam rolling (Aboodarda et al., 2015c). Since these studies have successfully demonstrated that non-local effects are present in fatigue, range of motion and pain perception at the muscle which has given indications of neural effects, using a non-local study design to elicit potentiation may be an effective method for determining if there is an existence of neural effects with this phenomenon.

1.15 Non-Local Muscle Potentiation

To this point, there are very few studies that have investigated the global or non-local effects of PAP. The first study used a pyramid-style protocol with Bulgarian split-squats to examine if it could elicit PAP effects in the contralateral limb (Andrews et al., 2016). Five repetitions of dominant leg Bulgarian split-squats at 50% of 1RM, followed by two repetitions at 70% of 1RM, and then one repetition at 90% of 1RM was performed (Andrews et al., 2016). On one day, the exercised dominant leg was tested, and significant improvements in countermovement jump height and power occurred (Andrews et al., 2016). On the other day, the unexercised non-dominant leg was tested, and there were slight decrements in countermovement jump height and power (Andrews et al., 2016), giving no evidence for non-local PAP. The other study was a non-local muscle fatigue protocol that produced some non-local PAP effects (Hamilton & Behm, 2017). The dominant knee extensors were fatigued using an isometric knee extension fatigue protocol, and non-dominant isometric knee extension force was measured before and after the protocol, among other measures (Hamilton & Behm, 2017). The study gave evidence for non-local PAP effects, as there was an increase in the force of the non-dominant knee extensors following fatigue to the dominant knee extensors (Hamilton & Behm, 2017).

Due to the lack of non-local PAP focused studies, and the minimal knowledge around the neural effects which may cause PAP, it is crucial to further explore this topic. Specifically, to develop a protocol that can elicit PAP in an unexercised muscle and then determine which types of muscle performance are most affected and what population is most and least susceptible to non-local PAP effects. This can help develop a further understanding of the phenomenon.

1.16 Methodological Considerations

Developing an effective protocol and recruiting an appropriate population are both crucial factors in order to ensure the best opportunity for PAP to occur in non-local muscles.

Testing Measures

As previously mentioned, PAP can be observed as an increase in force, rate of force development or both. In many previous studies of lower body PAP, isometric MVCs (Behm, Button, Barbour, Butt, & Young, 2004; Gilbert, Lees, & Graham-Smith, 2001; Guellich et al., 1996), drop jumps (French et al., 2003; Gullich & Schmidtbleicher, 1996; Jones & Lees, 2003), and countermovement jumps (Chiu et al., 2003; French et al., 2003; Gourgoulis et al., 2003; Kilduff et al., 2010; Mangus, Takahashi, Mercer, & Holcomb, 2006) have been used as tests for PAP. From the MVC, peak force, and the force in the first 100 milliseconds (F100) of the contraction can indicate changes to force and rate of force development, respectively. In addition to force characteristics, electromyography (EMG) recorded during the MVCs, can give information regarding how muscle activity may change following a conditioning activity. There is currently very little literature on EMG during PAP studies. Furthermore, drop and countermovement jumps can also provide information regarding reactive strength index (RSI), as an indicator of power and rate of force development. Reaction time testing has not been previously used as a tool to measure PAP. However, a quick reaction, and particularly a quick movement time, could indicate an improved rate of force development.

Potentiation Protocol

In order for the tests to be able to detect potentiation, it is crucial to design a protocol that has the best chance of eliciting PAP in the participants. Since fatigue coexists with PAP, the protocol must be able to maximize PAP and minimize fatigue. When choosing a conditioning activity for studying PAP in the lower body, previous studies have often used back squats or a more explosive squat variety such as a half-squat (Chiu et al., 2003; Duthie et al., 2002; Gourgoulis et al., 2003; Jensen & Ebben, 2003; Jones & Lees, 2003; Scott & Docherty, 2004; Young et al.,

1998) or isometric MVCs of the knee extensors (Behm et al., 2004; French et al., 2003; Gossen & Sale, 2000; Guellich et al., 1996).

In terms of volume, the previous studies using MVCs performed 1 to 5 repetitions of MVCs of 3, 5 and 10 seconds duration (Behm et al., 2004; French et al., 2003; Gossen & Sale, 2000; Guellich et al., 1996). The findings of these studies were that 10-second MVCs either had no performance changes or a reduction in performance measures, suggesting fatigue effects (Behm et al., 2004; Gossen & Sale, 2000). Meanwhile, the shorter duration MVCs (3 and 5 seconds) did show evidence for improvements in jumping performance measures (French et al., 2003; Gullich & Schmidtbleicher, 1996). Therefore, performing MVCs lasting between 3 and 5 seconds appears to maximize potentiating effects while reducing the impact of fatigue. As for the number of repetitions, the studies which elicited PAP effects used both 3 and 5 repetitions of MVCs, and there was evidence for PAP with three (French et al., 2003; Gullich & Schmidtbleicher, 1996) and five repetitions (Gullich & Schmidtbleicher, 1996). Neither of these studies performed four repetitions of MVCs, and it could be interesting to note if performing four repetitions has an improved PAP effect. Another important factor is the amount of rest between MVC repetitions. The study by French and colleagues (2003) performed three repetitions of three and five-second MVCs with 3 minutes of rest between repetitions, while Gullich and Schmidtbleicher (1996) used both 1 and 5 minutes between sets. While both rest intervals elicited PAP effects, the 1-minute rest interval had slightly higher effects (Gullich & Schmidtbleicher, 1996). While 1 minute of rest was able to produce PAP effects with three repetitions of 5-second MVCs, it is possible that adding a fourth repetition could enhance the fatigue with the shorter break.

Based on previous literature, when observing PAP effects on performance measures, potentiation can be present immediately following the conditioning activity (French et al., 2003;

Gourgoulis et al., 2003) and up to 10-12 minutes after (Gilbert et al., 2001; Gullich & Schmidtbleicher, 1996; Kilduff et al., 2010). This appears to be due to the interaction between PAP and fatigue (Anthony & Bishop, 2009). Whether muscle performance is increased or decreased at a particular time point is determined by the relative contribution of PAP and fatigue at that point. It appears that initially, both fatigue and PAP effects are high; if PAP is higher than fatigue at this time, performance increases will be present (Anthony & Bishop, 2009). As time progresses, fatigue effects tend to mask any PAP effects that may be present, and performance decreases (Anthony & Bishop, 2009). However, there is also some evidence to show that fatiguing effects subside quicker than PAP effects, and around 10 minutes following the conditioning activity, a window where performance is once again increased is present (Anthony & Bishop, 2009).

Participant Characteristics

There have been several studies that have analyzed differences in participants characteristics, which could play a part in the level of PAP occurring. As previously mentioned, several studies found a stronger (Duthie et al., 2002; Gourgoulis et al., 2003; Kilduff et al., 2010) and more athletic (Chiu et al., 2003) population had increased levels of PAP. An explanation for this could be that increased strength is associated with an increase in type II muscle fibres (Maughan et al., 1983; Thorstensson et al., 1976). Type II muscle fibres have been shown to elicit greater PAP (Hamada, Sale, MacDougall, & Tarnopolsky, 2003; Moore & Stull, 1984; Sweeney et al., 1993) through a more exceptional ability for myosin regulatory light chains to become phosphorylated (Moore & Stull, 1984). Additionally, it is hypothesized that more athletic populations, as in participants who take part in higher-level sport, have an increased resistance to fatigue compared to a population that recreationally resistance trains (Chiu et al., 2003). With reduced fatigue effects following a conditioning activity, the impact of PAP effects would be emphasized, therefore increasing improvements in muscle performance.

Additionally, another study analyzed the effect of the cross-sectional area and volume of the quadriceps muscle on PAP (Seitz et al., 2016). A positive correlation was found between quadriceps cross-sectional area, volume, and also torque with PAP (Seitz et al., 2016). This further supports that there are more significant signs of PAP effects in stronger populations. When comparing male and females participants, the findings are conflicting, with some studies finding similar PAP effects between males and females (Evetovich et al., 2015; Wilson et al., 2013), but also evidence for more significant PAP effects in males (Arabatzi et al., 2014). The findings of more significant PAP effects in males may be because males typically have larger muscles and greater strength, which both have been shown to increase PAP effects. Based on these findings, it appears that an ideal population to induce PAP effects on would be an athletically trained male population, with high type II muscle fibres in their quadriceps and a large cross-sectional area. However, there have only been a few studies to compare differences between males and females, and athletically trained versus recreationally trained participants.

Another factor to consider is whether conditioning the dominant limb and testing the non-dominant limb or vice versa would be more effective at producing PAP. The two current studies which have elicited non-local PAP effects either intentionally or unintentionally have both conditioned the dominant limb and tested the non-dominant limb (Andrews et al., 2016; Hamilton & Behm, 2017). Crossover fatigue studies which have targeted the quadriceps and have used isometric contractions to elicit fatigue have almost exclusively used a crossover from dominant to non-dominant limb (Arora et al., 2015; Halperin et al., 2014; Kennedy et al., 2015; Martin & Rattey, 2007; Rattey et al., 2006). Only one study was found which randomized the fatigued limb (Doix et al., 2013). While almost all studies have analyzed crossover from dominant to non-dominant, there have been no rationales given to why this is the case. Therefore, it would be interesting to analyze how and if conditioning the non-dominant limb and testing the dominant limb differs from the usual dominant to non-dominant crossover.

1.17 Summary

To summarize the current findings related to PAP, enhancements to peak twitch torque following both tetanic stimulation and maximal or near-maximal voluntary activity has been well-established in the literature. The predominant mechanism attributed to the twitch potentiation may be the phosphorylation of myosin regulatory light chains, a peripheral mechanism within the muscle. Tetanic stimulation and maximal or near-maximal voluntary activation have also produced H-reflex potentiation. While its existence in studies is less consistent than twitch potentiation, it does indicate mechanisms at the neural level. The potential neural mechanisms could include changes to presynaptic inhibition and changes to alpha motoneuron excitability, among other possibilities.

When changing the PAP testing measures from evoked changes, such as twitch and H-reflex, to functional performance changes, such as jump height and peak voluntary force production, the existence of PAP becomes much more variable. The main reason for this is hypothesized to be the co-existence of PAP and fatigue. Both mechanisms are working at the same time, at different magnitudes, and the external changes are the net product of the PAP and fatigue effects. Therefore, in order to see PAP in functional performance measures, PAP effects on the muscle must have a stronger influence than fatigue effects. Consequently, the details of the conditioning activity are essential in order to consistently elicit PAP in functional performance measures. Developing a better understanding of the mechanisms underlying PAP would be beneficial in creating an effective conditioning protocol.

In muscle fatigue literature, researchers have studied non-local muscle fatigue effects in order to further discover the mechanisms, specifically the neural mechanisms associated with fatigue. This type of research has received minimal attention in PAP research. Therefore, performing a non-local study of PAP could help better understand the presence or lack of a presence of neural mechanisms associated with the phenomenon.

Finally, to have the best chances of eliciting PAP, results of previous research will be used to develop an appropriate protocol, target population, and testing measures. An athletically trained population, consisting of both males and females, will have their knee extensors conditioned using four repetitions of five-second isometric knee extension MVCs, with 1-minute rest following the first and third repetitions and 3-minutes of rest following the second repetition. The presence of PAP will then be tested by comparing participants' performance of an isometric knee extension MVC, single-leg drop jump, single-leg countermovement jump, and reaction time test at 1 and 10 minutes following the conditioning activity to the performance of the same tests immediately before the conditioning activity.

1.18 References

Aboodarda, S. J., Copithorne, D. B., Power, K. E., Drinkwater, E., & Behm, D. G. (2015a). Elbow flexor fatigue modulates central excitability of the knee extensors. *Applied Physiology, Nutrition, and Metabolism*, *40*(9), 924-930.

Aboodarda, S. J., Šambaher, N., & Behm, D. G. (2015b). Unilateral elbow flexion fatigue modulates corticospinal responsiveness in non-fatigued contralateral biceps brachii. *Scandinavian Journal of Medicine & Science in Sports*, *26*(11), 1301-1312.

Aboodarda, S., Spence, A., & Button, D. C. (2015c). Pain pressure threshold of a muscle tender spot increases following local and non-local rolling massage. *BMC Musculoskeletal Disorders*, *16*(1).

Alway, S. E., Hughson, R. L., Green, H. J., Patla, A. E., & Frank, J. S. (1987). Twitch potentiation after fatiguing exercise in man. *European Journal of Applied Physiology and Occupational Physiology*, *56*(4), 461–466.

Amann, M., Venturelli, M., Ives, S. J., McDaniel, J., Layec, G., Rossman, M. J., & Richardson, R. S. (2013). Peripheral fatigue limits endurance exercise via a sensory feedback-mediated reduction in spinal motoneuronal output. *Journal of Applied Physiology*, *115*(3), 355–364.

Andrews, S. K., Horodyski, J. M., Macleod, D. A., Whitten, J., & Behm, D. G. (2016). The interaction of fatigue and potentiation following an acute bout of unilateral squats. *Journal of Sports Science and Medicine*, *15*(4), 625–632.

Anthi, X., Dimitrios, P., & Christos, K. (2014). On the mechanisms of post-activation potentiation: the contribution of neural factors. *Journal of Physical Education and Sport*, *14*(2), 134–137.

Anthony, N., & Bishop, D. (2009). Factors modulating post-activation potentiation and its effects on performance. *Sports Medicine*, *39*(2), 147–166.

Arabatzi, F., Patikas, D., Zafeiridis, A., Giavroudis, K., Kannas, T., Gourgoulis, V., & Kotzamanidis, C. M. (2014). The post-activation potentiation effect on squat jump performance: age and sex effect. *Pediatric Exercise Science*, *26*(2), 187–194.

Arora, S., Budden, S., Byrne, J. M., & Behm, D. G. (2015). Effect of unilateral knee extensor fatigue on force and balance of the contralateral limb. *European Journal of Applied Physiology*, *115*(10), 2177–2187.

Baker, D. G. (2003). Acute effect of alternating heavy and light resistances on power output during upper-body complex power training. *Journal of Strength and Conditioning Research*, *17*(3), 493–497.

Bangsbo, J., Madsen, K., Kiens, B., & Richter, E. A. (1996). Effect of muscle acidity on muscle metabolism and fatigue during intense exercise in man. *Journal of Physiology*, *495*(2), 587–596.

Behm, David G. (2004). Force maintenance with submaximal fatiguing contractions. *Canadian Journal of Applied Physiology*, *29*(3), 274–290.

Behm, David G., Button, D. C., Barbour, G., Butt, J. C., & Young, W. B. (2004). Conflicting effects of fatigue and potentiation on voluntary force. *Journal of Strength and Conditioning Research*, *18*(2), 365–372.

Behm, David George, Cavanaugh, T., Quigley, P., Reid, J. C., Silva Monteiro Nardi, P., & Marchetti, P. H. (2016). Acute bouts of upper and lower body static and dynamic stretching increase non-local joint range of motion. *European Journal of Applied Physiology*, *116*, 241–249.

Belanger, A. Y., McComas, A. J., & Elder, G. B. C. (1983). Physiological properties of two antagonistic human muscle groups. *European Journal of Applied Physiology and Occupational Physiology*, *51*(3), 381–393.

Belanger, A. Y., & Quinlan, J. (1982). Muscle function studies in human plantar-flexor and dorsi-flexor muscles. *Canadian Journal of Neurological Sciences*, *9*(3), 359.

Bellemare, F., & Garzaniti, N. (1988). Failure of neuromuscular propagation during human maximal voluntary contraction. *Journal of Applied Physiology*, *64*(3), 1084–1093.

Bergstrom, M., & Hultman, E. (1988). Energy cost and fatigue during intermittent electrical stimulation of human skeletal muscle. *J Appl Physiol*, *65 (4)*, 1500–1505.

Bigland-Ritchie, B., Furbush, F., & Woods, J. J. (1986). Fatigue of intermittent submaximal voluntary contractions: central and peripheral factors. *Journal of Applied Physiology*, *61*(2), 421–429.

Bigland-Ritchie, B., Kukulka, C. G., Lippold, O. C., & Woods, J. J. (1982). The absence of neuromuscular transmission failure in sustained maximal voluntary contractions. *The Journal of Physiology*, *330*(1), 265–278.

Binder-Macleod, S. A., Dean, J. C., & Ding, J. (2002). Electrical stimulation factors in potentiation of human quadriceps femoris. *Muscle & Nerve*, *25*(2), 271–279.

Blom, S., Hagbarth, K. E., & Skoglund, S. (1964). Post-tetanic potentiation of h-reflexes in human infants. *Experimental Neurology*, *9*(3), 198–211.

Botelho, S. Y., & Cander, L. (1953). Post-tetanic potentiation before and during ischemia in intact human skeletal muscle. *Journal of Applied Physiology*, *6*(4), 221–228.

Brown, G. L., & Von Euler, U. S. (1938). The after effects of a tetanus on mammalian muscle. *The Journal of Physiology*, *93*(1), 39–60.

Chaouachi, A., Padulo, J., Kasmi, S., Othmen, A. Ben, Chatra, M., & Behm, D. G. (2015).

Unilateral static and dynamic hamstrings stretching increases contralateral hip flexion range of motion. *Clinical Physiology and Functional Imaging, 37*(1), 23–29.

Chiu, L. Z. F., Fry, A. C., Weiss, L. W., Schilling, B. K., Brown, L. E., & Smith, S. L. (2003). Postactivation potentiation response in athletic and recreationally trained individuals. In *National Strength & Conditioning Association Res* (Vol. 17, Issue 4).

Corrie, W. S., & Hardin, W. B. (1964). Post-tetanic potentiation of h reflex in normal man. *Archives of Neurology, 11*(3), 317.

Danneels, L. A., Vanderstraeten, G. G., Cambier, D. C., Witvrouw, E. E., Stevens, V. K., & De Cuyper, H. J. (2003). A functional subdivision of hip, abdominal, and back muscles during asymmetric lifting. *Spine*, *26*(6), E114–E121.

Dietz, V. (1978). Analysis of the electrical muscle activity during maximal contraction and the influence ischaemia. *Journal of the Neurological Sciences*, *37*, 187–197.

Doix, A. C. M., Lefèvre, F., & Colson, S. S. (2013). Time course of the cross-over effect of fatigue on the contralateral muscle after unilateral exercise. *PLoS ONE*, *8*(5), 64910.

Duthie, G. M., Young, W. B., & Aitken, D. A. (2002). The acute effects of heavy loads on jump squat performance: an evaluation of the complex and contrast methods of power development. In *National Strength & Conditioning Association J. Strength Cond. Res* (Vol. 16, Issue 4).

Enoka, R. M., Hutton, R. S., & Eldred, E. (1980). Changes in excitability of tendon tap and hoffmann reflexes following voluntary contractions. *Electroencephalography and Clinical Neurophysiology, 48*(6), 664–672.

Evetovich, T. K., Conley, D. S., & McCawley, P. F. (2015). Postactivation potentiation enhances upper-and lower-body athletic performance in collegiate male and female athletes. *The*

Journal of Strength & Conditioning Research, *29*(2), 336–342.

French, D. N., Kraemer, W. J., & Cooke, C. B. (2003). Changes in dynamic exercise performance following a sequence of preconditioning isometric muscle actions. *Journal of Strength and Conditioning Research*, *17*(4), 678–685.

Gandevia, S. C. (2001). Spinal and supraspinal factors in human muscle fatigue. *Physiological Reviews*, *81*(4), 1726–1789.

Gilbert, G., Lees, A., & Graham-Smith, P. (2001). Temporal profile of post-tetanic potentiation of muscle force characteristics after repeated maximal exercise. *J Sports Sci*, *19*(6).

Gollhofer, A., Schoè, A., Rapp, W., & Stroinik, V. (1998). Changes in reflex excitability following isometric contraction in humans. *European Journal of Applied Physiology*, *77*, 89–97.

Gossen, E., & Sale, D. (2000). Effect of postactivation potentiation on dynamic knee extension performance...: deakin university library search. *Eur J Appl Physiol*, *83*, 524–530.

Gourgoulis, V., Aggeloussis, N., Kasimatis, P., Mavromatis, G., & Garas, A. (2003). Effect of a submaximal half-squats warm-up program on vertical jumping ability. *Journal of Strength and Conditioning Research*, *17*(2), 342–344.

Grant, M. C., Robergs, R., Baird, M. F., & Baker, J. S. (2014). The effect of prior upper body exercise on subsequent wingate performance. *BioMed Research International*, *2014*, 1–7.

Green, H. J., & Jones, S. R. (1989). Does post-tetanic potentiation compensate for low frequency fatigue? *Clinical Physiology*, *9*(5), 499–514.

Gullich, A., & Schmidtbleicher, D. (1996). Potentiation of explosive force. *New Studies in Athletics*, *4*(October), 67–80.

Hagbarth, K. E. (1962). Post-tetanic potentiation of myotatic reflexes in man. *Journal of*

Neurology, Neurosurgery, and Psychiatry, 25, 1–10.

Halperin, I., Chapman, D. W., & Behm, D. G. (2015). Non-local muscle fatigue: effects and possible mechanisms. *European Journal of Applied Physiology*, *115*(10), 2031–2048.

Halperin, I., Aboodarda, S. J., & Behm, D. G. (2014). Knee extension fatigue attenuates repeated force production of the elbow flexors. *European Journal of Sport Science*, *14*(8), 823-829.

Halperin, I., Copithorne, D., & Behm, D. G. (2014). Unilateral isometric muscle fatigue decreases force production and activation of contralateral knee extensors but not elbow flexors. *Applied Physiology, Nutrition, and Metabolism*, *39*(12), 1338–1344.

Hamada, T., MacDougall, J. D., Sale, D. G., & Moroz, J. (1997). Twitch potentiation of triceps surae and triceps brachii following voluntary contraction in trained athletes and sedentary controls. *Medicine &Science in Sports & Exercise*, *29*(Supplement), 26.

Hamada, T., Sale, D. G., MacDougall, J. D., & Tarnopolsky, M. A. (2003). Interaction of fibre type, potentiation and fatigue in human knee extensor muscles. *Acta Physiologica Scandinavica*, *178*(2), 165–173.

Hamilton, A. R., & Behm, D. G. (2017). The effect of prior knowledge of test endpoint on non-local muscle fatigue. *European Journal of Applied Physiology*, *117*(4), 651–663.

Hodgson, M., Docherty, D., & Robbins, D. (2005). Post-activation potentiation: underlying physiology and implications for motor performance. *Sports Medicine, 35*(7), 585–595.

Houston, M. E., & Grange, R. W. (1990). Myosin phosphorylation, twitch potentiation, and fatigue in human skeletal muscle. *Canadian Journal of Physiology and Pharmacology*, *68*(7), 908–913.

Houston, M. E., Green, H. J., & Stull, J. T. (1985). *Myosin light chain phosphorylation and* *isometric twitch potentiation in intact human muscle* (Vol. 403).

Hrysomallis, C., & Kidgell, D. (2001). Effect of heavy dynamic resistive exercise on acute upper-body power. *Journal of Strength and Conditioning Research, 15*(4), 426–430.

Hughes, J. R., & Morrell, R. M. (1957). Posttetanic changes in the human neuromuscular system. *Journal of Applied Physiology*, *11*(1), 51–57.

Jami, L., Murthy, K. S., Petit, J., & Zytnicki, D. (1983). After-effects of repetitive stimulation at low frequency on fast-contracting motor units of cat muscle. *The Journal of Physiology*, *340*(1), 129–143.

Jensen, R. L., & Ebben, W. P. (2003). Kinetic analysis of complex training rest interval effect on vertical jump performance. *Journal of Strength and Conditioning Research*, *17*(2), 345–349.

Johnson, M. A., Mills, D. E., Brown, P. I., & Sharpe, G. R. (2014). Prior upper body exercise reduces cycling work capacity but not critical power. *Medicine and Science in Sports and Exercise*, *46*(4), 802–808.

Jones, P., & Lees, A. (2003). A biomechanical analysis of the acute effects of complex training using lower limb exercises. *Journal of Strength and Conditioning Research*, *17*(4), 694–700.

Kelly, S., & Beardsley, C. (2016). Specific and cross-over effects of foam rolling on ankle dorsiflexion range of motion. *International Journal of Sports Physical Therapy*, *11*(4), 544–551.

Kennedy, D. S., Fitzpatrick, S. C., Gandevia, S. C., & Taylor, J. L. (2015). Fatigue-related firing of muscle nociceptors reduces voluntary activation of ipsilateral but not contralateral lower limb muscles. *Journal of Applied Physiology*, *118*(4), 408–418.

Kilduff, L. P., Bevan, H. R., Kingsley, M. I. C., Owen, N. J., Bennett, M. A., Bunce, P. J., Hore, A. M., Maw, J. R., & Cunningham, D. J. (2010). Postactivation potentiation in professional rugby players. *Journal of Strength and Conditioning Research*, *21*(4), 1134–1138.

Kitago, T., Mazzocchio, R., Liuzzi, G., & Cohen, L. G. (2004). Modulation of h-reflex excitability by tetanic stimulation. *Clinical Neurophysiology*, *115*(4), 858–861.

Krarup, C. (1977). Electrical and mechanical responses in the platysma and in the adductor pollicis muscle: in patients with myasthenia gravis. *Journal of Neurology, Neurosurgery &Amp; Psychiatry*, *40*(3), 241 LP – 249.

Krarup, Christian, & Horowitz, S. H. (1979). Evoked responses of the elbow flexors in control subjects and in myopathy patients. *Muscle & Nerve*, *2*(6), 465–477.

Lagerquist, O., & Collins, D. F. (2010). Influence of stimulus pulse width on m-waves, h-reflexes, and torque during tetanic low-intensity neuromuscular stimulation. *Muscle and Nerve*, *42*(6), 886–893.

Lance, J. W., Gail, P. d., & Neilson, P. D. (1966). Tonic and phasic spinal cord mechanisms in man. *Journal of Neurology, Neurosurgery & Psychiatry*, *29*(6), 535–544.

Lloyd, D. (1949). Post-tetanic potentiation of response in monosynaptic reflex pathways of the spinal cord. *The Journal of General Physiology*, *33*(2), 147–170.

Mangus, B. C., Takahashi, M., Mercer, J. A., & Holcomb, W. R. (2006). Investigation of vertical jump performance after completing heavy squat exercises. *Journal of Strength and Conditioning Research*, *20*(3), 597.

Marcora, S. M., Staiano, W., & Manning, V. (2009). Mental fatigue impairs physical performance in humans. *Journal of Applied Physiology*, *106*(3), 857–864.

Martin, P. G., & Rattey, J. (2007). Central fatigue explains sex differences in muscle fatigue and contralateral cross-over effects of maximal contractions. *Pflugers Archiv European Journal of Physiology*, *454*(6), 957–969.

Maton, B., & Gamet, D. (1989). The fatigability of two agonistic muscles in human isometric voluntary submaximal contraction: an emg study. *European Journal of Applied Physiology and Occupational Physiology*, *58*(4), 369–374.

Matsuura, R., & Ogata, T. (2015). Effects of fatiguing unilateral plantar flexions on corticospinal and transcallosal inhibition in the primary motor hand area. *Journal of Physiological Anthropology*, *34*(1).

Maughan, R. J., Watson, J. S., & Weir, J. (1983). Relationships between muscle strength and muscle cross-sectional area in male sprinters and endurance runners. *European Journal of Applied Physiology and Occupational Physiology*, *50*(3), 309–318.

Moore, M. A., & Kukulka, C. G. (1991). Depression of hoffmann reflexes following voluntary contraction and implications for proprioceptive neuromuscular facilitation therapy. *Physical Therapy*, *71*(4), 321–329.

Moore, R. L., & Stull, J. T. (1984). Myosin light chain phosphorylation in fast and slow skeletal muscles in situ. *American Journal of Physiology-Cell Physiology*, *247*(5), C462–C471.

Nordsborg, N., Mohr, M., Pedersen, L. D., Nielsen, J. J., Langberg, H., & Bangsbo, J. (2003). Muscle interstitial potassium kinetics during intense exhaustive exercise: effect of previous arm exercise. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, *285*(1), 143–148.

Nybo, L. (2003). CNS fatigue and prolonged exercise: effect of glucose supplementation. *Medicine and science in sports and exercise*, *35*(4), 589-594.

O’Leary, D. D., Hope, K., & Sale, D. G. (1997). Posttetanic potentiation of human dorsiflexors.

Journal of Applied Physiology, *83*(6), 2131–2138.

Pageaux, B., Lepers, R., Dietz, K. C., & Marcora, S. M. (2014). Response inhibition impairs subsequent self-paced endurance performance. *Eur J Appl Physiol*, *114*, 1095–1105.

Petrella, R. J., Cunningham, D. A., Vandervoort, A. A., & Paterson, D. H. (1989). Comparison of twitch potentiation in the gastrocnemius of young and elderly men. *European Journal of Applied Physiology and Occupational Physiology*, *58*(4), 395–399.

Prieske, O., Behrens, M., Chaabene, H., Granacher, U., & Maffiuletti, N. A. (2020). Time to Differentiate Postactivation "Potentiation" from "Performance Enhancement" in the Strength and Conditioning Community. *Sports Medicine (Auckland, NZ)*.

Rasmussen, P., Nielsen, J., Overgaard, M., Krogh-Madsen, R., Gjedde, A., Secher, N. H., & Petersen, N. C. (2010). Reduced muscle activation during exercise related to brain oxygenation and metabolism in humans. *Journal of Physiology*, *588*(11), 1985–1995.

Rassier, D. E., & MacIntosh, B. R. (2000). Coexistence of potentiation and fatigue in skeletal muscle. *Brazilian Journal of Medical and Biological Research*, *33*(5), 499–508.

Rattey, J., Martin, P. G., Kay, D., Cannon, J., & Marino, F. E. (2006). Contralateral muscle fatigue in human quadriceps muscle: evidence for a centrally mediated fatigue response and cross-over effect. *Pflugers Archiv : European Journal of Physiology*, *452*(2), 199–207.

Rosenblueth, A., & Morison, R. S. (1937). Curarization, fatigue and wedensky inhibition. *American Journal of Physiology-Legacy Content*, *119*(2), 236–256.

Sale, D. (2002). Postactivation potentiation: role in performance. *British Journal of Sports Medicine*, *38*(4), 386–387.

Scott, S. L., & Docherty, D. (2004). Acute effects of heavy preloading on vertical and horizontal jump performance. *Journal of Strength and Conditioning Research*, *18*(2), 201–205.

Seitz, L. B., Trajano, G. S., Haff, G. G., Dumke, C. C. L. S., Tufano, J. J., & Blazevich, A. J. (2016). Relationships between maximal strength, muscle size, and myosin heavy chain isoform composition and postactivation potentiation. *Applied Physiology, Nutrition, and Metabolism*, *41*(5), 491–497.

Sjogaard, G., Kiens, B., Jorgensen, K., & Saltin, B. (1986). Intramuscular pressure, emg and blood flow during low-level prolonged static contraction in man. *Acta Physiologica Scandinavica*, *128*(3), 475–484.

Stephens, J. A., & Taylor, A. (1972). Fatigue of maintained voluntary muscle contraction in man. *The Journal of Physiology*, *220*(1), 1–18.

Stuart, D. S., Lingley, M. D., Grange, R. W., & Houston, M. E. (1988). Myosin light chain phosphorylation and contractile performance of human skeletal muscle. *Canadian Journal of Physiology and Pharmacology*, *66*(1), 49–54.

Sweeney, H. L., Bowman, B. F., & Stull, J. T. (1993). Myosin light chain phosphorylation in vertebrate striated muscle: regulation and function. *American Journal of Physiology-Cell Physiology*, *264*(5), C1085–C1095.

Takahashi, K., Maruyama, A., Hirakoba, K., Maeda, M., Etoh, S., Kawahira, K., & Rothwell, J. C. (2011). Fatiguing intermittent lower limb exercise influences corticospinal and corticocortical excitability in the nonexercised upper limb. *Brain Stimulation*, *4*(2), 90–96.

Tarnanen, S. P., Ylinen, J. J., Siekkinen, K. M., Mälkiä, E. A., Kautiainen, H. J., & Häkkinen, A. H. (2008). Effect of isometric upper-extremity exercises on the activation of core stabilizing muscles. *Arch Phys Med Rehabil*, *89*.

Thorstensson, A., Grimby, G., & Karlsson, J. (1976). Force velocity relations and fiber composition in human knee extensor muscles. *Journal of Applied Physiology*, *40*(1), 12–16.

Trimble, M. H., & Enoka, R. M. (1991). Mechanisms underlying the training effects associated with neuromuscular electrical stimulation. *Physical Therapy*, *71*(4), 273-280.

Trimble, M. H., & Harp, S. S. (1998). Postexercise potentiation of the h-reflex in humans. *Medicine and Science in Sports and Exercise, 30*(6), 933–941.

Van Boxtel, A. (1986). Differential effects of low-frequency depression, vibration-induced inhibition, and posttetanic potentiation on h-reflexes and tendon jerks in the human soleus muscle. *Journal of Neurophysiology*, *55*(3), 551–568.

Vandervoort, A. A., Quinlan, J., & McComas, A. J. (1983). Twitch potentiation after voluntary contraction. *Experimental Neurology*, *81*(1), 141–152.

Wilson, J. M., Duncan, N. M., Marin, P. J., Brown, L. E., Loenneke, J. P., Wilson, S. M. C., Jo, E., Lowery, R. P., & Ugrinowitsch, C. (2013). Meta-analysis of postactivation potentiation and power: effects of conditioning activity, volume, gender, rest periods, and training status. *The Journal of Strength & Conditioning Research*, *27*(3), 854–859.

Young, W. B., Jenner, A., & Griffiths, K. (1998). Acute enhancement of power performance from heavy load squats. *The Journal of Strength & Conditioning Research*, *12*(2).

Chapter 2: Co-Authorship Statement

The following details my role in the preparation of the manuscript.

Research Design

Methodology was developed based on previous research by Dr. David Behm. Discussions with Dr. David Behm helped to refine details of the experiment. With assistance from Dr. David Behm I was able to obtain approval from the Interdisciplinary Committee on Ethics in Human Research (ICEHR) to conduct this research.

Data Collection

Data was collected by me with assistance from Ms. Emily Colwell, Mr. Gregory Furlong, Mr. Mitchel Elliott, Mr. Zachary Thorne, Mr. Jeff Combden, Ms. Rebecca Dyer, Mr. Ryan George, and Ms. Shania Clancey, and supervision from Dr. David Behm.

Data Analysis

I performed all data analysis procedures.

Manuscript Preparation

I wrote the manuscript with assistance from Dr. David Behm.

Chapter 3: Manuscript

Title: Evidence for the co-existence of non-local fatigue and potentiation

Authors: Gerard MJ Power, Emily Colwell, Gregory Furlong, Mitchel Elliott, Zachary Thorne, Jeff Combden, Rebecca Dyer, Ryan George, Shania Clancey and David G Behm

Institution: School of Human Kinetics and Recreation
Memorial University of Newfoundland
St. John’s, Newfoundland and Labrador, Canada, A1M 3L8

3.1 Abstract

Introduction: Post-activation potentiation (PAP) is an increase in twitch torque following an appropriate conditioning activity. Whereas post-activation performance enhancement (PAPE) is an overall improvement to muscle performance. A coexistence of PAP and fatigue has been reported. With evidence of fatigue in unconditioned muscles, the purpose of this study was to determine if a PAP conditioning protocol could cause non-local PAPE. **Methods:** Thirty-two participants were split into two groups; one conditioned the dominant quadriceps (D-ND) and the other conditioned the non-dominant (ND-D). A testing protocol was performed before and one and ten minutes after a high intensity, low volume conditioning protocol (2 sets of 2 x 5s maximum voluntary isometric contractions (MVIC)). The testing protocol included a MVIC, drop jump (DJ), countermovement jump (CMJ) and reaction time (RT) test. **Results:** There were four significant ($p < .05$) non-local effects, including a decrease in MVIC performance for the D-ND group ($d = 0.61$), an increase in MVIC performance for the ND-D group ($d = 0.21$), a decrease in DJ performance for the D-ND group ($d = 0.05$), and an increase in DJ performance for the ND-D group. There were also several significant ($p < .05$) main effects for time, including performance decrements at one-minute post (MVIC ($d = 0.29$), DJ ($d = 0.22$)), and decrements (MVIC ($d = 0.30$), DJ ($d = 0.21$)) and enhancements (CMJ ($d = 0.07$), RT ($d = 0.26$)) at ten-minutes post. **Discussion:** Overall, there was evidence for performance changes with the conditioning activity, however there was a high inter-individual variability. Some participants had improvements following the conditioning activity, while others had decreases in performance. These findings give early evidence that unilateral exercise does not only cause fatigue in contralateral muscles, but can also lead to enhancements, which can benefit both sport performance and rehabilitation settings.

Keywords*:* *post-activation potentiation; post-activation performance enhancement; fatigue*

3.2 Introduction

Post-activation potentiation (PAP) is a neuromuscular phenomenon which can increase force, and rate of force development following a conditioning stimulus (Hodgson et al., 2005). The conditioning stimulus to elicit PAP is often a maximum or near maximum voluntary contraction (Houston et al., 1985; Houston & Grange, 1990; Stuart et al., 1988; Vandervoort et al., 1983). The presence of PAP can be assessed in studies by measuring changes in peak twitch tension following the conditioning stimulus (Alway et al., 1987; Belanger & Quinlan, 1982; Green & Jones, 1989; Hamada et al., 1997). The most commonly cited mechanism for this increase in peak twitch tension is the intramuscular phosphorylation of myosin light chains (Grange et al., 1993; Houston et al., 1985; Houston & Grange, 1990; Sweeney et al., 1993; Vandenboom et al., 1995; Vandervoort et al., 1983). Recently, this phosphorylation has been described as the “classic” PAP (Blazevich & Babault, 2019). This PAP has a relatively short time course, with a half-life of around 30 seconds (Vandervoort et al., 1983).

However, some PAP studies have used external performance measures to assess PAP such as jump performance (Chiu et al., 2003; French et al., 2003; Gourgoulis et al., 2003; Gullich & Schmidtbleicher, 1996; Jensen & Ebben, 2003; Jones & Lees, 2003; Nibali et al., 2015; Scott & Docherty, 2004; Witmer et al., 2010; Young et al., 1998) and power (Baker, 2003; Duthie et al., 2002; Gossen & Sale, 2000; Hrysomallis & Kidgell, 2001; Mola et al., 2014). In some of these studies, PAP effects have been measured several minutes following the conditioning stimulus (Baker, 2003; Chiu et al., 2003; Gullich & Schmidtbleicher, 1996; Young et al., 1998). This time-course does not follow that of the myosin phosphorylation, and therefore suggests that there are likely other contributing mechanisms. These potentiation effects have been termed post-activation performance enhancements (PAPE) to distinguish them from the “classic” PAP, which is related to myosin phosphorylation (Blazevich & Babault, 2019).

Compared to the consistent increases in peak twitch tension with PAP studies, the effects upon external performance measures are much more variable. While a number of studies showed evidence of potentiation of voluntary measures (PAPE) (Baker, 2003; Chiu et al., 2003; Duthie et al., 2002; French et al., 2003; Gourgoulis et al., 2003; Gullich & Schmidtbleicher, 1996; Young et al., 1998); others did not (Gossen & Sale, 2000; Hrysomallis & Kidgell, 2001; Jensen & Ebben, 2003; Jones & Lees, 2003; Scott & Docherty, 2004), and some presented variable findings (Mola et al., 2014; Nibali et al., 2015; Witmer et al., 2010). The type of conditioning activity, testing and training status of the participant appeared to play a critical role in eliciting PAPE in these aforementioned studies. Differences in the volume and intensity of the exercise contrast the conditioning activities in studies with improved performance to studies with a lack of improvements. For example, studies with no significant PAPE used relatively higher volumes of repetitions (5-10) at lower intensities (Gossen & Sale, 2000; Hrysomallis & Kidgell, 2001; Jensen & Ebben, 2003; Jones & Lees, 2003; Scott & Docherty, 2004), while the studies demonstrating potentiation emphasized higher, explosive intensities, with less than five repetitions (Chiu et al., 2003; Duthie et al., 2002; French et al., 2003; Gourgoulis et al., 2003; Gullich & Schmidtbleicher, 1996; Young et al., 1998). The literature also shows that, in general, strong and resistance trained participants had a higher incidence of performance enhancement (Chiu et al., 2003; Duthie et al., 2002; Gourgoulis et al., 2003) compared to recreationally trained participants (Gossen & Sale, 2000; Hrysomallis & Kidgell, 2001; Jones & Lees, 2003; Scott & Docherty, 2004).

The testing protocols also could have impacted the ability to measure performance enhancement. First of all, according to the concept of training specificity (Behm & Sale, 1993), it is important that the testing exercises are specific to the conditioning exercise. Having specificity will ensure that the appropriate muscles and movement patterns are targeted. While most studies target similar muscles for the conditioning and testing exercise, there is extensive variety in the timing of the testing protocols. In a number of studies, PAPE tends to occur approximately five minutes after the conditioning exercise (Baker, 2003; Chiu et al., 2003; Gullich & Schmidtbleicher, 1996; Young et al., 1998), whereas PAPE is often not evident when tested immediately post-conditioning activity (Hrysomallis & Kidgell, 2001; Jensen & Ebben, 2003; Jones & Lees, 2003). The lack of PAPE with immediate post-testing may be related to the coexistence of PAP and fatigue (Behm, 2004; Behm et al., 2004; Rassier & MacIntosh, 2000). External manifestations of PAP may not be evident if fatigue processes are more predominant (Behm, 2004). The timing of the PAP and fatigue processes (Vandenboom & Houston, 1996) is one reason why the detection of PAPE with functional voluntary measures is so variable.

Muscle fatigue mechanisms have been identified at the muscle (Jami et al., 1983; Sjogaard et al., 1986), motoneuron (Bellemare & Garzaniti, 1988; Stephens & Taylor, 1972), spinal cord (Bigland-Ritchie et al., 1986; Maton & Gamet, 1989), and brain (Bergstrom & Hultman, 1988; Bigland-Ritchie et al., 1982; Dietz, 1978). Although the effects of fatigue and PAP on subsequent performance are intertwined (Behm, 2004; Rassier & MacIntosh, 2000), the scientific literature on PAP-related neural mechanisms is not conclusive. Strong evidence for neural mechanisms are evident with crossover or non-local muscle fatigue studies (unilateral fatigue of a muscle group leads to fatigue of contralateral, homologous or heterologous muscles)(Halperin et al., 2015; Martin & Rattey, 2007; Matsuura & Ogata, 2015; Rasmussen et al., 2010; Takahashi et al., 2011). Similar crossover or global effects have been reported with unilateral stretching (Behm et al., 2016; Chaouachi et al., 2015) and foam rolling (Aboodarda et al., 2015; Kelly & Beardsley, 2016). The only study to examine crossover effects of a unilateral conditioning exercise reported potentiation of the conditioned leg but significant impairments of the homologous, contralateral limb (Andrews et al., 2016). More studies are necessary to determine possible neural contributions to PAPE with the use of a crossover limb design.

Cross education studies have demonstrated a crossover effect from the dominant to the non-dominant side (Andrushko et al., 2018; Farthing et al., 2005, 2009, 2011), however, the crossover effects from non-dominant to dominant side are usually found to be weaker or absent (Farthing, 2009; Farthing et al., 2005; Imamizu & Shimojo, 1995; Parlow & Kinsbourne, 1989; Stoddard & Vaid, 1996). However, there are also studies that show a symmetry in the direction of crossover (Coombs et al., 2016; Othman et al., 2019). To this point, there have been no studies investigating if there are differences in the crossover direction for PAPE studies, and therefore it would be beneficial to explore.

Having a better understanding of the mechanisms contributing to PAPE and how the conditioning activity and training status of the participant affects the timing of the enhancements is important for both the fields of athletic performance and rehabilitation. In terms of athletic performance training methods and warm-up routines could be established which can help athletes enhance performance of targeted muscles at specific times to either improve their training or improve performance in their specific discipline. In terms of rehabilitation, a stronger muscle or side could be conditioned in order to potentiate weak or injured muscle(s) and improve the effectiveness of the rehabilitation exercises.

The objective of this study was to examine the crossover effects using voluntary conditioning stimuli between dominant and non-dominant leg on unilateral MVIC, jump performance and reaction time of the knee extensors among resistance- and recreational trained participants. It was hypothesized that there would be performance enhancements in the exercised quadriceps as well as the contralateral non-exercised quadriceps; albeit of a lower magnitude.

3.3 Methods

Participants

Based on three prior potentiation studies using voluntary conditioning stimuli (Andrews et al. 2016, Boullosa et al. 2013, Low et al. 2019) a statistical, “a priori” power analysis of force measures (G*Power (software package 3.1.9.2, Dusseldorf, Germany) to achieve an alpha of 0.05 with a power of 0.8 indicated that 14-30 participants would be needed to achieve sufficient power. Hence, a purposeful sample of 32 participants (16 males; age: 22.9 ± 2.03 years; height: 180.5 ± 5.92 cm; weight: 82.8 ± 9.43 kg, and 16 females; age: 23.1 ± 2.80 years; height: 166.6 ± 7.35 cm; weight: 66.4 ± 11.09 kg;) volunteered to take part in the study. Of the 32 participants, 16 were considered recreationally trained (regularly participating in physical activity for recreational purposes), and 16 were considered athletically trained (an athlete on a varsity or provincial sports team). The dominant leg of each participant was determined by asking which leg they would use to kick a soccer ball. Each participant was required to complete a physical activity readiness questionnaire (PAR-Q) with no positive responses and read and sign the informed consent form before participating in the study. Exclusion criteria included any neurological conditions or serious musculoskeletal injuries in the past year. The Interdisciplinary Committee on Ethics in Human Research (ICEHR) of the Memorial University of Newfoundland approved the study (Approval #: 20171234-HK).

Research Design

The study followed a two-group mixed design. In order to examine the influence of limb dominance, participants were randomly assigned to either the dominant to non-dominant (D-ND) group or the non-dominant to dominant (ND-D) group. Based on the tendency for greater potentiation in strength trained individuals (Chiu et al., 2003; Duthie et al., 2002; Gossen & Sale, 2000; Gourgoulis et al., 2003; Hrysomallis & Kidgell, 2001; Jones & Lees, 2003; Scott & Docherty, 2004), the randomization was controlled to ensure an equal number of recreationally trained and athletically trained participants. Participants attended the lab on four different days, separated by a minimum of 48 hours, to complete four different sessions in a random order. The four sessions included one intervention and control day per leg. The conditioning intervention was always performed on the dominant leg for the D-ND group and always performed on the non-dominant leg for the ND-D group. The rest on control days was equal to the length of the intervention. A testing protocol was performed immediately before the voluntary conditioning intervention, and 1- and 10-minutes after the intervention. The tests consisted of a unilateral maximum voluntary isometric contraction (MVIC) of the knee extensors, single-leg drop jump (DJ), single-leg countermovement jump (CMJ), and unilateral reaction time test. Due to practical reasons related to equipment preparation and time constraints, the testing protocol always began with the MVIC, followed by the DJ, the final two tests, the CMJ and reaction time test were then randomized for each participant, on each day.

Experimental Protocol

Each day followed the same protocol. First, participants were prepared with electromyography (EMG) electrodes for the vastus lateralis (VL), and biceps femoris (BF). VL was chosen as an indicator of changes to the agonist muscle group, while BF was chosen in order to detect if there was any change in co-contraction during the study. The midpoint of each muscle, halfway between the anterior superior iliac spine and the top of the patella for VL and halfway between the gluteal fold and the popliteal space for the BF, and the lateral condyle of the tibia were marked to identify where the two muscle points and the ground (Cavanaugh et al., 2017), respectively, would be located for EMG electrodes. Each location was prepared by shaving any hair, removing dead skin cells with an abrasive pad, and cleaning the area with an alcohol swab. Researchers placed two recording electrodes (1-cm 162 Ag/AgCl; MediTrace 133, Kendall, Technical products Toronto, Ontario, Canada) at each of the specified muscle locations, two centimetres apart, parallel to the muscle fibre, and one recording electrode was placed on the fibular lateral condyle, acting as the ground electrode. Once the resting EMG was checked for a low noise signal (<0.05 mV amplitude), the participant began their warm-up. Electrode placement was traced with a permanent marker to allow for consistent placement between days.

The warm-up consisted of 5 minutes on a cycle ergometer (Monark Ergomedic 828E Exercise Test Cycle, Monark Exercise AB, Vansbro, Sweden) with 1 kilopond of resistance at 70 revolutions per minute, followed by ten isometric knee extension contractions at 50% of their perceived maximal intensity on the leg to be tested. One minute after the warm-up, the pre-test protocol began with the MVIC test, followed by the DJ test. EMG was recorded for both of these tests. Researchers removed EMG leads, and the CMJ test and reaction time test were performed in a random order. Immediately following the pre-test, either the intervention or control protocol was performed. Upon completion of the intervention or control, a 1- and 10-minute post-test was performed. Participants returned to the lab three more times to complete the other sessions.

Testing Protocol

The testing protocol consisted of four different unilateral exercises, a knee extension MVIC, DJ, CMJ and reaction time test.

Knee Extension Maximum Voluntary Isometric Contraction (MVIC)

For the MVIC, the participant was seated on a specially made table with an adjustable backrest (constructed by Technical Services of Memorial University of Newfoundland). Researchers positioned participants so that when they were in an upright, comfortable position, the backrest was flush against their back, and the crease of their knees was on the edge of the table. Restraints were put in place across the participant's chest and thighs to stabilize them. The tested leg was inserted in a strap, attached to a chain that was hooked into a load cell containing a Wheatstone bridge strain gauge (Omega Engineering Inc., LCCA 250, St. Eustache, Quebec, Canada) so that the knee was flexed at approximately 80 degrees (visual inspection with goniometer). During the MVICs, the participant would cross their arms over their chest and be instructed to push against the strap as hard and fast as possible, and researchers provided verbal encouragement throughout the contraction. Two MVICs were performed with one minute of rest between if the second MVIC was greater than 5% larger than the first, a third and final MVIC was performed a minute later.

Drop Jump (DJ)

For the DJ, the participant was positioned on top of a step with three pairs of risers underneath, totalling 25.4 cm in height. Participants stood on the untested leg, with the leg to be tested positioned in front of the step, over the force plate (Advanced Mechanical Technology Inc; BP400600HF-2000, Watertown MA, USA) and arms in the akimbo position. Participants were instructed to drop onto the force plate passively, then once their foot made contact with the force plate, to jump straight up as quickly and as high as possible, before once again making contact with the force plate on the landing. Two DJ trials were performed; if participants did not follow the proper DJ protocol, they were required to repeat the trial.

Countermovement Jump (CMJ)

For the CMJ, the participant was positioned to the side of a Vertec vertical jump tester, balancing on their tested leg with their arms extended in front of them. The participant was oriented so that their dominant arm, the arm they felt most comfortable reaching with, was closest to the Vertec testing device. The Vertec was set up so that when the participant was standing with their feet flat and dominant arm reaching up as high as possible, they could reach the first vane and only the first vane. Participants were instructed to squat down on their tested leg and without a pause, jump up as high as they could, reach for the vanes with their dominant arm, and land on two feet. A minimum of two jumps were performed; if the participants jump increased by 5.08 cm (4 vanes) or more, a third jump was performed.

Reaction Time Test

The reaction time device was built by the Memorial University Technical Services (St. John’s NL, Canada) and consisted of two push buttons, 40 cm apart, installed on a box, positioned on the floor, a switch, which activated a light and signalled the beginning of the test; and two clocks. The participant was positioned so that the foot of their tested leg was rested on one of the buttons, and the other leg was positioned along the side of the box. They were in the akimbo position. The participant was instructed to focus on the second button and the light, and once the light turned on, to move as quickly as possible to the second button. Both clocks began as soon as the switch was activated, the first clock stopped when the foot was released from the first button (reaction time), and the second clock stopped when the foot pressed the second button (movement time). A total of two reaction and movement time tests were performed.

Intervention Protocol

Four different sessions were performed for each participant:

1) Dominant control day: Testing protocols performed on the dominant leg, 6 minutes and 20 seconds rest between pre-test and 1-minute post-test.
2) Non-dominant control day: Testing protocols performed on the non-dominant leg, 6 minutes and 20 seconds of rest between pre-test and 1-minute post-test
3) Ipsilateral intervention day: Intervention and testing protocol performed on the dominant leg for the D-ND group and non-dominant leg for the ND-D group.
4) Contralateral intervention day: Intervention protocol performed on the dominant leg for the D-ND group and a non-dominant leg for the ND-D group, testing protocols performed on the contralateral leg.

The conditioning intervention consisted of four repetitions of five-second knee extension MVICs. The same equipment setup was used as with the testing MVIC. Participants were instructed to push as hard and fast as possible against the strap and were given verbal encouragement during each repetition. One-minute of rest was given after the first and third repetition, and three-minutes of rest was given after the second repetition. The total duration of the intervention was 5 minutes and 20 seconds.

Data Analysis

Knee Extension Maximum Voluntary Isometric Contraction

Peak force and instantaneous strength (the force produced in the first 100 milliseconds (F100) of the MVIC: Grabow et al. 2017, Low et al. 2019) was recorded. EMG of the VL and BF was recorded, filtered using a bandpass filter and the root mean square of the rectified EMG over a one second period at the peak of the MVIC (500ms before and after the peak force) was calculated using AcqKnowledge III software (Biopac Systems Inc., Holliston, MA).

Drop Jump

Initial contact time and flight time measured by the force plate were recorded. Using this data and calculations, jump height and reactive strength index (RSI) were determined.

Jump height = $^1/_2\, g(^t/_2)^2$, where g = 9.81 m/s$_2$, t = flight time in the air (s) (Moir,

2008) RSI = jump height (m) / contact time (s) (Flanagan et al., 2008)

Countermovement Jump

The Vertec device was able to determine jump height to the nearest 0.5 inch. Participants' peak jump was recorded in inches and converted to metres.

Reaction and Movement Time

The reaction time test measured reaction time and total response time (from test start to push of the second button). Reaction time was subtracted from response time to determine movement time.

Statistical Analysis

Statistical analyses were completed using the SPSS software (Version 23.0, SPSS, Inc. Chicago, IL). The assumption of sphericity and normality were tested for all dependent variables and if a violation was noted, the corrected values for non-sphericity with Greenhouse-Geisser were reported. Each dependent variable was analyzed using a separate 3 (Times; Pre, 1Post, 10Post) x 2 (Conditions; Control, Intervention) x 2 (Conditioned Leg; Dominant, Non-Dominant) x 2 (Tested Leg; Exercised, Contralateral) mixed-design analysis of variance (ANOVA) with repeated measures (within-group) on the first two factors and between-group measures on the last two factors. Significance was set at $p \leq 0.05$. If significant main or interaction effects were found, a simple planned contrast analysis was performed. Cohen's "d" effect sizes were assessed to determine the magnitude of differences. Classifications of the effect sizes were in accordance with Cohen (small: $d < 0.5$; medium: $0.5 \leq d < 0.8$; large: $d \geq 0.8$) (Cohen 1988).

3.4 Results

Maximum Voluntary Isometric Contraction Variables

Peak Force and F100

There was a significant interaction effect between condition, time, group and leg being tested on F100 performance ($F_{(2, 120)} = 3.105$, $p = .048$). The first contrast showed a significant difference of condition, group and leg being tested between the pre-test and the 1-minute post-test. Means revealed that for the D-ND group, for the contralateral (non-dominant) leg, F100 values were similar during the pre-test, for both conditions, however during the 1-minute post-test, there was a greater decrease in performance during the intervention condition (-16.1%, d = 0.61), compared to the control condition (-4.9%, d = 0.21, figure 1). However, in the exercised (dominant) leg of the D-ND group, initially, there were higher values during the control condition compared to the intervention condition in the pre-test, but at the 1-minute post-test, there was an increase in performance during the intervention condition (3.9%, d = 0.13), and a decrease in performance during the control condition (-16.8%, d = 0.57, figure 1). With the ND-D group, for the contralateral (dominant) leg, pre-test values were 18.1% higher in the control condition (d = 0.53), but at 1-minute post-test, performance decreased during the control condition (-5.7%, d = 0.21) and increased during the intervention condition (8.0%, d = 0.21, figure 1). Finally, for the exercised (non-dominant) leg of the ND-D group, values were similar for both conditions during the pre-test, but at 1-minute post-test, there was a greater decrease in performance during the control condition (-14.8%, d = 0.47), compared to the intervention condition (-6.1%, d = 0.22, figure 1). The second contrast comparing condition, group, and leg being tested at pre-test, and 10-minute post-test, was not significant ($F_{(1,60)} = 2.519$, $p = .118$) . Finally, there was a significant effect of group on F100 performance ($F_{(1, 60)} = 4.952$, $p = .030$). The D-ND group had a 7.1% greater F100 than the ND-D group ($d = 0.23$).

There was a significant effect of group on MVIC peak force ($F_{(1, 60)} = 4.201$, $p = .045$). Group means showed that the D-ND group had a 15.5% greater peak force than the ND-D group ($d = 0.50$). There was a significant main effect of time on F100 performance ($F_{(2, 120)} = 9.096$, $p < .001$). Contrasts showed that there was a decreased F100 at 1- (-8.5%, $d = 0.29$) and 10-minutes (-8.5%, $d = 0.30$) post-test compared to the pre-test.

EMG

There was a significant effect of group on BF EMG ($F_{(1, 60)} = 14.543$, $p < .001$). Group means showed that the D-ND group had 122.6% higher BF EMG activity than the ND-D group ($d = 0.83$). There was also a significant effect of leg being tested on BF EMG ($F_{(1, 60)} = 4.048$, $p = .049$). Means showed that there was 17.7% greater BF EMG activity in the exercised leg compared to the contralateral leg ($d = 0.35$). There were no significant effects of time ($F_{(2,120)} = 3.105$, $p = .066$) or condition ($F_{(1,60)} = 0.606$, $p = .44$) for VL EMG.

Drop Jump

Contact Time

There was a significant interaction effect between condition, group, and leg being tested ($F_{(1, 60)} = 7.482$, $p = .008$). Contrasts revealed that, compared to the control condition, the intervention condition had 2.1% ($d = 0.11$) and 4.1% ($d = 0.21$) longer contact times for the contralateral and exercised leg, respectively, of the ND-D group and the contralateral leg of the D-ND group had a 4.0% ($d = 0.29$) longer contact time. While, the exercised leg of the D-ND group had a 5.9% shorter contact time ($d = 0.41$).

There was a significant main effect of time on DJ contact time ($F_{(2, 120)} = 10.02$, $p < .001$). Contrasts revealed that compared to the pre-test, contact time increased (decreased performance) 3.7% at 1-minute (d = 0.22), and 3.4% at 10-minutes post-test (d = 0.21).

Jump Height

There was a significant interaction effect between time, group and leg being tested ($F_{(2,120)} = 4.757$, $p = .010$). The first contrast revealed a significant effect of group and leg being tested between the pre-test and one-minute post-test. Means revealed that, compared to the pre-test, regardless of the condition, the D-ND group had a small 1.8% increase in jump height for the exercised leg (d = 0.05) and a small 1.7% decrease in jump height for the contralateral leg (d = 0.05) at 1-minute post-test. For the ND-D group, compared to the D-ND group, the changes were greater. Regardless of condition, at the 1-minute post-test there was a decrease in jump height for the exercised leg (-5.5%, d = 0.18) and an increase in jump height for the contralateral leg (4.6%, d = 0.16) compared to the pre-test. The second contrast showed no significant effect of group and leg being tested between the pre-test and ten-minute post-test ($F_{(1,60)} = 0.692$, $p = .409$).

RSI

There was a significant ($F_{(2, 120)} = 3.853$, $p = .024$) main effect of time on RSI performance. Contrasts indicated that compared to the pre-test, RSI performance showed trivial magnitude decreases of 3.1% at 1-minute (d = 0.08) and 3.1% at 10-minutes post-test (d = 0.08).

Countermovement Jump

Jump Height

There was a significant ($F_{(2, 120)} = 8.693$, $p < .001$) main effect of time on CMJ jump height. Contrasts showed that compared to the pre-test, jump height was a trivial magnitude

1.8% greater at 10-minutes post-test (d = 0.07). There was also a significant effect of group on jump height ($F_{(1,60)}$ = 5.129, p = .027). Group means showed that D-ND group performed 14.9% better overall than the ND-D group (d = 0.56).

Reaction Time Test

Reaction and Movement Time

There was a significant ($F_{(2, 120)}$ = 4.711, p = .011) main effect of time on reaction time. Contrasts indicated that compared to pre-test, reaction time was 4.6% less (increased performance) during the ten-minute post-test (d = 0.26). There were no significant movement time effects.

3.4 Discussion

Overall, the experimental protocol caused variable changes to performance. The first set of findings worth noting is that of the 10 variables, 5 variables had a significant main effect for time. Of these, two variables, CMJ jump height (1.8%) and reaction time (4.6%), had performance enhancements at 10-minutes post-test compared to pre-test and three variables, F100 (-8.5% at both 1- and 10-minutes post), DJ CT (-3.7% at 1-minute post and -3.4% at 10-minutes post) and RSI (-3.1% at both 1- and 10-minutes post) had performance decrements compared to pre-test. For these variables, with control and intervention measures combined, there was an effect on performance from pre- to post-test. Therefore, it appears that the testing protocol interacted with the intervention protocol, and both had an effect on subsequent performance.

Previous PAPE studies that measured changes in functional performance such as the current study, also have evidence for variable findings. There were some studies, that had relatively clear evidence of performance enhancements without any decrements (Baker, 2003;

Gourgoulis et al., 2003; Gullich & Schmidtbleicher, 1996; Young et al., 1998), but it was more common for PAPE-type studies to have variability, including possible evidence for fatigue (Chiu et al., 2003; Duthie et al., 2002; French et al., 2003; Gossen & Sale, 2000; Hrysomallis & Kidgell, 2001; Jensen & Ebben, 2003; Jones & Lees, 2003; Scott & Docherty, 2004).

The main reason for the variability in performance changes was thought to be related to the coexistence of fatigue and potentiation (Chiu et al., 2003; Duthie et al., 2002; French et al., 2003; Gossen & Sale, 2000). As the literature has already established, performance measures are determined by the interaction of fatigue and potentiation (Behm, 2004; Behm et al., 2004; Rassier & MacIntosh, 2000). Chiu et al. (2003) explains how the fatigue effect is of a high amplitude but short duration, while performance enhancement is present at a lower amplitude but longer duration. As a result, as the effect of fatigue diminishes, performance enhancements have been found. This would explain why the two enhancements in performance of the present study were found during the 10-minutes post-test. Additionally, there has been evidence to show that if the total volume of MVCs exceeds 10-seconds, the resultant fatiguing effects could overcome the potential potentiation effects (French et al., 2003; Vandervoort et al., 1983). The conditioning protocol of the present study had an MVC volume that exceeded 10-seconds, and even on control days, when these conditioning MVCs were not performed, the pre-test required participants to perform 2-3 MVCs of 4 seconds, which could have increased the volume to over 10-seconds. The study by Gullich and Schmidtbleicher (1996) did have conditioning MVCs that exceeded 10-seconds. However, they also had more rest during their study, which could have allowed time for the fatiguing effects to decrease.

In addition to the significant effects of time on several variables, there were also some significant interaction effects of the group and leg being tested with time and condition. Starting with the exercised leg of the D-ND group, from pre-test to 1-minute post-test, F100 increased by 3.9% during the intervention condition and decreased by 16.8% during the control condition. This significant interaction gives evidence that the conditioning protocol had a PAPE effect on F100 performance for the conditioned leg. This change to F100 occurred without any significant changes to MVC peak force. This finding demonstrates two important concepts. The first concept is that PAP has been found to more substantially affect rate of force development than force (Sale, 2002). This helps explain why F100, a proxy measure of the rate of force development would improve, without the MVC peak force improving. The second concept is training specificity (Behm & Sale, 1993). Since the conditioning and the testing exercise were both MVCs, there was an increased likelihood of performance enhancements.

The exercised leg of the D-ND group also saw a 5.9% briefer drop jump contact time during the intervention compared to control and an increase in drop jump height of 1.7% from pre-test to 1-minute post-test, regardless of condition. The condition specific difference in contact time, is also evidence that the intervention was successful in inducing PAPE effects to the exercised leg. Like the F100, drop jump contact time is a measurement related to rate of force absorption and development, and this most likely explains why performance was enhanced for this measure with the intervention. The time specific improvement in drop jump height, is not direct evidence that the conditioning protocol induced PAPE, but rather that the combination of the conditioning protocol and the pre-test collectively contributed to an enhancement in drop jump height. These changes to drop jump performance are consistent with the other potentiation studies that used MVICs as the conditioning exercise and measured changes to drop jump performance (French et al., 2003; Gullich & Schmidtbleicher, 1996). Jones and Lees (2003) also investigated drop jump performance, however they recorded no changes. However, they used back squats instead of MVICs as the conditioning exercise. It is possible that the increased energy demand of a multi-jointed exercise like the back squat, may have caused more fatigue and prevented drop jump improvements.

The findings with the exercised leg of the ND-D group are almost completely opposite. F100 performance decreased for both the intervention (6.1%) and control (14.8%) conditions from pre-test to 1-minute post-test, drop jump contact time was 4.1% longer during the intervention condition compared to control, and drop jump height decreased 5.5% from pre-test to 1-minute post-test. There are two differences between the groups that could explain these opposing effects. First, the exercised leg of the D-ND group was the dominant leg, whereas, the exercised leg of the ND-D group was the non-dominant leg. There are conflicting findings, when investigating if there are asymmetries in the lower limbs, similar to those of the upper limbs. There are studies which show enhanced strength, fatigue resistance, coordination, and other functional measures in the dominant leg (Bahamonde et al., 2012; Demura et al., 2001; Desai et al., 2016; Ditroilo et al., 2010; Hunter et al., 2000; Jacobs et al., 2005; Jacobs et al., 1996; Kramer & Balsor, 1990; Ross et al., 2004), however, there are a similar number of studies, which show no significant differences between the dominant and non-dominant leg (Burnie & Brodie, 1986; Greenberger & Paterno, 1995; Hageman et al., 1988; Henderson et al., 1993; Hoffman et al., 1998; Holmes & Alderink, 1984; Lindström et al., 1995; Magalhaes et al., 2004; Masuda et al., 2003; McCurdy & Langford, 2005; Mohtadi et al., 1990; Neumann et al., 1988; Ostenberg et al., 1998; Willems & Ponte, 2013). The pre-test MVC peak force values of the present study show non-significantly different values in the dominant (574 N) and non-dominant leg (565 N). Based on the prior literature and the present findings, it is possible that there is increased strength in the dominant limb contributing to the performance difference, however, there is no clear evidence for this. PAP has been shown to be more predominant in individuals with greater strength (Chiu et al., 2003; Duthie et al., 2002; Gourgoulis et al., 2003), if there were minor muscle strength and endurance asymmetries between the dominant and non-dominant leg, this could have led to a greater influence of fatigue than potentiation in the non-dominant leg. There are no known potentiation studies that have investigated limb differences in PAP or PAPE, however, these findings may indicate that there are differences, and this should be further explored.

The second difference between the groups is the significant between-group differences that were found in the present study. It was found that the D-ND group had a 15.5% greater MVC peak force, a 7.1% greater F100, and a 14.9% higher countermovement jump. Although participants were randomly assigned to their group, there is clear evidence that the D-ND group had increased strength and jumping ability. There is clear evidence to support that stronger (Duthie et al., 2002; Gourgoulis et al., 2003; Kilduff et al., 2008) and more athletic (Chiu et al., 2003) populations have increased levels of PAPE. This seems to be a likely contributor to the evidence of PAPE in the D-ND group, but not in the ND-D group.

As for the contralateral legs, in the D-ND group, F100 decreased for both intervention (16.1%) and control (4.9%) from pre-test to 1-minute post-test, drop jump contact time was 4.0% longer (impaired) in the intervention condition compared to control, and drop jump height was decreased by 1.8% from pre-test to 1-minute post. These effects give indications that there was an overall decrease in performance over time for the contralateral leg of the D-ND group, but also that the conditioning intervention enhanced the influence of fatigue. There are only two relevant crossover PAPE studies to compare to the present study. Andrews et al. (2016) used Bulgarian split squats as the conditioning exercise and found post-intervention deficits to the countermovement jump and no change to the drop jump in the contralateral limb. Hamilton and Behm (2017) conducted a study on non-local muscle fatigue, but in the study, found evidence for enhancements of MVIC force in the contralateral limb following two 100-seconds knee extensor MVICs.

The finding of performance decrements in the present study are similar to the findings of Andrews et al. (2016). They suggested two possible reasons for the performance decrease in the contralateral leg. First, the contralateral leg could have performed better in the pre-test due to the general warm-up that was performed, and the subsequent cooling due to inactivity may have reduced performance during the post-tests (Andrews et al., 2016). Second, the contralateral leg may have been affected by the central fatigue that was caused by the intervention without the benefit of the PAP or PAPE effects that only acted on the previously exercised muscles (Andrews et al., 2016). These mechanisms could also be relevant for the present study. In terms of the muscle warming and cooling, the general warmup was the same in both studies and the time between pre-test and post-test was also similar, so the time course of the muscle temperature could have been similar. In terms of central fatigue, previous research has shown that the effort required to maximally activate muscles will lead to greater central fatigue than a submaximal effort (Kennedy et al., 2013). The decrements in the present study could be due to the central fatigue that is occurring from the required repeated maximal efforts. The testing exercises and the conditioning exercises of the present study were all performed at maximal intensity. The relationship between maximally activating muscles and central fatigue could explain why decreased performance happened on both control and intervention days, and why the additional maximal intensity exercises that were present on the intervention day caused larger decreases in force.

The findings of Hamilton and Behm (2017), do not agree with the findings of the present study. The present study used four 5-second MVCs and elicited fatigue effects in the contralateral leg, while Hamilton and Behm (2017) used two 100-second MVCs and elicited PAP effects. It was postulated that the enhancement was due to enhanced neural mechanisms such as firing frequency, synchronization and recruitment of higher order motor units (Hamilton & Behm, 2017). It is unclear why 200-seconds of MVICs would cause PAPE effects in the contralateral leg, but 20-seconds of MVICs and 3 sets of Bulgarian split squats did not. More research should be performed to confirm if fatiguing protocols can cause improvements in short-term maximal intensity activities of the contralateral leg.

Performance of the contralateral leg of the ND-D group was slightly different. The F100 did also decrease (5.7%) during the control session for the ND-D group, however, it increased 8.0% during the intervention session. This is the strongest evidence for a crossover PAPE effect in this study. The potentiation mechanism is not likely to be due to myosin light chain kinase phosphorylation (“classic” PAP). The more likely mechanisms are those mentioned by Hamilton & Behm (2017) including increases in firing frequency, motor unit recruitment, and enhanced synchronization. The difference between the ND-D group and the D-ND group may be related to the leg being tested. Crossover PAPE effects were seen in this study in the dominant leg. As previously mentioned, there is conflicting evidence related to differences in strength, or fatigability between the dominant and non-dominant leg. The results of the current study do seem to indicate differences with crossover PAPE. While it cannot be said that the dominant leg is stronger or more resistant to fatigue, there is evidence to show improved performance of the dominant limb in more complex activities, such as a single leg hop test (Desai et al., 2016) or kicking a soccer ball (Barbieri et al., 2015; Dörge et al., 2002), where coordination is an essential component . This increased coordination could potentially be a reason for why there are performance enhancements in the dominant leg, but not the non-dominant leg. In other words, the dominant leg may be able to take better advantage of the enhanced synchronization that occurs from the conditioning exercise.

For drop jump measures, contact time was 2.1% longer during the intervention condition compared to control, but drop jump height was shown to have an overall increase of 4.6% from pre-test to one-minute post-test. Potentiation studies have shown increased drop jump height with no changes to contact time (French et al., 2003; Gullich & Schmidtbleicher, 1996). The change in contact time for the contralateral leg of the ND-D group, could be due to altered coordination and synchronization and with a prolonged impulse (force x time) could have enhanced drop jump height performance. It seems possible that similar PAPE effects that improved F100 performance, also improved drop jump performance.

While there were significant changes to performance throughout the study, giving evidence for both fatigue and potentiation. There was just as much evidence that showed no changes in performance. This is consistent with the current PAPE research that shows a high inter-individual variability (Crewther et al., 2011; Lim et al., 2016; Mola et al., 2014; Nibali et al., 2015) and a complex interaction of potentiation and fatigue (Behm, 2004; Behm et al., 2004; Rassier & MacIntosh, 2000; Sale, 2002).

Further analysis was performed for each test score at 1 and 10-minutes post-test which were classified as either a potentiated (improvement of greater than 5%), fatigue (decrement of greater than 5%), or trivial effect (change of 5% or less in either direction). Of the 2,559 test scores, 843 (33%) were classified as potentiation, 991 (39%) were classified as fatigue, and 725 (28%) were classified as trivial. Since there were similar incidences of potentiation and fatigue, the data could not attain significance for potentiation or fatigue effects. This analysis gives evidence that there was a high incidence of changes to performance (72%). However, whether the protocol elicited enhancements or decrements to performance, was highly variable. A study using self-selected rest, has been shown to be more effective at enhancing performance than a pre-determined rest time (do Carmo et al., 2018). The conditioning protocol in the current study, may have shown more evidence for performance enhancement with the use of a self-selected rest interval.

Summary

The present study does provide some evidence for non-local PAPE effects to occur. However, the magnitude and overall presence of these effects was greatly reduced due to the coexistence of fatigue and potentiation. In order for future research to find more convincing findings of non-local potentiation, it is important to continue to understand the coexistence of potentiation and fatigue, particularly as it relates to unconditioned limbs. Inter-individual variability always played an impact on the unpredictability of performance enhancements and decrements in this study. Therefore, it is important for future non-local potentiation studies, that participant characteristics that contribute to potentiation be better understood and that study designs implement a method for better individualizing conditioning and testing protocols.

3.6 References

Aboodarda, S. J., Spence, A.-J., & Button, D. C. (2015). Pain pressure threshold of a muscle tender spot increases following local and non-local rolling massage. *BMC Musculoskeletal Disorders*, *16*(1). https://doi.org/10.1186/s12891-015-0729-5

Alway, S. E., Hughson, R. L., Green, H. J., Patla, A. E., & Frank, J. S. (1987). Twitch potentiation after fatiguing exercise in man. *European Journal of Applied Physiology and Occupational Physiology*, *56*(4), 461–466. https://doi.org/10.1007/BF00417776

Andrews, S. K., Horodyski, J. M., Macleod, D. A., Whitten, J., & Behm, D. G. (2016). The interaction of fatigue and potentiation following an acute bout of unilateral squats. *Journal of Sports Science and Medicine*, *15*(4), 625–632.

Andrushko, J. W., Gould, L. A., & Farthing, J. P. (2018). Contralateral effects of unilateral training: Sparing of muscle strength and size after immobilization. *Applied Physiology, Nutrition and Metabolism*, *43*(11), 1131–1139. https://doi.org/10.1139/apnm-2018-0073

Bahamonde, R., Weyer, J., Velotta, J., & Middleton, A. (2012). Effects of leg dominance on the single leg hop functional test in non-injured adults. *30th Annual Conference of Biomechanics in Sports*, *218*, 31–34.

Baker, D. (2003). Acute effect of alternating heavy and light resistances on power output during upper-body complex power training. *Journal of Strength and Conditioning Research*, *17*(3), 493–497. https://doi.org/10.1519/1533-4287(2003)017<0493:AEOAHA>2.0.CO;2

Barbieri, F. A., Gobbi, L. T. B., Santiago, P. R. P., & Cunha, S. A. (2015). Dominant–non-dominant asymmetry of kicking a stationary and rolling ball in a futsal context. *Journal of Sports Sciences*, *33*(13), 1411–1419. https://doi.org/10.1080/02640414.2014.990490

Behm, D. G. (2004). Force maintenance with submaximal fatiguing contractions. *Canadian Journal of Applied Physiology*, *29*(3), 274–290. https://doi.org/10.1139/h04-019

Behm, D. G., Button, D. C., Barbour, G., Butt, J. C., & Young, W. B. (2004). Conflicting effects of fatigue and potentiation on voluntary force. *Journal of Strength and Conditioning Research*, *18*(2), 365–372.

Behm, D. G., Cavanaugh, T., Quigley, P., Reid, J. C., Silva Monteiro Nardi, P., & Marchetti, P. H. (2016). Acute bouts of upper and lower body static and dynamic stretching increase non-local joint range of motion. *European Journal of Applied Physiology*, *116*, 241–249. https://doi.org/10.1007/s00421-015-3270-1

Behm, D. G., & Sale, D. G. (1993). Velocity specificity of resistance training. *Sports Medicine: Evaluations of Research in Exercise Science and Sports Medicine*, *15*(6), 374–388. https://doi.org/10.2165/00007256-199315060-00003

Belanger, A. Y., & Quinlan, J. (1982). Muscle function studies in human plantar-flexor and dorsi-flexor muscles. *Canadian Journal of Neurological Sciences*, *9*(3), 359.

Bellemare, F., & Garzaniti, N. (1988). Failure of neuromuscular propagation during human maximal voluntary contraction. *Journal of Applied Physiology*, *64*(3), 1084–1093. https://doi.org/10.1152/jappl.1988.64.3.1084

Bergstrom, M., & Hultman, E. (1988). Energy cost and fatigue during intermittent electrical stimulation of human skeletal muscle. *J Appl Physiol*, *65 (4)*, 1500–1505.

Bigland-Ritchie, B., Furbush, F., & Woods, J. J. (1986). Fatigue of intermittent submaximal voluntary contractions: central and peripheral factors. *Journal of Applied Physiology*, *61*(2), 421–429. https://doi.org/10.1152/jappl.1986.61.2.421

Bigland-Ritchie, B., Kukulka, C. G., Lippold, O. C., & Woods, J. J. (1982). The absence of neuromuscular transmission failure in sustained maximal voluntary contractions. *The Journal of Physiology*, *330*(1), 265–278. https://doi.org/10.1113/jphysiol.1982.sp014340

Binder-Macleod, S. A., Dean, J. C., & Ding, J. (2002). Electrical stimulation factors in potentiation of human quadriceps femoris. *Muscle & Nerve*, *25*(2), 271–279. https://doi.org/10.1002/mus.10027

Blazevich, A. J., & Babault, N. (2019). Post-activation potentiation versus post-activation performance enhancement in humans: Historical perspective, underlying mechanisms, and current issues. *Frontiers in Physiology, 10*. https://doi.org/10.3389/fphys.2019.01359

Botelho, S. Y., & Cander, L. (1953). Post-tetanic potentiation before and during ischemia in intact human skeletal muscle. *Journal of Applied Physiology*, *6*(4), 221–228.

Brown, G. L., & Von Euler, U. S. (1938). The after effects of a tetanus on mammalian muscle. *The Journal of Physiology*, *93*(1), 39–60.

Burnie, J., & Brodie, D. (1986). Isokinetic measurement in preadolescent males. *International Journal of Sports Medicine*, *07*(4), 205–209. https://doi.org/10.1055/s-2008-1025759

Cavanaugh, M. T., Aboodarda, S. J., Hodgson, D. D., & Behm, D. G. (2017). Foam rolling of quadriceps decreases biceps femoris activation. *Journal of Strength and Conditioning Research*, *31*(8), 2238–2245.

Chaouachi, A., Padulo, J., Kasmi, S., Othmen, A. Ben, Chatra, M., & Behm, D. G. (2015). Unilateral static and dynamic hamstrings stretching increases contralateral hip flexion range of motion. *Clinical Physiology and Functional Imaging*, *37*(1), 23–29. https://doi.org/10.1111/cpf.12263

Chiu, L., Fry, A., Weiss, L., Schilling, B., Brown, L., & Smith, S. (2003). Postactivation potentiation response in athletic and recreationally trained individuals. *Journal of Strength and Conditioning Research*, *17*(4), 671–677.

Coombs, T. A., Frazer, A. K., Horvath, D. M., Pearce, A. J., Howatson, G., & Kidgell, D. J. (2016). Cross-education of wrist extensor strength is not influenced by non-dominant training in right-handers. *European Journal of Applied Physiology*, *116*(9), 1757–1769. https://doi.org/10.1007/s00421-016-3436-5

Crewther, B. T., Kilduff, L. P., Cook, C. J., Middleton, M. K., Bunce, P. J., & Yang, G. Z. (2011). The acute potentiating effects of back squats on athlete performance. *Journal of Strength and Conditioning Research*, *25*(12), 3319–3325. https://doi.org/10.1519/JSC.0b013e318215f560

Demura, S., Goshi, F., Yamaji, S., & Nagasawa, Y. (2001). Lateral dominance of legs in maximal muscle power, muscular endurance, and grading ability. *Perceptual and Motor Skills*, *93*(1), 11–23. https://doi.org/10.2466/pms.2001.93.1.11

Desai, M. S., Patil, V., & Naik, R. (2016). Assessment of functional performance of lower extremity and effect of leg dominance on the same in young asymptomatic individuals. *International Journal of Physiotherapy and Research*, *4*(2), 1423–1428. https://doi.org/10.16965/ijpr.2016.110

Dietz, V. (1978). Analysis of the electrical muscle activity during maximal contraction and the influence of ischaemia. *Journal of the Neurological Sciences*, *37*, 187–197.

Ditroilo, M., Forte, R., Benelli, P., Gambarara, D., & De Vito, G. (2010). Effects of age and limb dominance on upper and lower limb muscle function in healthy males and females aged 40-

80 years. *Journal of Sports Sciences*, *28*(6), 667–677. https://doi.org/10.1080/02640411003642098

do Carmo, E. C., De Souza, E. O., Roschel, H., Kobal, R., Ramos, H., Gil, S., & Tricoli, V. (2018). Self-selected rest interval improves vertical jump post-activation potentiation. *Journal of Strength and Conditioning Research*, *15*(April), 1. https://doi.org/10.1519/jsc.0000000000002519

Dörge, H. C., Andersen, T. B., SØrensen, H., & Simonsen, E. B. (2002). Biomechanical differences in soccer kicking with the preferred and the non-preferred leg. *Journal of Sports Sciences*, *20*(4), 293–299. https://doi.org/10.1080/026404102753576062

Duthie, G. M., Young, W. B., & Aitken, D. A. (2002). The acute effects of heavy loads on jump squat performance: An evaluation of the complex and contrast methods of power development. *Journal of Strength and Conditioning Research*, *16*(4), 530–538. https://doi.org/10.1519/1533-4287(2002)016<0530:TAEOHL>2.0.CO;2

Farthing, J. P. (2009). Cross-education of strength depends on limb dominance: Implications for theory and application. *Exercise and Sport Sciences Reviews*, *37*(4), 179–187. https://doi.org/10.1097/JES.0b013e3181b7e882

Farthing, J. P., Chilibeck, P. D., & Binsted, G. (2005). Cross-education of arm muscular strength is unidirectional in right-handed individuals. *Medicine and Science in Sports and Exercise*, *37*(9), 1594–1600. https://doi.org/10.1249/01.mss.0000177588.74448.75

Farthing, J. P., Krentz, J. R., & Magnus, C. R. A. (2009). Strength training the free limb attenuates strength loss during unilateral immobilization. *Journal of Applied Physiology*, *106*(3), 730–736. https://doi.org/10.1152/japplphysiol.91331.2008

Farthing, J. P., Krentz, J. R., Magnus, C. R. A., Barss, T. S., Lanovaz, J. L., Cummine, J., Esopenko, C., Sarty, G. E., & Borowsky, R. (2011). Changes in functional magnetic resonance imaging cortical activation with cross education to an immobilized limb. *Medicine and Science in Sports and Exercise*, *43*(8), 1394–1405. https://doi.org/10.1249/MSS.0b013e318210783c

Flanagan, E. P., Ebben, W. P., & Jensen, R. L. (2008). Reliability of the reactive strength index and time to stabilization during depth jumps. *Journal of Strength and Conditioning Research*, *22*(5), 1677–1682. https://doi.org/10.1519/JSC.0b013e318182034b

French, D. N., Kraemer, W. J., & Cooke, C. B. (2003). Changes in dynamic exercise performance following a sequence of preconditioning isometric muscle actions. *Journal of Strength and Conditioning Research*, *17*(4), 678–685. https://doi.org/10.1519/00124278-200311000-00009

Gossen, E., & Sale, D. (2000). Effect of postactivation potentiation on dynamic knee extension performance. *Eur J Appl Physiol*, *83*, 524–530.

Gourgoulis, V., Aggeloussis, N., Kasimatis, P., Mavromatis, G., & Garas, A. (2003). Effect of a submaximal half-squats warm-up program on vertical jumping ability. *Journal of Strength and Conditioning Research*, *17*(2), 342–344. https://doi.org/10.1519/1533-4287(2003)017<0342:EOASHW>2.0.CO;2

Grange, R. W., Vandenboom, R., & Houston, M. E. (1993). Physiological significance of myosin phosphorylation in skeletal muscle. *Canadian Journal of Applied Physiology = Revue Canadienne de Physiologie Appliquée*, *18*(3), 229–242. https://doi.org/10.1139/h93-020

Green, H. J., & Jones, S. R. (1989). Does post-tetanic potentiation compensate for low frequency fatigue? *Clinical Physiology*, *9*(5), 499–514. https://doi.org/10.1111/j.1475-097X.1989.tb01003.x

Greenberger, H. B., & Paterno, M. V. (1995). Relationship of knee extensor strength and hopping test performance in the assessment of lower extremity function. *Journal of Orthopaedic and Sports Physical Therapy*, *22*(5), 202–206. https://doi.org/10.2519/jospt.1995.22.5.202

Gullich, A., & Schmidtbleicher, D. (1996). Potentiation of explosive force. *New Studies in Athletics*, *11*(4), 67–81.

Hageman, P. A., Gillaspie, D. M., & Hill, L. D. (1988). Effects of speed and limb dominance on eccentric and concentric isokinetic testing of the knee. *Journal of Orthopaedic and Sports Physical Therapy*, *10*(2), 59–65. https://doi.org/10.2519/jospt.1988.10.2.59

Halperin, I., Chapman, D. W., & Behm, D. G. (2015). Non-local muscle fatigue: effects and possible mechanisms. *European Journal of Applied Physiology*, *115*(10), 2031–2048. https://doi.org/10.1007/s00421-015-3249-y

Hamada, T., MacDougall, J. D., Sale, D. G., & Moroz, J. (1997). Twitch potentiation of triceps surae and triceps brachii following voluntary contraction in trained athletes and sedentary controls. *Medicine &Science in Sports & Exercise*, *29*(Supplement), 26. https://doi.org/10.1097/00005768-199705001-00153

Hamilton, A. R., & Behm, D. G. (2017). The effect of prior knowledge of test endpoint on non-local muscle fatigue. *European Journal of Applied Physiology*, *117*(4), 651–663. https://doi.org/10.1007/s00421-016-3526-4

Henderson, R. C., Howes, C. L., Erickson, K. L., Heere, L. M., & DeMasi, R. A. (1993). Knee flexor-extensor strength in children. *Journal of Orthopaedic and Sports Physical Therapy*, *18*(4), 559–563. https://doi.org/10.2519/jospt.1993.18.4.559

Hodgson, M., Docherty, D., & Robbins, D. (2005). Post-activation potentiation: Underlying physiology and implications for motor performance. *Sports Medicine*, *35*(7), 585–595. https://doi.org/10.2165/00007256-200535070-00004

Hoffman, M., Schrader, J., Applegate, T., & Koceja, D. (1998). Unilateral postural control of the functionally dominant and nondominant extremities of healthy subjects. *Journal of Athletic Training*, *33*(4), 319–322.

Holmes, J. R., & Alderink, G. J. (1984). Isokinetic strength characteristics of the quadriceps femoris and hamstring muscles in high school students. *Physical Therapy*, *64*(6), 914–918. https://doi.org/10.1093/ptj/64.6.914

Houston, M. E., & Grange, R. W. (1990). Myosin phosphorylation, twitch potentiation, and fatigue in human skeletal muscle. *Canadian Journal of Physiology and Pharmacology*, *68*(7), 908–913. https://doi.org/10.1139/y90-139

Houston, M. E., Green, H. J., & Stull, J. T. (1985). Myosin light chain phosphorylation and isometric twitch potentiation in intact human muscle. *Pflugers Archiv European Journal of Physiology*, *403*, 348–352.

Hrysomallis, C., & Kidgell, D. (2001). Effect of heavy dynamic resistive exercise on acute upper-body power. *Journal of Strength and Conditioning Research*, *15*(4), 426–430. https://doi.org/10.1519/1533-4287(2001)015<0426:EOHDRE>2.0.CO;2

Hughes, J. R., & Morrell, R. M. (1957). Posttetanic changes in the human neuromuscular system. *Journal of Applied Physiology*, *11*(1), 51–57. https://doi.org/10.1152/jappl.1957.11.1.51

Hunter, S. K., Thompson, M. W., & Adams, R. D. (2000). Relationships among age-associated strength changes and physical activity level, limb dominance, and muscle group in women. *Journals of Gerontology - Series A Biological Sciences and Medical Sciences*, *55*(6), 264–273. https://doi.org/10.1093/gerona/55.6.B264

Imamizu, H., & Shimojo, S. (1995). The locus of visual-motor learning at the task or manipulator level: Implications from intermanual transfer. *Journal of Experimental Psychology: Human Perception and Performance*, *21*(4), 719–733.

Jacobs, C., Uhl, T. L., Seeley, M., Sterling, W., & Goodrich, L. (2005). Strength and fatigability of the dominant and nondominant hip abductors. *Journal of Athletic Training*, *40*(3), 203–206.

Jacobs, R., Bobbert, M. F., Jan, G., Schenau, V. I., & Universiteit, V. (1996). Mechanical output from individual muscles during explosive leg extensions: The role of biarticular muscles. *Journal of Biomechanics*, *29*(4), 513–523.

Jami, L., Murthy, K. S., Petit, J., & Zytnicki, D. (1983). After-effects of repetitive stimulation at low frequency on fast-contracting motor units of cat muscle. *The Journal of Physiology*, *340*(1), 129–143. https://doi.org/10.1113/jphysiol.1983.sp014754

Jensen, R. L., & Ebben, W. P. (2003). Kinetic analysis of complex training rest interval effect on vertical jump performance. *Journal of Strength and Conditioning Research*, *17*(2), 345–349.

Jones, P., & Lees, A. (2003). A biomechanical analysis of the acute effects of complex training using lower limb exercises. *Journal of Strength and Conditioning Research*, *17*(4), 694–700. https://doi.org/10.1519/1533-4287(2003)017<0694:ABAOTA>2.0.CO;2

Kelly, S., & Beardsley, C. (2016). Specific and cross-over effects of foam rolling on ankle dorsiflexion range of motion. *International Journal of Sports Physical Therapy*, *11*(4), 544–551.

Kennedy, A., Hug, F., Sveistrup, H., & Guével, A. (2013). Fatiguing handgrip exercise alters maximal force-generating capacity of plantar-flexors. *European Journal of Applied Physiology*, *113*(3), 559–566. https://doi.org/10.1007/s00421-012-2462-1

Kilduff, L. P., Owen, N., Bevan, H., Bennett, M., Kingsley, M. I. C., & Cunningham, D. (2008). Influence of recovery time on post-activation potentiation in professional rugby players. *Journal of Sports Sciences*, *26*(8), 795–802. https://doi.org/10.1080/02640410701784517

Kramer, J. F., & Balsor, B. E. (1990). Lower extremity preference and knee extensor torques in intercollegiate soccer players. *Canadian Journal of Sport Sciences = Journal Canadien Des Sciences Du Sport*, *15*(3), 180—184.

Krarup, C., & Horowitz, S. H. (1979). Evoked responses of the elbow flexors in control subjects and in myopathy patients. *Muscle & Nerve*, *2*(6), 465–477. https://doi.org/10.1002/mus.880020608

Lim, J., Barley, C., & Chua, Y. (2016). Intra complex recovery intervals for acute lower body post activation potentiation in elite badminton athletes. *Journal of Athletic Enhancement*, *5*(5). https://doi.org/10.4172/2324-9080.1000237

Lindström, B., Karlsson, S., & Gerdle, B. (1995). Knee extensor performance of dominant and non-dominant limb throughout repeated isokinetic contractions, with special reference to peak torque and mean frequency of the EMG. *Clinical Physiology*, *15*(3), 275–286. https://doi.org/10.1111/j.1475-097X.1995.tb00518.x

Lloyd, D. (1949). Post-tetanic potentiation of response in monosynaptic reflex pathways of the spinal cord. *The Journal of General Physiology*, *33*(2), 147–170. https://doi.org/10.1085/jgp.33.2.147

Magalhaes, J., Oliveira, J., Ascensao, A., & Soares, J. (2004). Concentric quadriceps and hamstrings isokinetic strength in volleyball and soccer players. *Journal of Sports Medicine and Physical Fitness*, *44*(2), 119–125.

Martin, P. G., & Rattey, J. (2007). Central fatigue explains sex differences in muscle fatigue and contralateral cross-over effects of maximal contractions. *Pflugers Archiv European Journal of Physiology*, *454*(6), 957–969. https://doi.org/10.1007/s00424-007-0243-1

Masuda, K., Kikuhara, N., Takahashi, H., & Yamanaka, K. (2003). The relationship between muscle cross-sectional area and strength in various isokinetic movements among soccer players. *Journal of Sports Sciences*, *21*(10), 851–858. https://doi.org/10.1080/0264041031000102042

Maton, B., & Gamet, D. (1989). The fatigability of two agonistic muscles in human isometric voluntary submaximal contraction: an EMG study. *European Journal of Applied Physiology and Occupational Physiology*, *58*(4), 369–374. https://doi.org/10.1007/bf00643511

Matsuura, R., & Ogata, T. (2015). Effects of fatiguing unilateral plantar flexions on corticospinal and transcallosal inhibition in the primary motor hand area. *Journal of Physiological Anthropology*, *34*(1). https://doi.org/10.1186/s40101-015-0042-x

McCurdy, K., & Langford, G. (2005). Comparison of unilateral squat strength between the dominant and non-dominant leg in men and women. *Journal of Sports Science and Medicine*, *4*(2), 153–159.

Mohtadi, N. G., Kiefer, G. N., Tedford, K., & Watters, S. (1990). Concentric and eccentric quadriceps torque in pre-adolescent males. *Canadian Journal of Sport Sciences*, *15*(4), 240—243.

Moir, G. L. (2008). Three different methods of calculating vertical jump height from force platform data in men and women. *Measurement in Physical Education and Exercise Science, 12*(4), 207–218. https://doi.org/10.1080/10913670802349766

Mola, J. N., Bruce-Low, S. S., & Burnet, S. J. (2014). Optimal recovery time for postactivation potentiation in professional soccer players. *Journal of Strength and Conditioning Research*, *28*(6), 1529–1537. https://doi.org/10.1519/JSC.0000000000000313

Neumann, D. A., Soderberg, G. L., & Cook, T. M. (1988). Comparison of maximal isometric hip abductor muscle torques between hip sides. *Physical Therapy, 68*(4), 496–502. https://doi.org/10.1093/ptj/68.4.496

Nibali, M. L., Chapman, D. W., Robergs, R. A., & Drinkwater, E. J. (2015). Considerations for determining the time course of post-activation potentiation. *Applied Physiology, Nutrition and Metabolism, 40*(11), 1163–1170. https://doi.org/10.1139/apnm-2015-0175

O'Leary, D. D., Hope, K., & Sale, D. G. (1997). Posttetanic potentiation of human dorsiflexors. *Journal of Applied Physiology, 83*(6), 2131–2138. https://doi.org/10.1152/jappl.1997.83.6.2131

Ostenberg, A., Roos, E., Ekdah, C., & Roos, H. (1998). Isokinetic knee extensor strength and functional performance in healthy female soccer players. *Scandinavian Journal of Medicine & Science in Sports, 8*(5), 257–264. https://doi.org/10.1111/j.1600-0838.1998.tb00480.x

Othman, A. Ben, Chaouachi, A., Chaouachi, M., Makhlouf, I., Farthing, J. P., Granacher, U., &

Behm, D. G. (2019). Dominant and nondominant leg press training induce similar contralateral and ipsilateral limb training adaptations with children. *Applied Physiology, Nutrition and Metabolism, 44*(9), 973–984. https://doi.org/10.1139/apnm-2018-0766

Parlow, S. E., & Kinsbourne, M. (1989). Asymmetrical transfer of training between hands: Implications for interhemispheric communication in normal brain. *Brain and Cognition, 11*(1), 98–113. https://doi.org/10.1016/0278-2626(89)90008-0

Rasmussen, P., Nielsen, J., Overgaard, M., Krogh-Madsen, R., Gjedde, A., Secher, N. H., & Petersen, N. C. (2010). Reduced muscle activation during exercise related to brain oxygenation and metabolism in humans. *Journal of Physiology, 588*(11), 1985–1995. https://doi.org/10.1113/jphysiol.2009.186767

Rassier, D. E., & MacIntosh, B. R. (2000). Coexistence of potentiation and fatigue in skeletal muscle. *Brazilian Journal of Medical and Biological Research*, *33*(5), 499–508. https://doi.org/10.1590/S0100-879X2000000500003

Rosenblueth, A., & Morison, R. S. (1937). Curarization, fatigue and Wedensky inhibition. *American Journal of Physiology-Legacy Content, 119*(2), 236–256.

Ross, S., Guskiewicz, K., Prentice, W., Schneider, R., & Yu, B. (2004). Comparison of biomechanical factors between the kicking and stance limbs. *Journal of Sport Rehabilitation*, *13*, 135–150.

Sale, D. (2002). Postactivation potentiation: Role in performance. *British Journal of Sports Medicine, 38*(4), 386–387. https://doi.org/10.1136/bjsm.2002.003392

Scott, S. L., & Docherty, D. (2004). Acute effects of heavy preloading on vertical and horizontal jump performance. *Journal of Strength and Conditioning Research, 18*(2), 201–205.

https://doi.org/10.1519/R-13123.1

Sjogaard, G., Kiens, B., Jorgensen, K., & Saltin, B. (1986). Intramuscular pressure, EMG and blood flow during low-level prolonged static contraction in man. *Acta Physiologica Scandinavica*, *128*(3), 475–484. https://doi.org/10.1111/j.1748-1716.1986.tb08002.x

Standaert, F. G. (1964). The mechanisms of post-tetanic potentiation in cat soleus and gastrocnemius muscles. *The Journal of General Physiology*, *47*(5), 987–1001. https://doi.org/10.1085/jgp.47.5.987

Stephens, J. A., & Taylor, A. (1972). Fatigue of maintained voluntary muscle contraction in man. *The Journal of Physiology*, *220*(1), 1–18. https://doi.org/10.1113/jphysiol.1972.sp009691

Stoddard, J., & Vaid, J. (1996). Asymmetries in intermanual transfer of maze learning in right- and left-handed adults. *Neuropsychologia, 34*(6), 605–608. https://doi.org/10.1016/0028-3932(95)00158-1

Stuart, D. S., Lingley, M. D., Grange, R. W., & Houston, M. E. (1988). Myosin light chain phosphorylation and contractile performance of human skeletal muscle. *Canadian Journal of Physiology and Pharmacology*, *66*(1), 49–54. https://doi.org/10.1139/y88-009

Sweeney, H. L., Bowman, B. F., & Stull, J. T. (1993). Myosin light chain phosphorylation in vertebrate striated muscle: regulation and function. *American Journal of Physiology-Cell Physiology*, *264*(5), C1085–C1095. https://doi.org/10.1152/ajpcell.1993.264.5.c1085

Takahashi, K., Maruyama, A., Hirakoba, K., Maeda, M., Etoh, S., Kawahira, K., & Rothwell, J. C. (2011). Fatiguing intermittent lower limb exercise influences corticospinal and corticocortical excitability in the nonexercised upper limb. *Brain Stimulation*, *4*(2), 90–96. https://doi.org/10.1016/j.brs.2010.07.001

Vandenboom, R., Grange, R. W., & Houston, M. E. (1995). Myosin phosphorylation enhances rate of force development in fast-twitch skeletal muscle. *American Journal of Physiology - Cell Physiology*, *268*(3 37-3). https://doi.org/10.1152/ajpcell.1995.268.3.c596

Vandenboom, R., & Houston, M. E. (1996). Phosphorylation of myosin and twitch potentiation in fatigued skeletal muscle. *Canadian Journal of Physiology and Pharmacology*, *74*(12), 1315–1321. https://doi.org/10.1139/y96-144

Vandervoort, A. A., Quinlan, J., & McComas, A. J. (1983). Twitch potentiation after voluntary contraction. *Experimental Neurology*, *81*(1), 141–152. https://doi.org/10.1016/0014-4886(83)90163-2

von Euler, U. S., & Swank, R. L. (1940). Tension changes during tetanus in mammalian and avian muscle. *Acta Physiologica Scandinavica*, *1*(3), 203–219. https://doi.org/10.1111/j.1748-1716.1940.tb00269.x

Willems, M. E. T., & Ponte, J. P. G. (2013). Divergent muscle fatigue during unilateral isometric contractions of dominant and non-dominant quadriceps. *Journal of Science and Medicine in Sport*, *16*(3), 240–244. https://doi.org/10.1016/j.jsams.2012.06.005

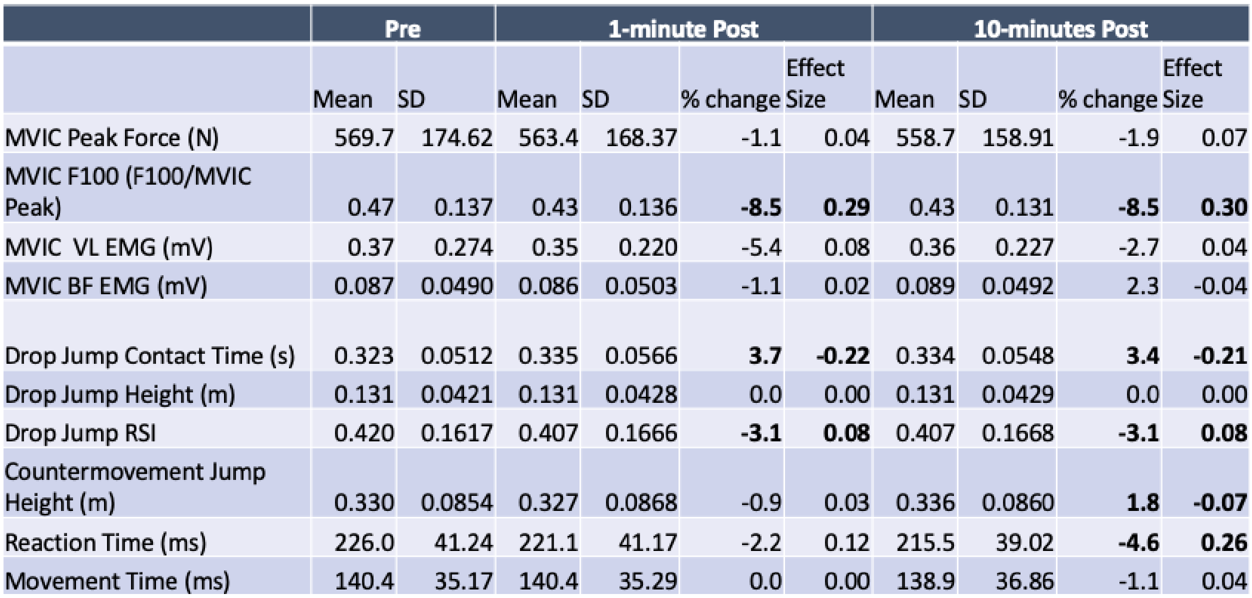
Witmer, C. A., Davis, S. E., & Moir, G. L. (2010). The acute effects of back squats on vertical jump performance in men and women. *Journal of Sports Science and Medicine*, *9*(2), 206–213.

Young, W. B., Jenner, A., & Griffiths, K. (1998). Acute enhancement of power performance from heavy load squats. *The Journal of Strength & Conditioning Research*, *12*(2), 82–84.

3.7 Tables

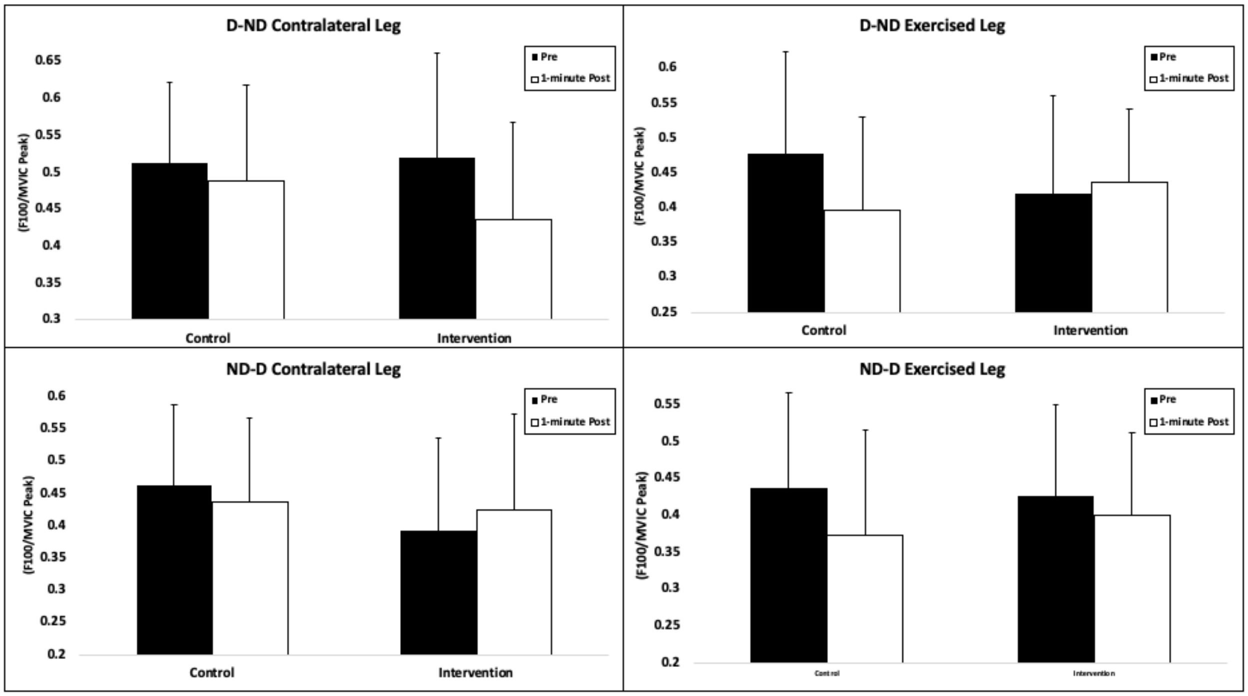
Table 1.

Means and standard deviations of performance measures at pre-test, 1-minute post-test and 10 minutes post-test. Percent changes and effect sizes are provided for the 1-minute and 10-minutes post-tests compared to the pre-test values. Significant differences ($p < .05$) are **bolded**.



	Pre		1-minute Post				10-minutes Post			
	Mean	SD	Mean	SD	% change	Effect Size	Mean	SD	% change	Effect Size
MVIC Peak Force (N)	569.7	174.62	563.4	168.37	-1.1	0.04	558.7	158.91	-1.9	0.07
MVIC F100 (F100/MVIC Peak)	0.47	0.137	0.43	0.136	**-8.5**	**0.29**	0.43	0.131	**-8.5**	**0.30**
MVIC VL EMG (mV)	0.37	0.274	0.35	0.220	-5.4	0.08	0.36	0.227	-2.7	0.04
MVIC BF EMG (mV)	0.087	0.0490	0.086	0.0503	-1.1	0.02	0.089	0.0492	2.3	-0.04
Drop Jump Contact Time (s)	0.323	0.0512	0.335	0.0566	**3.7**	**-0.22**	0.334	0.0548	**3.4**	**-0.21**
Drop Jump Height (m)	0.131	0.0421	0.131	0.0428	0.0	0.00	0.131	0.0429	0.0	0.00
Drop Jump RSI	0.420	0.1617	0.407	0.1666	**-3.1**	**0.08**	0.407	0.1668	**-3.1**	**0.08**
Countermovement Jump Height (m)	0.330	0.0854	0.327	0.0868	-0.9	0.03	0.336	0.0860	**1.8**	**-0.07**
Reaction Time (ms)	226.0	41.24	221.1	41.17	-2.2	0.12	215.5	39.02	**-4.6**	**0.26**
Movement Time (ms)	140.4	35.17	140.4	35.29	0.0	0.00	138.9	36.86	-1.1	0.04

3.8 Figures



D-ND Contralateral Leg

D-ND Exercised Leg

ND-D Contralateral Leg

ND-D Exercised Leg

Figure 1.

Top Left: F100/MVC Peak values during the pre-test and 1-minute post-test on control day and intervention day for the contralateral leg of the D-ND group. **Top Right:** F100/MVC Peak values during the pre-test and 1-minute post-test on control day and intervention day for the exercised leg of the D-ND group. **Bottom Left:** F100/MVC Peak values during the pre-test and 1-minute post-test on control day and intervention day for the contralateral leg of the ND-D group. **Bottom Right:** F100/MVC Peak values during the pre-test and 1-minute post-test on control day and intervention day for the exercised leg of the ND-D group.

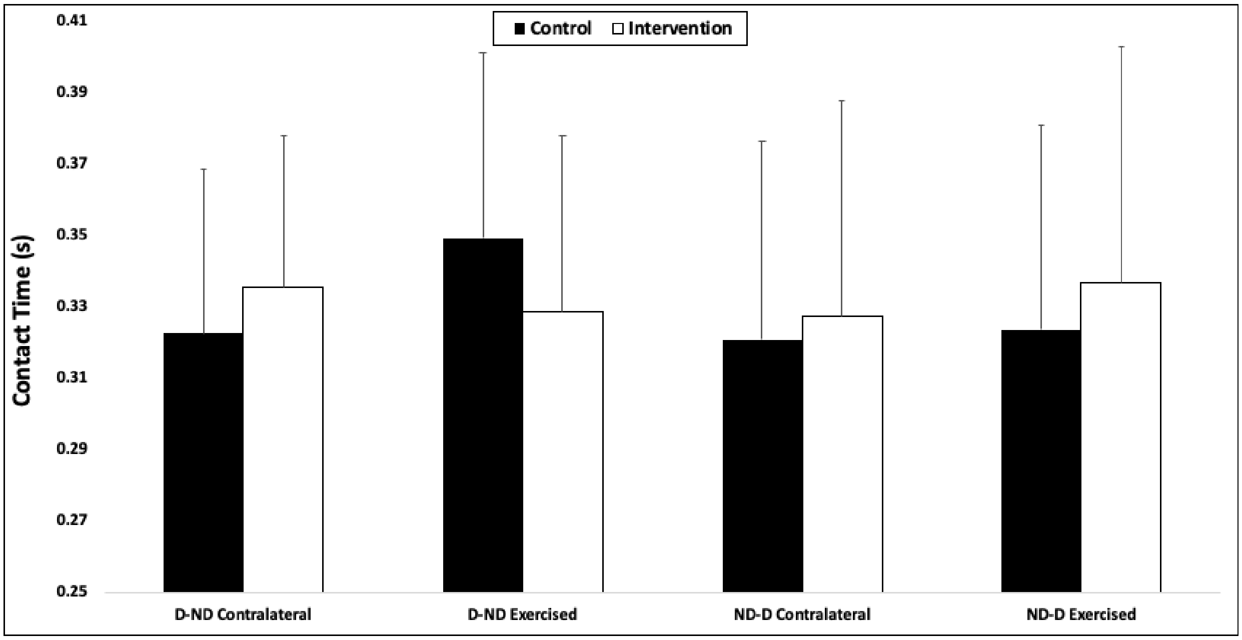


Figure 2.

Contact times during control and intervention days for each leg and each group.

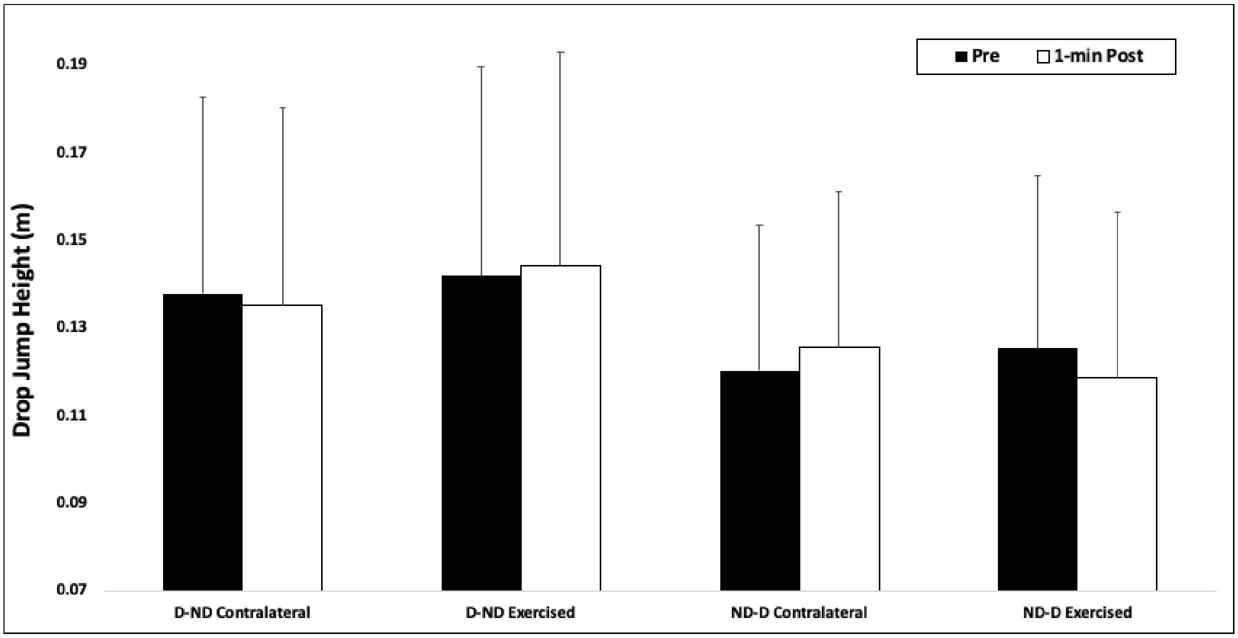


Figure 3.

Drop jump height at pre-test and one-minute post-test for each leg and each group.