THE EFFECT OF AN INVERTED BODY POSITION ON MUSCLE FORCE AND ACTIVATION

NATASHA RUBY PADDOCK

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The Effect of an Inverted Body Position on Muscle Force and Activation

By

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ABSTRACT

Orthostatic pressure changes have been shown to significantly affect sympathetic nervous system responses in order to maintain balance and homeostasis. Neuromuscular responses have not been extensively, if at all, investigated in an inverted body position. Muscle force, activation and other neuromuscular factors are necessary, for instance, to successfully complete escape procedures from a secured inverted seated position of a overturned car or aircraft.

It is known that both central and peripheral factors contribute to muscle force output. With an increase in pressure to levels above the heart in an inverted body position, cerebral blood pooling is likely. Even though there is evidence of a decrement in sympathetic functioning in similar circumstances to inversion, specific vestibulosympathetic responses during inversion are unknown, but possibly contribute to neuromuscular impairment. Peripheral factors such as lower levels of blood flow to the contracting muscles leading to decreased perfusion pressure and an oxygen deficit within the muscle results in a decreased force output. Decreased hydrostatic pressure in areas below the heart during inversion may also be a contributing hindrance to neuromuscular performance, but this has not been demonstrated.

Based on the lack of literature in this area, the following experiment was implemented. Maximal and submaximal voluntary and evoked forces and EMG were recorded, and the contractions were analyzed for peak force, rate of force development and activation with upright and inverted seated positions. It was expected that inversion

induced deficits in muscle force and activation would suggest impairment in neuromuscular efficiency in this tilt position.

It was found that both quadriceps EMG activity during submaximal contractions, as well as instantaneous strength during maximal contractions, demonstrated a deficit in the inverted position. Therefore, during the inverted seated position it seems that neuromuscular function is impaired.

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This work is dedicated to my beautiful niece, Isabella.

PERSEVERANCE

When all the world is looming dark

And things seem not so clear,

When shadows seem to hover 'round

Lord, may I persevere.

When it seems everything's been tried

And there's no way to go,

Just let me keep remembering

Sometimes the journey's slow.

I may just need to stop and rest

Along the path I trod,

A time to try to understand

And have my talk with God.

As I gain new strength to carry on

Without a doubt or fear,

Somehow I know things will be right,

And so, I persevere.

~ Anne Stortz

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LIST OF ABBREVIATIONS

ATP – Adenosine Triphosphate

BP – Blood Pressure

CNS – Central Nervous System

CO – Cardiac Output

CVP – Central Venous Pressure

EMG – Electromyography

HDR – Head Down Rotation

HDT – Head Down Tilt

HR – Heart Rate

HUT – Head Up Tilt

iEMG – Integrated EMG

LBNP – Lower Body Negative Pressure

MSNA – Muscle Sympathetic Nerve Activity

MVC – Maximal Voluntary Contraction

NTS – Nucleus Tactus Solitarius

SV – Stroke Volume

VO_2 – Maximal Oxygen Consumption

LITERATURE REVIEW

1. INTRODUCTION

Neuromuscular performance during an inverted body position has not been widely studied. However, there are various situations where muscle tension is required in the lower limbs to escape or perform optimally while inverted (i.e. aircraft accidents).

Muscle force output is controlled by central and peripheral factors (Bigland & Lippold, 1954; Schneider & Chandler, 1973). Hence, anything that may inhibit these factors will have an adverse affect on muscle force. During an upright body position, hydrostatic pressure in the lower limbs is regulated by venovasoconstriction and muscle pumps that act to limit blood pooling (Vissing, Secher & Victor, 1997; Miller, Pegelow, Jacques & Dempsey, 2005; Delp & Laughlin, 1998). However, it is not known if the same mechanisms present during upright activities act in a similar manner, or are adequate, to maintain neuromuscular function during knee extension while inverted. The baroreceptor reflex may be desensitized during inversion due to the increased resistance against gravity to pump blood below the heart (Jennings, Seaworth, Howell, Tripp & Goodyear, 1985). The vestibulospinal reflex normally acts to maintain or restore postural tone (Berne & Levy, 2001). While some studies showed that sympathetic activity is decreased in a supine body position (Bosone, 2004), the vestibulosympathetic reflex has not been studied during inversion. There also may be other unknown mechanisms that are active during inversion to maintain homeostasis, while competing with the large increase in cerebral pressure. If neither of these mechanisms proves to be effective in maintaining the perfusion pressure to the exercising muscle in the lower limb while inverted, a decrease in force output and/or activation may be the result since there is a linear relationship between perfusion pressure and force production in the supine body position (Koga, Shibasaki, Kondo, Fukuba & Barstow, 1999; Hogan, Richardson & Kurdak, 1994).

Accordingly, additional research is required to find out if an inverted body position hinders neuromuscular performance. Thus, the proposed study will employ a novel rotational chair about the horizontal axis to test a subject's level of muscle activation and force output during complete seated inversion.

2. MUSCLE FORCE OUTPUT IS DUE TO CENTRAL AND PERIPHERAL FACTORS

Muscle force is controlled by central and peripheral factors. Central factors control muscle force mainly through motor unit recruitment (Kukulka & Clamann, 1981), firing frequency (Bigland & Lippold, 1954) and synchronicity (Milner-Brown, Stein & Lee, 1975). Peripheral variables involved in muscle force production include the synergy of excitation-contraction coupling and myofilament cross bridge kinetics. Changes in twitch responses are associated with alterations with excitation-contraction coupling, whereas modifications in tetanic force are more reflective of changes in cross bridge kinetics. The following section will discuss work that has been published related to how changes in hydrostatic pressure affect the production of muscle tension.

3. WHY WOULD CENTRAL FACTORS BE INHIBITED WHILE INVERTED?

3.1. FACTORS REGULATING HYDROSTATIC PRESSURES IN LIMBS

Pressure at the lower limbs when upright is regulated by various mechanisms, such as veno-vasoconstriction (Vissing, Secher & Victor, 1997), respiratory muscle pump (Miller *et al,* 2005) and the skeletal muscle pump (Delp & Laughlin, 1998). All of these mechanisms contribute to limiting the pooling of blood in the lower limbs. It is unclear what mechanism(s) are active in the cerebrum with inverted body positions to regulate the high pressures, or alternatively control the consequent decreased pressures on the lower limbs in order to try and maintain neuromuscular function.

3.2. IS THERE A DECREASE IN HYDROSTATIC PRESSURE AT THE LOWER LIMBS DURING INVERSION?

The following are possible mechanisms of the gravity-induced increase in arterial pressure resulting in an increase in perfusion pressure and muscle blood flow after muscle contraction. The muscle pump allows for increased perfusion to exercising muscles during whole body tilt upwards, due to low venous hydrostatic pressure during relaxation (Folkow *et al.* 1971). Intramuscular pressure is another factor that contributes to blood flow alterations via mechanisms such as the muscle pump, therefore any modifications to intramuscular pressure (i.e. whether due to muscle contraction itself or some extraneous factor) can influence muscle function (Sejersted & Hargens, 1995). In the supine position, the effects of hydrostatic pressure seem to be minimal and therefore there is not much of a change in perfusion pressure (Laughlin and Schrage, 1999). Vascular tone is likely to increase with body tilt (MacDonald *et al.* 1999), and a gravity-induced rise in arterial pressure and vasodilation increases blood flow while inclined. Although not researched to date, a similar muscle pump effect as experienced in the lower limbs while upright may not be as efficient in the upper body when inverted. Hence, in an inverted body position the muscle pump effect may not be adequate to increase perfusion to the lower body musculature. Relative to the extensive volume of lower limb skeletal muscles, the muscle pump's influence on the cerebrum may be minimal or non-existent. Therefore, when inverted, the limited muscle pump action may lead to a limited or restricted ability to prevent cerebral blood pooling. If the preceding postulates are correct, then what are the effects of possible cerebral blood pooling and increased hydrostatic pressure on central nervous system (CNS) functioning? Furthermore, what are the inversion-induced effects of decreased lower body hydrostatic pressure on lower limb function?

3.3. AMOUNT OF PERFUSION AND THUS O_2 DELIVERY EFFECTS

It has been demonstrated that there are variations in the rate of alveolar oxygen uptake, perfusion and distribution (Cerretelli et al. 1977; Convertino, Goldwater & Sandler, 1984 & Hughson, Cochrane & Butler, 1993), time to task failure (Rochette et al. 2003), and changes in endurance and fatigue (Egana & Green, 2005) with changes in body position. Supine exercise resulted in increased oxygen deficit and decreased VO_2 capacity (Conventino, Goldwater & Sandler, 1984), further supporting the idea that a peripheral oxygen deficit may contribute to neuromuscular impairment.

MacDonald et al. (1998) investigated blood flow at the femoral artery during the onset of supine and upright exercise involving larger muscles. Results indicate drops in mean arterial pressure, heart rate (HR), VO_2 and rate of blood flow in the supine versus upright position. These findings led to the suggestion that alterations in metabolic control by the availability of oxygen at the onset of supine exercise may limit the amount of muscle oxygen uptake. Hence, the reduction in leg blood flow and oxygen delivery during supine exercise may be attributed to reduced perfusion pressure at that body position.

In support of these findings, Koga et al. (1999) stated that the blood flow availability to the working muscles is decreased in the supine position (Eiken, 1988 & Folkow et al. 1971). In the supine position, the majority of the blood flow is at the same level as the heart and brain, and therefore there is no need to compensate for about 750 ml of thoracic blood being rapidly pushed downward as with standing upright (Stewart, 2000). Koga et al. (1999) also put forth the possible contributions of the hydrostatic gradient effect loss in supine positions, lending to a decrease in arterial pressure in the lower extremities followed by a blunt in the cardiovascular response.

The changes in postural blood distribution seem to be dependent upon peripheral circulation, with the duration of graded exercise performance reported to be significantly longer during standing upright (Egana & Green, 2005). Leg blood flow was increased with acute supine exercise due to the gravity-induced differences in arterial pressure at the working muscle, attributed to hyperemia and vasodilation.

During orthostasis there is an increase in blood hydrostatic pressure below the heart, resulting in increased arterial and venous pressures (Egana & Green, 2005). In support of previous finding, the arterial and thus perfusion pressures increase between muscular contractions during orthostasis (Folklow et al. 1971), which may explain the larger blood flow in the limbs during submaximal supine exercise, and decreased VO_2 at the onset of upright exercise compared with supine (MacDonald et al. 1998). These results may also apply to submaximal activity, and are thought to be improved with maximal contractions. During inversion, there is an increased hydrostatic pressure above the heart at the cerebral level (in relation to the anatomical position), but the effects of this pressure change on neuromuscular function are unknown.

Oxygen availability is important in regulating recruitment of high-threshold motor units. It is suggested that the VO_2 slow component may be largely attributed to the motor unit recruitment of fast twitch muscle fibers, with lower efficiency and higher oxygen cost (Barstow, 1994; Barstow, Casaburi & Wasserman, 1993). The results indicate that there is a larger recruitment of fast twitch fibers in the supine position compared to upright heavy exercise. It was also suggested that during high intensity supine exercise, there is a reduction in oxygen delivery and use by the muscles. With an increase in fast twitch fiber recruitment and decrease in oxygen delivery and use by the muscles in the supine position, it could be hypothesized that there will also be a change in the force-EMG relationship.

A key point related to this study is that force output is directly affected by blood flow in contracting muscles (Hogan, Richardson & Kurdak, 1994). Therefore, muscle force output during submaximal and moderately intense work is affected by changes in blood flow mediated by oxygen availability, which may be modified by altered hydrostatic pressure on both the muscle and the cerebrum during inversion. Therefore, it is hypothesized that inversion-induced decreased blood flow to the contracting quadriceps will result in a decreased force output.

3.4. BARORECEPTOR FUNCTIONING

Orthostasis literally refers to standing upright. When an individual stands to an upright position, the baroreceptor reflex is activated due to the force of gravity pulling blood towards the legs and away from upper parts of the body. There is an immediate drop in blood pressure, which is counteracted by the baroreceptor reflex that acts to increase blood pressure to ensure cerebral perfusion (Ponte & Purves, 1974). If this baroreceptor reflex is inhibited in any way, there is a potential risk of lack of blood reaching the brain and subsequent syncope.

Baroreceptors are stretch receptors found in the carotid sinuses and aortic arch which respond to stretch of the vessel due to increased arterial pressure. An increased firing rate coincides with inhibition of the vasoconstrictor regions, followed by peripheral vasodilation and decreased blood pressure (Berne & Levy, 2001). Baroreceptors play a key role in short term blood pressure regulation. Hence, it is clear that baroreceptors are crucial to acute changes in body posture for maintaining homeostasis.

3.4.1. LOWER BODY NEGATIVE PRESSURE

The lower body negative pressure (LBNP) test is another way of testing features of altered body positions. The LBNP test uses external negative pressure from the waist down, under well-controlled conditions, to simulate certain features. LBNP increases the pressure gradient at the heart with a reduction at the lower extremities, which is what is expected for an inverted body position.

The effect of supine and upright submaximal exercise on cardiovascular parameters was investigated by Hughson, Cochrane and Butler (1993). Subjects were placed on a cycle ergometer positioned in upright and supine positions while LBNP was applied in a supine position trial. During supine exercise, LBNP sends more blood to the lower body, thereby activating the baroreceptor reflex. It has been put forth that oxygen transport is rate-limiting in the supine body position, since exercising in the supine position during LBNP results in a faster rate of increase in VO_2 than without LBNP. A study by Cooper and Hainsworth in 2001, found that a LBNP of -40 mmHg did not have any effect on cardiac responses. However, it did enhance vascular resistance responses and increase the peak gain of the baroreceptor reflex, helping maintain BP during orthostatis, as well as lower the pressure decreases during prolonged periods of stress (Cooper & Hainsworth, 2001).

Surprisingly, a study by Jennings et al. (1985) found a significant increase in diastolic BP at the 60 degree head down tilt (HDT) position, which was said to be reflective of the increased resistance against gravity to pump blood to levels below the heart. Jauregui-Renaud et al. (2005) found that the activation of carotid and aortic baroreceptors by HDT induced a decrease of pulse rate within seconds. Hence increased hydrostatic pressure may decrease cardiac output to relieve the perceived increase in systemic blood pressure in an attempt to decrease the perfusion pressure in the lower extremities when inverted.

In a study by Arbeille and Herault (1998), during the 70 degree, three minute head up tilt (HUT) procedure, along with lower body negative pressure (LBNP) at four decreasing levels, at post-HDT the femoral resistances increased less and femoral flow reduced less compared to pre-HDT. It seems from this study that four days in HDT were enough to alter the lower limb arterial and venous response to HUT and LBNP. The HDT also reduced the flow redistribution in favor of the brain (Arbeille & Herault, 1998).

3.4.2. FUNCTION OF BARORECEPTORS DURING INVERSION

Stimulation of the baroreceptors will inhibit vasoconstrictor tone of resistance vessels. Small increases in central venous pressure reduce the sensitivity of the baroreflex control of sympathetic nerve activity in healthy individuals (Charkoudian *et al,* 2004). A study using 60-degree HUT on a tilt table for 20 minutes, resulted in decreased stroke volume (SV) and central venous pressure (CVP), suggesting pooling of blood in the dependent veins (Minson *et al.,* 1999). Since hydrostatic pressure to the brain may be increased in a supine position, and to a greater extent in the inverted position, it can be postulated that CVP will acutely increase, therefore decreasing the sensitivity of the baroreflex during inversion. However, as the previous studies had conflicting reports on cardiac function with the LBNP, it is difficult to predict the pressure consequences of an inverted position. If baroreceptors fail to properly adjust central and peripheral blood pressure under inverted conditions, there could be consequences for the peripheral metabolism subsequently affecting performance. It is unclear how the baroreceptors react to inverted body positions.

4. EFFECT OF PRESSURE ALTERATIONS ON THE CENTRAL NERVOUS SYSTEM

4.1. VESTIBULAR SYSTEM CONTRIBUTIONS

The vestibular system is a component of the sensory system. Changes in the head's position in space are quickly and accurately detected by vestibular input. The main components of the vestibular system, with regards to postural adjustments, are the otolith organs and the semi-circular canals. The otolith organs therefore sense linear acceleration and orientation relative to gravity, including head tilted to left, right, forward, backward making the otoliths move along their gravity gradient. Maximal splanchnic activity resulting from firing of the otolith afferents is produced by head rotation in vertical planes (Yates & Miller, 1994). Yates and Miller (1994) also demonstrated that head down rotation (HDR) and nose-up pitch in cats signal the otolith organs to produce the vestibulosympathetic reflexes, resulting in positive changes in blood pressure. The vestibular effects on respiratory (i.e. vestibulorespiratory reflex) and sympathetic systems during postural changes are instrumental in maintaining homeostasis with regards to blood oxygenation and blood pressure as well (Yates, 1996; Kerman & Yates, 1998). Yates *et al.* (1994) also noted that the same response as seen in a cat should be dually found in humans during movements that may threaten homeostasis. The vestibulosympathetic reflex results in increased sympathetic nerve activity (Kaufmann *et al,* 2002) with differential outflow. In fact, otolith activation creates an increase in muscle sympathetic nerve activity (MSNA) but not skin sympathetic nerve activity (Ray, Hume & Shortt, 1997). The semicircular canals are activated by angular acceleration, including rotational movements. Both parts of the vestibular system evoke vestibulospinal reflexes acting on the limbs, especially by roll (Wilson *et al,* 1986). It is unknown how the vestibulosympathetic reflex will respond to inversion.

There are various methods to naturally create a change in vestibular nerve activity. Whole body tilt, in particular off-vertical axis rotation (Kaufmann *et al,* 2002), can disrupt the release of vasoconstrictor efferents. Animal vestibular stimulation studies suggest positive activity changes in the vasoconstrictor fibers (Kerman & Yates, 1998) and other sympathetic afferents (Yates & Miller, 1994). During postural alteration, both vascular resistance and vasoconstriction are imperative (Wilson *et al,* 2006). Evidently, gravitational stressed rats with the inner ear intact are better able to regulate blood pressure than vestibular deficient rats (Tanaka *et al,* 2006). Therefore, gravity plays a large role in the vestibulosympathetic reflex, and since gravity causes many changes in how the body responds to inversion, it can be inferred that the vestibulosympathetic reflex is crucial to maintain homeostasis at inversion. The question is how the mechanism(s) change to accommodate to an inverted body position and if any possible adjustments maintain or negatively impact quadriceps muscle function.

In order to maintain homeostasis in the body, there must be patterns in the vestibular system adjustments to ensure that blood flow is adequately distributed throughout the body (Kerman, McAllen & Yates, 2000). The vestibulosympathetic reflex patterns according to the target organ, and the nerve's rostro-caudal location (Kerman, Yates, and McAllen, 2000). It has been shown that the solitary tract, contributes to the vestibulosympathetic reflex by adding to cardiovascular control and sympathetic regulation (Costa *et al.* 1995). The solitary trac receives third order afferent inputs from the vestibular system (Yates *et al.* 1994). As well, nuclei tractus solitarius (NTS) synapse with the carotid sinus baroreflex (Spyer, 1981), and send inhibitory signals to the rostral ventrolateral medulla. Moreover, the vestibular system exhibits autonomic adjustments during postural changes to achieve autonomic control of visceral functions (Doba & Reis, 1974). This could have implications for neuromuscular performance during downwards tilt.

Furthermore, the vestibulospinal system may respond to downwards body tilts as a threat to balance by increasing co-contractions. Increased co-contractions have been suggested to be related to lower force outputs (Behm & Anderson, 2006). Although an individual may be fully strapped while inverted, the altered afferent feedback (i.e. dangling feet) and the change in vestibular functioning could induce a sense of instability.

Ray and Carter (2003) examined the effect of sympathetic activity by inducing head-down rotation (HDR) in subjects to physically alter the vestibular system. It has been concluded that the alterations in MSNA observed during HDR are a direct result of alterations in the otolith organs.

Further investigations in the area of vestibular control and the neuromuscular mechanisms associated with it, may have practical implications in actual or simulated weightless environments. There has been evidence put forth of decreased sympathetic activity in such circumstances (Beckers *et al,* 2003), which may contribute to inhibited muscle function.

4.2. SYMPATHETIC SYSTEM CONTRIBUTIONS

Both peripheral and central processing factors are involved with postural adjustments (Ivanenko *et al.* 2000). Efferent and afferent signals within the sensorimotor system provide feedback from somatosensory, vestibular, and visual inputs (Kollmitzer *et al.* 2000), and consistent anticipatory postural adjustments (Slijper and Latash, 2000) contribute to balance.

The efferent nerves send signals to adjust posture, thereby producing and/or maintaining muscle contraction. The efferent system also provides autonomic outflow and ensures optimal blood flow to the contracting muscles and brain, via somatic motoneurons. Output from the brain's central command acts in a feed-forward manner, affecting both autonomic and somatic outflow. However, input from somatic and visceral afferents act in a feedback fashion. Therefore, decreases in blood volume, pressure and muscle contractions provide changes in afference (Kerman, McAllen & Yates, 2000). This also provides evidence to indicate that altered sympathetic activation due to an inverted body position could affect the ability to activate motoneurons. Thus, quantification of the changes in sympathetic activity to the vessels involved in postural alterations can be achieved by the direct recording of the neural sympathetic discharge from the peroneal nerve (Furlan, 2002).

MSNA causes vasoconstriction in skeletal muscle in response to standing upright (Wallin & Sundlof, 1982). During orthostasis the immediate increase of sympathetic activity to the vessels is accompanied by an excessive cardiac sympathetic response, resulting in an abnormally rapid heart rate (Furlan, 2001). Furthermore, it was proposed that at high levels of sympathetic activity, postsynaptic adrenergic receptors may become saturated, resulting in maximum smooth muscle constriction (Fu, Witkowski & Levine, 2004). It has also been shown that short-term vasoconstriction of skeletal muscles is gravity dependent (Cui *et al,* 1997). Prolonged HUT is associated with a greater innervation density of the hindlimb blood vessels (Monos, Lorant & Feher, 2001). This in turn causes a potentiated acute myogenic response to pressure and an increased neural vasoconstrictor capacity of the blood vessels important to venous return and cardiac output (Dornyei, 1996). The response in MSNA to inversion has not been directly studied. Therefore, we cannot assume to expect opposite results as seen in the upright position.

As the central nervous system becomes increasingly stressed, there are reports of elevated intracranial pressures in rabbits subjected to 45 degree head down body tilt (Tatebayashi, Doi & Kawai, 2002) and humans positioned at 30 degree head down body tilt (Bosone, 2004). The effect of increased intracranial pressure on human neuromuscular performance has not been previously investigated.

The combination of increased intracranial pressures and decreased sympathetic outflow might reduce the neural outflow to the motor neurons adversely affecting the ability to fully activate all motor neurons, thus reducing maximal force output or the ability to sustain submaximal intensity contractions.

In summary, there have been no studies performed with complete inversion, but it has been shown that acute head down body tilt lowers sympathetic nervous activity (Bosone, 2004; Cooke, Carter & Kussela, 2004;Cooke & Dowlyn, 2000), while having no effect on parasympathetic activity (Cooke, Carter & Kussela, 2004). Inhibition of sympathetic activity has been shown to decrease HR (Sundblad, 2000), blood pressure (BP) (Bosone, 2004) and total peripheral resistance (Goodman & LeSage, 2002). In order to balance the decreased HR, cardiac output (CO) reactively increases with 6 degree head down body tilt (Yao, 1999). Kowanokuchi et al. (2001) used 6-8.5 degree head down body tilt with LBNP to illustrate that sympathetic inhibition can be attributed more to a vestibulosympathetic reflex rather than cardiopulmonary baroreceptors. Since changes in body tilt have significant impact on cardiovascular and sympathetic responses it would be of interest to investigate inversion effects on neuromuscular performance.

5. LINKING CARDIOVASCULAR CHANGES TO NEUROMUSCULAR PERFORMACE

As there are limited inversion studies in the literature, the effects of changes in peripheral perfusion pressure and ischemia are discussed.

The distance the muscle being tested is above or below the heart is one determining factor of perfusion pressure in the muscle. Neilsen (1983) demonstrated a decrease in perfusion pressure in the hand while the arm is raised above the heart. It has also been shown that lower limbs altered by positive pressures of up to 50 mmHg, reduces muscle perfusion and consequently decreases muscle performance (Eiken, 1987; Sundberg & Kaisjer 1992). Fitzpatrick et al. (1996) discovered that when the hand was raised above the heart, perfusion pressure in the hand decreased by 35 mmHg (ie. hydrostatic pressure of a 45 cm column of blood) resulting in decreased force production and increased mean arterial pressure. Alternatively, when the hand was lowered below the heart, perfusion pressure increased by 35 mmHg and there was an increase in muscle force production. It was also found that the evident dependence of force production on the amount of perfusion pressure was enhanced when the workload was increased. Furthermore, animal studies performed with an isolated cat soleus muscle treated with a reduced mean blood pressure, resulted in decreased blood flow and force production with near maximal workloads (Hobbs & McCloskey, 1987).

Hobbs *et al.* (1987) also found increased integrated EMG (iEMG) during leg elevation. The results were evidence of force output being affected by the perfusion pressure into the muscle. However, it was still uncertain if the increase in iEMG was due to recruitment of additional motor units to balance the decrease in muscle force output with altered perfusion. Fitzpatrick et al (1996) modified the perfusion pressure in the adductor pollicis and found no systematic changes in EMG. However, there was an increase in muscle activation, thought to be responsible for the maintenance of constant force output with a decrease in perfusion pressure into the muscle.

Hobbs & McCloskey (1987) used the cat to show that muscles consisting of type I muscle fibers demonstrated the positive perfusion pressure - force development relationship, while muscles composed of mainly type II muscle fibers did not. In a human study by Fitzpatrick et al (1996) the adductor pollicis was the muscle investigated, which is mainly composed of fiber types I and IIA. Therefore, the demonstrated early rapid decline in muscle force, followed by an extended period of slower muscle force decline are reflective of these two muscle fiber types being present and exhibiting change. Whereas it is known that force production is decreased when perfusion is lowered, there was no direct evidence to suggest that changes in muscle performance were due to changes in oxygen delivery to the muscle or other factors related to blood flow.

Lanza et al (2006) investigated adenosine triphosphate (ATP) synthesis during ankle dorsiflexion in the supine position with cuff occlusion to the tibialis anterior. With a decrease in ATP synthesis by oxidative phosphorylation due to a decrease in PO_2, which is required for mitochondrial ATP synthesis, it was found that the ATP balance was maintained during ischaemia via decreased ATP demand. The lower demand for ATP was attributed to decreased muscle force production as well as increased metabolic economy.

The lower ATPase rates during ischaemic contraction were suggested to be an indication of greater decrease in muscle force output during ischaemia, since muscle force production controls the rate of ATP production. Other contributing factors to decrease in muscle force production may be the decrease in phosphocreatine and enhanced myoglobin desaturation with ischaemic contractions (Lanza et al. 2006). Even with the voluntarily maximal activation of the tibialis anterior, glycolytic ATP production was unchanged between free flow and ischaemic contractions (Lanza et al. 2006). However, a study by Greenhaff et al (1993) examined maximal electrical stimulation of the quadriceps and found opposite results. It was found that glycogenolytic rates were similar between ischaemic and free flow contractions in type II muscle fibers. Contrastingly, glycolytic flux was increased more with ischaemic contractions versus free flow contractions by type I fibers. Lanza et al. (2006) contributed the differences in observations between these two laboratories to the difference in muscle groups studied, muscle activation technique, as well as the glycolytic flux quantifying method.

Lanza et al. (2006) also demonstrated a decrease in the force-time integral, reflecting more muscle fatigue during ischaemic contractions. The greater decrease in muscle force generating capacity was party attributed to ATP hydrolysis becoming less favored, as apparent by ATP supply being closely connected to muscle force output (Dawson et al. 1978).

In summary, during maximal or near maximal muscle contractions, if there is a decrease in perfusion pressure (i.e. decrease in hydrostatic pressure), there is a decrease in muscle force production. Also, type I muscle fibers are the most sensitive to changes in perfusion pressure and therefore most likely to affect muscle force output. Furthermore, ischaemic muscle contractions result in decreased mitochondrial ATP synthesis and hence, since there is a larger decrease in muscle force production during such contractions there is also a decrease in ATP demand. Although ischaemic conditions do not exactly replicate the inverted posture these studies may give some indication of possible lesser fluctuations in energy output with inversion.

6. EFFECT OF INCREASED HYDROSTATIC PRESSURE ON MUSCLE FORCE OUTPUT

Early investigations into the effects of high pressure on muscle were conducted by Cattell & Edwards (1928), who began by studying the energy changes involved in contractions under high pressure, while Brown (1934) looked at the effect of rapid changes in hydrostatic pressure on muscle contraction. It was found that high pressure applied at the onset of contraction increased the twitch tension (Cattell & Edwards, 1928), while decreasing rates of contraction and relaxation (Brown, 1934). Since twitch tension was more adversely affected than tetanic tension, the changes in tension were attributed to excitation contraction coupling modifications (Cattell & Edwards, 1928). Both Brown (1958) and Ikkai and Ooi (1969) found that raised hydrostatic pressure decreased the attraction of actin to myosin, thereby hindering the actomyosin ATPase reaction.

Geeves and Ranatunga (1987) furthered these concepts by investigating how isometric tension production in a single rabbit psoas muscle fiber was affected by high hydrostatic pressures. Pressure was increased for 2-10 seconds and then held constant for 10-20 seconds. The result was a 15% decrease in isometric active tension in a maximally calcium activated fiber. It was thought that a lower number of active cross bridges and/or a decrease in the force per cross bridge was responsible for this linear relationship. It was later deduced that the amount of products of the ATPase reaction determines how much the maximum active tension is decreased (Fortune, Geeves & Ranatunga, 1989). With increased hydrostatic pressure applied, tension was decreased more by the presence of inorganic phosphate, while ADP lessened the amount of tension reduction, providing more evidence that a cross bridge incident is responsible for tension alterations induced by increased hydrostatic pressure.

The differences in a twitch and tetanus tension response to higher hydrostatic pressures were more thoroughly explored by Ranatunga & Geeves (1991). This study used the extensor digitorum longus of the rat, which is composed of mainly fast twitch fibers, to determine the isometric contraction response to augmented hydrostatic pressure. It was shown that during increased hydrostatic pressure the peak tension, time to peak and the time to half-relaxation of the elicited twitch contraction were enhanced. Alternatively, with the administration of a fused tetanus there was decreased tension production. This lowering of tension was thought to be composed of an increased half-time of exponential relaxation (i.e. due to hydrostatic compression of muscle fiber elasticity) and a decreased half-time of tension rise.

Fortune, Geeves & Ranatunga (1994) compared the effects of hydrostatic pressure on both maximally and submaximally contracted rabbit psoas muscle fibers. The results displayed opposite responses for each type of contraction. For contractions at low Ca^{2+} levels (i.e. submaximal contraction), there was a steady tension increase. However, at high levels of Ca^{2+} (i.e. maximal contraction), there was a decrease in steady tension. The reason for this difference was suggested to be due to the high hydrostatic pressure affecting other processes such as Ca^{2+} uptake and release. During a submaximal contraction of an intact muscle fiber, such an alteration in this process could increase contractile activation and force output. This theory provided further support for the idea that Ca^{2+} regulates cross bridge recruitment rather than the rate of a particular step within the cross bridge cycle. Another study also found that increased twitch tension due to enhanced hydrostatic pressure may be caused by increased release of Ca^{2+} (Vawda, Ranatunga & Geeves, 1996). Other studies have shown that high hydrostatic pressures causes pulsing acetylcholine receptor release, decreasing its effect on muscle firing frequency (Heinemann, Stuhmer & Conti, 1987), and another study demonstrated decreased enzymatic activity of lactic dehydrogenase (Schmid, Ludemann & Jaenicke, 1979). Both of these studies are further evidence that high hydrostatic pressures result in neuromuscular impairment.

All of these aforementioned studies were completed with animal models. There is very little research conducted, if any, on humans in this area. It is interesting that there are seemingly opposing results to the above animal skeletal muscle studies found in the rat cardiac muscle. Ornhagen & Sigurdsson (1981) found that high hydrostatic pressure resulted in increased force of atrial contraction.

An inverted position would be expected to increase blood pooling in the brain while decreasing blood perfusion in the lower limbs, and therefore less hydrostatic pressure acting on the lower limb vessels. The effect of less hydrostatic pressure as compared to the animal studies examining high hydrostatic pressure would not automatically translate into the opposite response (i.e. increases rather than decreases in maximum force). Due to the lack of literature in the area of reduced hydrostatic pressure (Parazynski *et al,* 1991) in human limbs due to inversion, it is of interest to investigate this question.

6.1. FORCE-EMG RELATIONSHIP

In addition to blood flow to the contracting muscle, the nervous system contributes to control of time to task failure of a submaximal sustained contraction (Akima *et al.* 2002) in varying body positions. Rochette *et al.* (2003) examined time to task failure and the patterns of EMG activity of the quadriceps in supine and seated postures. Increased EMG activity indicates recruitment of additional motor units during contraction along with progressive fatigue (Fallentin, Jorgensen & Simonsen, 1993). The results showed that the submaximal torque recorded before the fatiguing contraction was the greatest in the seated position. EMG activity increased throughout the fatiguing contraction in the supine position. The rate of increase in EMG was similar in both positions, while the average rate of torque increase did not differ. The time to task failure performed at the same relative target torque was unchanged by altered body positions (Rochette *et al.* 2003).

The results from this study concluded that sustained submaximal contraction of the quadriceps did not show the changes reported in the elbow flexor muscles reported by Hunter & Enoka (2003). These results suggest that control of muscle activation is related to the structural organization of the muscle group. However, the synergist muscle was unrepresentative of the activation patterns of the entire muscle group because the amplitude and rate of increase in EMG activity was not uniform among the quadriceps. The time to task failure was similar in both positions, but the decrease in maximal torque was greater in the seated position suggesting that they are controlled by differing mechanisms (Rochette *et al,* 2003).

Published research concerning the EMG-force relationship and muscle activation of the knee extensors while in static inverted seated positions are rare. Hence, it is important to investigate the general neuromuscular response during this type of contraction and body posture, with the practical applications possibly leading to enhancement of the preparation and training for accident situations and also influencing the working efficiency of individuals in the unique situation of whole body inversion.

7. CONCLUSIONS

In conclusion, this literature review has provided information to indicate that neuromuscular function to the lower limbs may be impaired during inverted body positions. Since muscle force output is due to central and peripheral factors, inhibition of either of these nervous systems will contribute to alterations in muscle force.

Presently, the only known hindrance to the cerebral area during inversion is an increased hydrostatic pressure above the heart, and a probable decrease in baroreflex sensitivity. However, these factors alone could result in cerebral blood pooling with drastic effects on central factors controlling lower limb function.

There is persuading evidence that inversion will result in neuromuscular impairment. Expected gravitation changes to certain areas of the body, for example during seated inversion, will induce otolith activation, consequently stimulating the vestibulosympathetic reflex and a resulting decrease in muscle sympathetic nerve activity to the leg muscles. Furthermore, since force output is directly affected by blood flow, a decrease in blood flow availability to the quadriceps during inversion may lead to oxygen deficit and a decreased VO_2 capacity within the muscle. A resultant decrease in perfusion pressure at the muscle will likely cause a decrease in force output, followed by a decrease in ATP production and demand. Likewise, a possible decrease in hydrostatic pressure below the heart during inversion can also lead to a decrease in tension production. For example, head down tilt has been shown to increase resistance against gravity to pump blood to levels below the heart. It is acknowledged that EMG activity is increased with high hydrostatic pressures; however, the EMG response to decrease hydrostatic pressure at the muscle is unknown.

The Effect of an Inverted Body Position on Muscle Force and Activation

Author: Natasha Paddock

School of Human Kinetics and Recreation
Memorial University of Newfoundland

Running Title: Inversion effects on muscle force and activation

ABSTRACT

Progressively tilting the body from supine to upright, have been utilized to examine changes in the vestibular, autonomic and cardiovascular responses. The purpose of this study was to investigate neuromuscular responses to upright and inverted seated positions. Sixteen subjects tested their knee extensors under upright and inverted seated positions for maximal voluntary contraction (MVC) force, level of muscle inactivity, electromyographic (EMG) activity and evoked contractile properties. Surface EMG electrodes were placed on the rectus femoris and semitendenosis. Stimulating electrodes were placed over the inguinal space and distal portions of the quadriceps. The evoked and voluntary contractions were analyzed for peak force, rate of force development and activation. During 50% and 75% MVC, the quadriceps EMG activity was significantly greater in the upright position compared to the inverted position. The results showed a trend for quadriceps MVC EMG activity to be greatest in the upright position. There were no significant differences in the force-EMG relationship between the conditions. Instantaneous strength in the inverted position was 19.3% lower than the upright position. It was concluded that the inverted seated position had detrimental effects upon muscle activation during submaximal contractions. These findings could have negative implications for individuals attempting to escape from trapped inverted seated positions such as an overturned aircraft or vehicle.

Keywords: inversion, electromyography, evoked contractile properties, strength

INTRODUCTION

Neuromuscular performance during upright positions is ubiquitous throughout the literature. The activation associated with force output produced by short duration maximal voluntary contractions (MVC) can be represented by EMG activity (Bigland & Lippold, 1954). This activity shows an increase in global action potential amplitude, which can be caused by many factors such as increased motor unit recruitment (Kukulka & Clamann, 1981), firing rate (Bigland & Lippold, 1954) and synchronicity (Milner-Brown, Stein & Lee, 1975). These parameters of analysis are quite helpful when examining fatigue and overall performance, and also provide a model to study various disease or disorder conditions, in addition to general muscle physiology mechanics. Muscle activation and force studies are typically conducted during seated or standing positions. However, there are a number of scenarios where an individual may have to perform maximal contractions under inverted conditions. The question arises regarding the neuromuscular responses to inversion while submerged in an overturned helicopter, motor vehicle, performing evasive maneuvers in military aircraft or other unique and dangerous environments. Therefore this research was initiated to increase our understanding of how force output and muscle activation changes in upright and inverted seated positions.

A number of studies have examined related neuromuscular function in upright whole body tilt from supine to upright positions (Furlan, 2001), head-up (Arbeille & Herault, 1998) head-down (Yasumasa, 2002), and head-rotation (Ray, 2000). It is possible that changes in hydrostatic pressure of both the cerebrum and the working muscle, in addition to changes in both the cardiovascular and sympathetic systems may contribute to alterations in neuromuscular performance during different body positions. This may be especially apparent in an inverted position compared to upright posture.

1. PURPOSE OF STUDY

This paper was developed to explore how neuromuscular function may change when the body is placed in an inverted body position. It was believed that the information provided by this study would contribute knowledge regarding the physiological changes associated with inversion, as well as shedding some light onto possible mechanisms behind these changes, by determining the extent to which neuromuscular performance is impaired during inversion.

2. RESEARCH HYPOTHESES

It was hypothesized that an inverted body position will induce neuromuscular impairments. More specifically, during inversion it was hypothesized that:

(1) MVC force output will decrease

(2) EMG activity will be decrease during MVC and increase with submaximal intensity contractions

(3) Muscle activation will decrease

METHODOLOGY

1. SUBJECTS

Sixteen male subjects (height = 178.25 cm +/- 7.59, weight = 82.04 kg +/- 12.29, age = 25.06 +/- 3.70) from Memorial University of Newfoundland participated in the study. All subjects performed the protocol in Memorial University's Exercise Physiology Laboratory. All participants had no previous history of any hypertensive or cerebral related conditions or serious injury, and were between 19 to 35 years old. Subjects included both competitive and recreational athletes; resulting in a heterogeneous group of active individuals. There were no sedentary participants. All participants were given an overview of the procedure, a Physical Activity Readiness Questionnaire (PAR-Q) form (Health Canada, 2004), and signed an informed consent form. They also participated in an orientation session prior to the data collection. The study was granted ethical approval by Memorial University's Human Investigations Committee.

2. EXPERIMENTAL DESIGN

2.1. PROTOCOL

Subjects were instructed to not smoke, drink alcohol or exercise at least 6 hours prior to testing and to not eat food at least two hours prior to testing (Health Canada, 2004). Subjects were given an orientation session at least 48 hours prior to testing. The orientation allowed them to become familiar with the protocol, as they performed all of the same procedures as they would during testing. All participants were required to perform a warm-up activity prior to testing, consisting of pedaling on a cycle ergometer set at 1kp and 70 rpm (70 Watts) for 5 minutes, keeping the heart rate above 70 beats per minute.

Every testing session began with an initial measure conducted from an upright seated position for consistency purposes. This measure involved progressively increasing twitch magnitude elicited to the subject until force output reached a plateau, indicating the maximum resting twitch. Hence, this twitch value was then utilized for each subsequent stimulation during the ITT. The following measures were then tested in the randomly selected tilt position (seated upright or inverted; Figures 1 & 2 respectively).

First, the subject performed 2-3 maximal voluntary contractions (MVC's). Secondly, a MVC was performed with the interpolated twitch technique (ITT). The first twitch was elicited at the peak voluntary force, and the second while the muscle was relaxed. Next, 25%, 50% and 75% MVC trials were collected in random fashion. Each percentage of the maximum force for each subject was displayed on a computer screen, and the subject was prompted to maintain the force at each level by way of visual interpretation. Lastly, a post-test maximum potentiated twitch was elicited. The preceding order of tests was maintained for all testing sessions since a voluntary contraction prior to the resting twitch would potentiate the force.

Blood pressure was monitored prior to testing, and again after each MVC to ensure the safety of the subject. Subjects were allowed a two minute rest period between each test condition. There were two testing sessions, with at least 48 hours between each one, and each subject was tested at similar times of the day for each subsequent session.

2.2. APPARATUS

The study was conducted with subjects in a seated position on a rotational chair with hips and knees at 90^{o}. To measure the moment about the knee joint, a reinforced strap was placed around the ankle, attached by a high tension wire to a Wheatstone bridge configuration strain gauge (Omea Engineering Inc., LCCA 250, Don Mills, Ontario, Canada), perpendicular to the lower limb. The subject's body was secured in the rotational chair via a 5 – point strap (waist, shoulders and groin), along with an additional leg brace located around both thighs. The securing of participants with strapping and a leg brace maintained posture and also helped to ensure stability, isolation and correct orientation of the quadriceps muscle and joints.

3. DEPENDENT VARIABLES

3.1. EVOKED CONTRACTILE PROPERTIES

Twitches were evoked with stimulating electrodes. Stimulating electrodes were constructed in the laboratory from aluminum foil and paper coated with conduction gel (Aquasonic, Fairfield, NJ) and immersed in a saline solution. The length of the electrode was sufficient to wrap the width of the inguinal space and distal portion of the quadriceps, in order to stimulate the femoral nerve. The amperage and voltage of the stimulation were progressively increased until reaching a force plateau, indicating peak twitch force. Torque about the knee joint was measured by the strain gauge, amplified (DA 100 and analog to digital converter MP100WSW, Biopac Systems, Inc., Holliston, MA), and monitored on a computer (Compaq, St. John's, Newfoundland, Canada). All data was collected at 2 kHz and then stored on a computer.

3.2. MVC-FORCE

Verbal instructions to maximally contract the quadriceps as hard and fast as possible were given to the subject for the MVC. The arms were crossed in front of the chest, and the ankle cable was maintained in a taut position to help prevent movement of the knee joint during the data collection. Verbal motivation was given by the investigator during the contraction to promote a maximal response. The contraction lasted for 4 seconds, followed by relaxation. If there was more than a five percent difference between the first two MVC trials, the subject was asked to perform a third trial, and the highest MVC force was recorded. All forces detected by the strain gauge were amplified and converted via an analog to digital (A/D) converter to be stored on a computer for further analysis.

3.3. INTERPOLATED TWITCH TECHNIQUE (ITT)

The ITT was incorporated during the MVC. The quadriceps muscles were subjected to interpolated stimulation by a doublet (two maximal twitches with a 100 ms interpulse interval). The superimposed twitch of the ITT activates any fibers that are not voluntarily recruited by the MVC. The segment of the MVC where peak force was achieved was identified in the preliminary MVC trials. This point in time was used to elicit the superimposed twitch for the MVC ITT trial. The same time frame was incorporated after the superimposed twitch to elicit the potentiated twitch. The subject was instructed to relax fully before the potentiated twitch was produced. An index of muscle inactivation was derived by expressing the potentiated twitch as a percentage of the superimposed twitch (Behm, St. Pierre & Perez, 1996).

3.4. FORCE-EMG RELATIONSHIP

The MVC peak force measured by the strain gauge was utilized to estimate 25%, 50% and 75% MVC force. These force levels were subsequently displayed on the computer monitor for the subject to see. The subject was then requested to perform isometric knee extension contractions at an intensity that would match the prescribed force level indicated on the computer monitor. There were separate trials for each percentage of MVC, and there were two minutes of recovery between each 4 second contraction.

3.5. Electromyography

The skin was prepared for surface and stimulating electrode placement by shaving the area, followed by rubbing with sand paper and then an alcohol swab to clean. Two bipolar surface electrodes (Kendall Medi-trace 100 series, Chikopee, MA) were placed 2 cm apart over the mid-belly of the vastus lateralis and the semitendinosis in alignment with the muscle fibers. The anterior superior iliac spine to the patella, and the gluteal fold to the knee fold were initially measured and the halfway mark recorded, so that for each successive session the surface electrodes were consistently placed. Ground electrodes were placed on the tibia and fibular head.

The EMG signal was sampled at 2kHz with a Blackman -61 dB band-pass filter between 10-500 Hz, amplified 1000 times (Biopac Systems MEC 100 amplifier, Santa Barbara, CA; input impedence = 2M, common mode rejection ratio > 100 dB [50/60 Hz];

noise > 5 UV), directed through an A/D converter (Biopac MP100) to be stored on a personal computer for further analysis.

4. DATA ANALYSIS

4.1. FORCE

Data were recorded and analyzed with proprietary software (AcqKnowledge III, Biopac Systems Inc.). All MVC forces were analyzed using the maximum value of force output. The resting and potentiated twitch forces were also analyzed using the highest value. Instantaneous strength was analyzed as the force generated in the first 100ms of the MVC. The half relaxation time was calculated as the time period to reach half of the peak twitch force. The time to peak twitch was measured as the time period of the peak to peak value from baseline to the peak twitch force.

4.2. EMG

The quadriceps EMG signal during the percentage trials, along with both the vastus lateralis and the semitendonosis muscles EMG activity during the MVC trials, were amplified, filtered (10-1,000 Hz), monitored, and stored on a computer. The post-collections analysis software than rectified and integrated (iEMG) the data over a 500-ms period during which peak voluntary force was produced. The muscle action potential wave (M-wave) amplitudes were analyzed from the stimulated resting twitches and maximum values were recorded.

5. STATISTICAL ANALYSIS

One-way analysis of variances (ANOVA) with repeated measures was conducted on all measures, in the upright and inverted positions (GB-STAT for MS WINDOWS V. 6.0.). Differences were considered significant when p-values were below an alpha level of 0.05. An EMG-Force relationship was derived for the MVC and percentage trials (25%, 50%,75% and 100% of MVC) and described with a second-order polynomial equation (GB-STAT for MS WINDOWS V. 6.0.). From the second-order polynomial, differences in slope and curvature were investigated. A post-hoc Bonferonni – Dunn's Procedure test was also utilized to determine the values of pair wise comparisons, and detect the location of significant differences between upright and inverted positions.

Effect sizes (ES = mean change / standard deviation of the sample scores) were calculated and reported (Cohen, 1988). Cohen applied qualitative descriptors for the effect sizes with ratios of less than 0.41, 0.41 - 0.7, and greater than 0.7 indication small, moderate and large changes respectively. Descriptive statistics and figures include means +/- standard deviation (SD).

RESULTS

1. EVOKED CONTRACTILE PROPERTIES

There were no significant changes in resting or potentiated twitch forces with changes in position. Likewise, there were no significant changes in half relaxation time or time to peak twitch. However, there was a numerical indication that time to peak twitch decreased in the inverted body position (ES = 2.273). There data also suggested a (small to moderate effect sizes) tendency for M-wave amplitudes from the upright position to be 17.1% higher than in the inverted (ES = 0.517) position ($p = 0.412$). There was a moderate effect size (ES = 0.168) for the resting twitch forces to be 17.1% higher in the upright position rather than inverted ($p = 0.168$; Tables 1 & 2).

2. MVC MUSCLE ACTIVATION AND FORCE

There were no significant changes with position for MVC force, muscle activation as measured with the ITT or semitendonosis EMG activity. However, instantaneous strength was 19.3% lower than upright, in the inverted position ($p = 0.0053$; ES = 0.782; Figure 5). There was also a trend for vastus lateralis MVC EMG activity to be 41.3% greater in the upright position as compared with the inverted (ES = 0.413) position ($p = 0.078$; Tables 1 & 2).

3. FORCE-EMG RELATIONSHIP

The EMG activity for the 50% quadriceps MVC appeared to be 24.7% higher in the upright position than the inverted position (ES = 0.828; p = 0.039; Figure 3). During the 75% MVC, the vastus lateralis EMG activity was 29.3% greater in the upright position compared to the inverted position (ES = 0.769; p = 0.016; Figure 4). The unadjusted r^2 has a p-value of 0.58, indicating a linear Force-EMG relationship (slope p = 0.389). There were no significant differences in position for slope (Table 3).

4. RELIABILITY

The reliability of the twitch forces using an ICC was 0.8. MVCs, ITTs and the associated EMG were not pre-tested in every condition but previous research from this laboratory have reported reliability values ranging from 0.91 - 0.99 (Behm, St. Pierre, & Perez, 1996; Behm, & St. Pierre, 1997; Behm, & St. Pierre, 1997; Behm, Button, Barbour, Butt & Young, 2004; Behm, Anderson & Curnew, 2002).

DISCUSSION

This is the first study to investigate the effects of an inverted body seated position on neuromuscular function. The main findings of this study were 1) a significant decrease in EMG activity of submaximal (i.e. 50% and 75% MVC) knee extensions during inverted tilt positions and 2) instantaneous strength was found to be significantly lower in the inverted position. Even though not statistically significant, there were important trends and numerical indications with considerably large effect sizes and percentage differences between tilt positions demonstrated. As this is the first study in this area, there are no comparable studies, which have replicated seated whole body inversion. However, other studies using whole body and head tilts may provide some insight into the mechanisms underlying these inversion-induced deficits.

1. CHANGES IN SUBMAXIMAL MVC EMG ACTIVITY

The initial hypothesis that EMG activity would be altered by changes in body tilt was substantiated in this study. There was a significant decrease in quadriceps EMG activity during both 50% and 75% MVC's while inverted. A decrease in EMG activity reflects inhibitory influences on activation, and can be due to multiple factors. A decrease in number of motor units recruited, size of motor units recruited, firing frequency of the motoneurone, synchronicity of action potential firing or a decreased muscle action potential amplitude or duration can all contribute to a decreased EMG signal (Bigland & Lippold, 1954; Kukulka & Clamann, 1981; Milner-Brown, Stein & Lee, 1975). Essentially, a drop in EMG activity due to inversion could be related to an inhibition of central or peripheral factors.

2. PERIPHERAL FACTORS AFFECTING CHANGES IN SUBMAXIMAL MVC EMG ACTIVITY

There is evidence that a decrease in blood volume, blood presure and muscle contractions cause changes in afference (Kerman, McAllen & Yates, 2000). Furthermore, a decrease in lower limb conductivity, which affects motor unit action potentials, was shown to decrease EMG spectral content during tilt from vertical to supine. Rochette *et al.* (2003) reported a decrease in EMG activity during 20% MVC while lying supine compared to seated upright. They attributed the decrease in EMG to a decrease in afferent neural outflow to the motor neurons. Likewise, whole body tilt, in particular off-vertical axis rotation, can disrupt the release of vasoconstrictor efferents. There could be further decreases in neural outflow to the motor neurons with increased hydrostatic pressure and altered sympathetic activation during inversion. A decrease in neuromuscular efficiency is also possible during inversion, which could result in an increased neural drive to perform the same intensity of submaximal contraction. Barstow (1994) found a larger recruitment of fast twitch fibers during activity in the supine position versus upright. However, these contrasting results may be due to the differences in intensity of contraction, since Barstow's protocol involved maximal exercise, whereas the findings of the present study involve submaximal isometric contractions. However, numerically, the vastus lateralis MVC EMG decreased by almost half in the inverted position compared to upright in the present study. However, the cause of the high MVC EMG variability in the present study which nullified significant results is not known and should be the study of further research. Furthermore, further studies are required to examine the underlying mechanisms of decreased EMG activity during seated inversion.

3. CENTRAL FACTORS AFFECTING CHANGES IN SUBMAXIMAL MVC EMG ACTIVITY

An inverted position would be expected to increase hydrostatic pressure in the cerebrum. During orthostasis increased hydrostatic pressure and consequent blood pooling in the lower limbs is offset by a number of mechanisms to ensure adequate venous return to the heart. These mechanisms include the muscle pump, thoracic or respiratory pump and ventricular pump effect as well as changes in vasomotor tone (Vissing, Secher & Victor, 1997; Miller *et al,* 2005; Delp & Laughlin, 1998). However, relative to the extensive volume of lower limb skeletal muscles, the muscle pump may be minimal or non-existent in the cerebrum. Therefore, when inverted, the limited muscle pump action may lead to a limited or restricted ability to prevent cerebral blood pooling. This increased hydrostatic pressure and possible blood pooling could have negative consequences on the ability of the brain to normally activate the motoneurones resulting in a decreased neuromuscular efficiency (increased EMG activity or activation for a similar submaximal resistance)

Secondly, stimulation of the baroreceptors inhibit vasoconstrictor tone of resistance vessels. Small increases in central venous pressure reduce the sensitivity of the baroreflex control of sympathetic nerve activity in healthy individuals (Charkoudian *et al,* 2004). Since hydrostatic pressure to the brain may be increased to a great extent in the inverted position, it might be postulated that central venous pressure would acutely increase, decreasing the sensitivity of the baroreflex control of sympathetic stimulation during inversion. In addition, it has been shown that acute head down body tilt lowers sympathetic nervous activity (Bosone, 2004; Cooke, Carter & Kussela, 2004;Cooke & Dowlyn, 2000), while having no effect on parasympathetic activity (Cooke, Carter & Kussela, 2004). Inhibition of sympathetic activity has been shown to decrease heart rate (Sundblad, 2000), blood pressure (Bosone, 2004) and total peripheral resistance (Goodman & LeSage, 2002). Kowanokuchi et al. (2001) used 6-8.5^0 head down body tilt with lower body negative pressure to illustrate that sympathetic inhibition can be attributed more to a vestibulosympathetic reflex rather than cardiopulmonary baroreceptors. A decrease in sympathetic activation may also play a role in the ability of the central nervous system to adequately activate the motoneurones.

4. INSTANTANEOUS STRENGTH

During the MVC, instantaneous strength was significantly lower in the inverted position, compared to upright in the present study. Instantaneous strength was defined in this study as the force produced in the first 100 ms of the MVC. As the subjects were asked to contract maximally and explosively, instantaneous strength would be related to the ability of the participant to increase their rate of force development. The rate of force development has been reported to be positively related to the firing frequency or rate coding of the motoneurone (Miller, Mirka & Maxfield, 1981). Hence, any changes in instantaneous strength would tend to affect this physiological parameter. Decreases in perfusion pressure can cause a decrease in muscle force output (Lanza *et al,* 2006). It is expected that both perfusion pressure and blood flow to the contracting muscle in the areas below the heart is reduced during inversion (Cerretelli et al. 1977; Convertino, Goldwater & Sandler, 1984 & Hughson, Cochrane & Butler, 1993). Force output is directly affected by blood flow in contracting muscles (Hogan, Richardson & Kurdak, 1994). Furthermore, oxygen availability to the working muscle is an important factor in the recruitment of high-threshold motor units (MacDonald *et al,* 1998), which would have a strong impact on the rate of force development. Fluctuations in hydrostatic pressure at the muscle and the brain, as well as alterations in the vestibulosympathetic reflex and baroreflex function expected with inversion (Charkoudian *et al,* 2004; Doba & Reis, 1974, Kerman, McAllen & Yates, 2000; Bosone, 2004; Fitzpatrick, 1996; Hobbs & McCloskey, 1987) would be expected to alter muscle rate of force development as well.

5. MVC FORCE OUTPUT

The hypothesis that MVC force and activation would decrease during inverted body position was not substantiated in the present study. This result was surprising, since there is much evidence of decreased muscle force output with increased hydrostatic pressures. The previously discussed rationale for decreased neuromuscular efficiency with submaximal contractions was not sufficient to inhibit force or activation during a MVC in the inverted position in this study.

6. EVOKED CONTRACTILE PROPERTIES

There was a numerical indication that time to peak twitch decreased in the inverted body position (i.e. faster muscle response). Ranatunga & Geeves (1991) found that in a mainly fast twitch muscle fiber from the rat, peak tension, time to peak and the time to half-relaxation of an elicited twitch were all increased during increased hydrostatic pressure (i.e. slower muscle response). Similarly, high pressure applied at the onset of a contraction increased the twitch tension (Cattell & Edwards, 1928), while decreasing rates of contraction and relaxation (Brown, 1934) in early animal studies. Another study also found increased twitch tension due to enhanced hydrostatic pressure that may have been caused by increased release of Ca^{2+} (Vawda, Ranatunga & Geeves, 1996). However, the quadriceps in the present inversion study would have been in an environment of decreased hydrostatic pressure. Hence, the slower muscle response associated with higher hydrostatic pressures in the aforementioned animal studies may be reversed to a certain extent with lower pressures in humans. Further studies are needed to study the effects of inverted body tilt on muscle force, activation and related twitch responses in humans.

7. LIMTITATIONS & CONSIDERATIONS FOR FUTURE RESEARCH

There are a number of limitations involved with the present research study. Therefore, considerations for future research are critical to the advancement in knowledge regarding this novel subject area of inversion and neuromuscular function.

Inverted body positions are a rare occurrence during daily activities; therefore precautions were taken in this study to ensure subject safety and accurate, reliable results. Prior health history was discussed with the subjects through the use of a PAR-Q form and a list of other health related factors that are not included on the PAR-Q form (see methodology for further details). However, subjects mentioned a feeling of light-headedness after the tilting protocol. This feeling may have decreased the subjects' ability and willingness to perform at optimal levels. Hence, future studies should monitor cerebral pressures and blood pressure (i.e. how does intracranial pressure correlate with performance).

With regards to the nervous system, future studies should consider the H-reflex function during inversion. Examining this variable was not possible during the present study since all electrically stimulated contractions performed were with maximal intensity. However, with submaximal contractions the excitability of the motoneuron could be investigated. There are currently conflicting results on tilt and the H-reflex. Knikou and Rymer (2003) reported a larger H-reflex response with 20 and 50 degree head down body tilt. However, Pacquet and Hui-Chan (1999) alternatively showed impedance of the H-reflex following head up body tilts. Moreover, a change from supine to vertical body position did not show any significant changes to the H-reflex (Alrowayeh, Sabbahi & Etnyre, 2005). Studies investigating the H-reflex will provide an even more comprehensive answer to the question of how neuromuscular function is impaired during inversion. Factors, such as those apparent in the present study (i.e. vestibular, cardiovascular, hydrostatic pressure at the limbs), may affect afferent excitability of motoneurones.

Furthermore, qualitative studies may need to be completed to see how individuals vary with their feelings of discomfort during a MVC while inverted. There may have also been some level of subject fear of both the protocol and apparatus. Therefore, it may be a good idea to include more orientation sessions prior to performing the actual protocol in future studies.

The heterogeneity of the subjects implies both strengths and weaknesses. A heterogeneous group does increase the variability of the study; however, it also helps in transferring the results to the population as a whole. Therefore, future studies may consider separate sample groups, as well as increasing the number of participants.

8. CONCLUSIONS

The inverted seated position had detrimental effects upon muscle activation with submaximal contractions and maximal instantaneous strength.

These findings are of interest at both basic physiological and applied levels. The impairments in submaximal muscle activation and instantaneous rate of force development likely illustrate the effects of changes in hydrostatic pressure, the cardiovascular parameters as well as sympathetic variables on muscle function. From an applied perspective, individuals confronted with inverted seated positions such as passengers within a helicopter that have crashed into water, military fighter pilots evading attack or drivers in overturned vehicles need a functional neuromuscular system to perform procedures allowing them to escape injury and survive.

Future studies are needed to determine what are the effects on the vestibular and cardiovascular systems and hydrostatic pressure at the muscle during inversion. The goal of these studies should be to provide a more in depth examination of the actual mechanisms responsible for the reported results of decreased neuromuscular performance during inversion.

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TABLES

Table 1: Means and standard deviations of both tilt positions

Condition	Upright	Inverted
MVC Forces (Newtons)	612 +/- 132	563 +/- 104
MVC EMG Hamstrings (mV.s)	0.00257 +/- 0.00342	0.00204 +/- 0.00104
Hamstrings EMG 25% (mV.s)	0.0006 +/- 0.00813	0.00047 +/- 0.00043
Hamstrings EMG 50% (mV.s)	0.00126 +/- 0.00126	0.00098 +/- 0.00067
Hamstrings EMG 75% (mV.s)	0.00179 +/- 0.00316	0.00138 +/- 0.00068
MVC EMG Quadriceps (mV.s)	0.0177 +/- 0.0163	0.01040 +/- 0.00431
Quadriceps EMG 25% (mV.s)	0.0027 +/- 0.00163	0.00212 +/- 0.00061
Quadriceps EMG 50% (mV.s)	0.00563 +/- 0.00168	0.00424 +/- 0.00171
Quadriceps EMG 75% (mV.s)	0.0103 +/- 0.0039	0.00725 +/- 0.00291
Hamstrings/Quadriceps Ratio 25%	0.262 +/- 0.308	0.235 +/- 0.185
Hamstrings/Quadriceps Ratio 50%	0.226 +/- 0.26 *	0.271 +/- 0.216
Hamstrings/Quadriceps Ratio 75%	0.203 +/- 0.255 *	0.281 +/- 0.307
Quadriceps EMG M-wave	2.463 +/- 0.814	2.042 +/- 1.292
ITT (% inactivation)	13.921 +/- 6.847	13.879 +/- 6.183
Resting Twitch Forces (Newtons)	139.652 +/- 60.237	138.541 +/- 50.312
Twitch Potentiation Ratio	0.87 +/- 0.0989	0.896 +/- 0.127
Instantaneous Strength	258.997 +/- 74.936 *	208.807 +/- 118.645
Half Relaxation Time (s)	0.0696 +/- 0.0187	0.066 +/- 0.025
Time to Peak Twitch (s)	0.177 +/- 0.236	0.133 +/- 0.230

Table 2: Statistical results for inverted values in relation to the upright position

Condition	ES	p-value	% difference
MVC Force	0.38	0.1964	8.2
MVC EMG Hamstrings	0.155	0.4031	20.6
Hamstrings EMG 25%	0.16	0.7714	21.7
Hamstrings EMG 50%	0.221	0.4895	22.2
Hamstrings EMG 75%	0.13	0.5227	22.9
MVC EMG Quadriceps	0.413	0.0778	41.3
Quadriceps EMG 25%	0.357	0.2857	21.5
Quadriceps EMG 50%	0.828	0.0395	24.7
Quadriceps EMG 75%	0.769	0.0156	29.3
Hamstrings/Quadriceps Ratio 25%	0.086	0.8893	10.1
Hamstrings/Quadriceps Ratio 50%	0.172	0.8097	-19.7
Hamstrings/Quadriceps Ratio 75%	0.304	0.7778	-38.0
Quadriceps EMG M-Wave	0.517	0.1682	17.1
ITT	0.006	0.5392	0.3
Resting Twitch Forces	0.412	0.1684	-10.4
Twitch Potentiation Ratios	0.267	0.781	-3.0
Instantaneous Strength	0.782	0.0053	-19.3
Half Relaxation Time	0.215	0.1347	6.2
Time to Peak Twitch	2.273	0.4294	-43.1

Table 3: Force-EMG position for slope values

	Slope	**r^2**
Upright	- 0.0000147 +/- 0.000116	0.966 +/- 0.0435
Inverted	0.0000201 +/- 0.0000317	0.926 +/- 0.11

FIGURES

Figure 1: Photo of subject oriented in the upright seated position

Figure 2: Photo of subject oriented in the inverted seated position

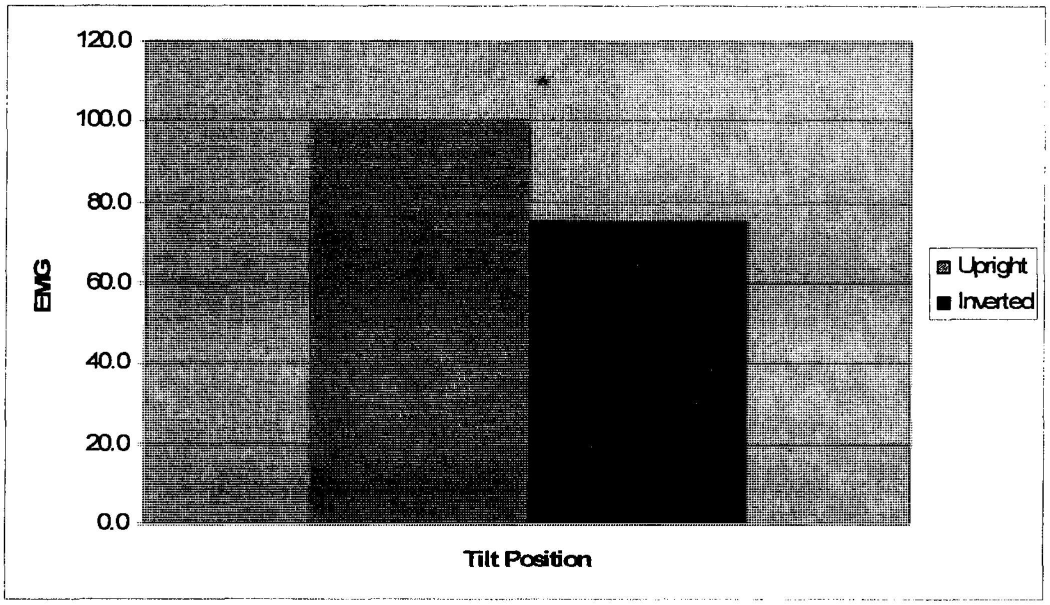

Figure 3: The graph depicts the mean EMG integral during 50% MVC knee extension, with values normalized so that the upright position is the control and set at 100%.

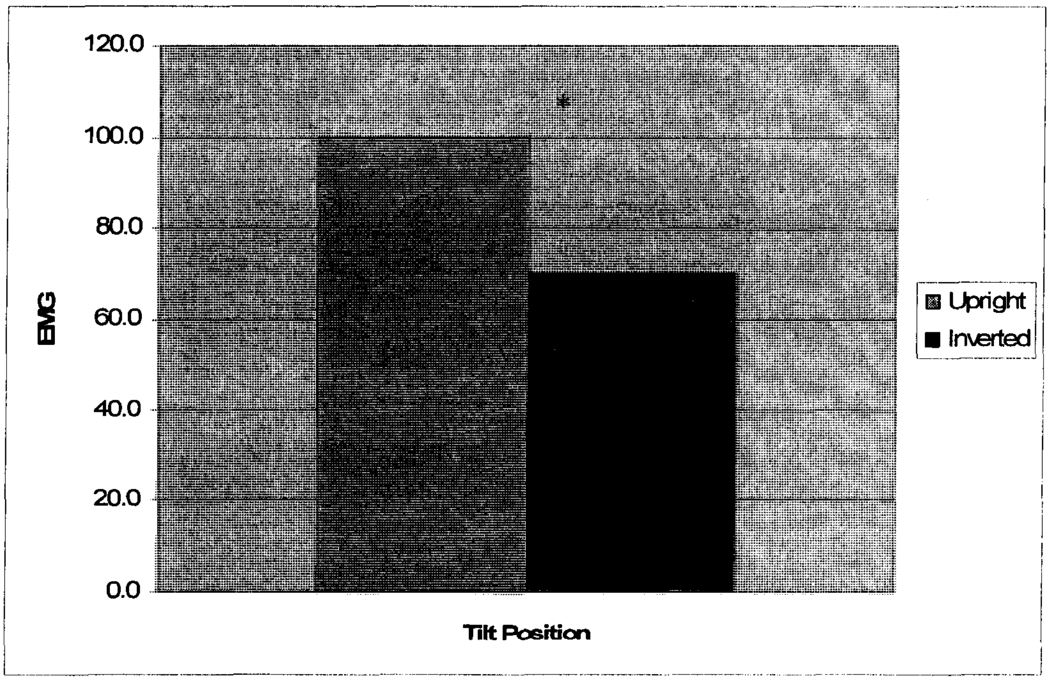

Figure 4: The graph depicts the mean EMG integral during 75% MVC knee extension, with values normalized so that the upright position is the control and set at 100%.

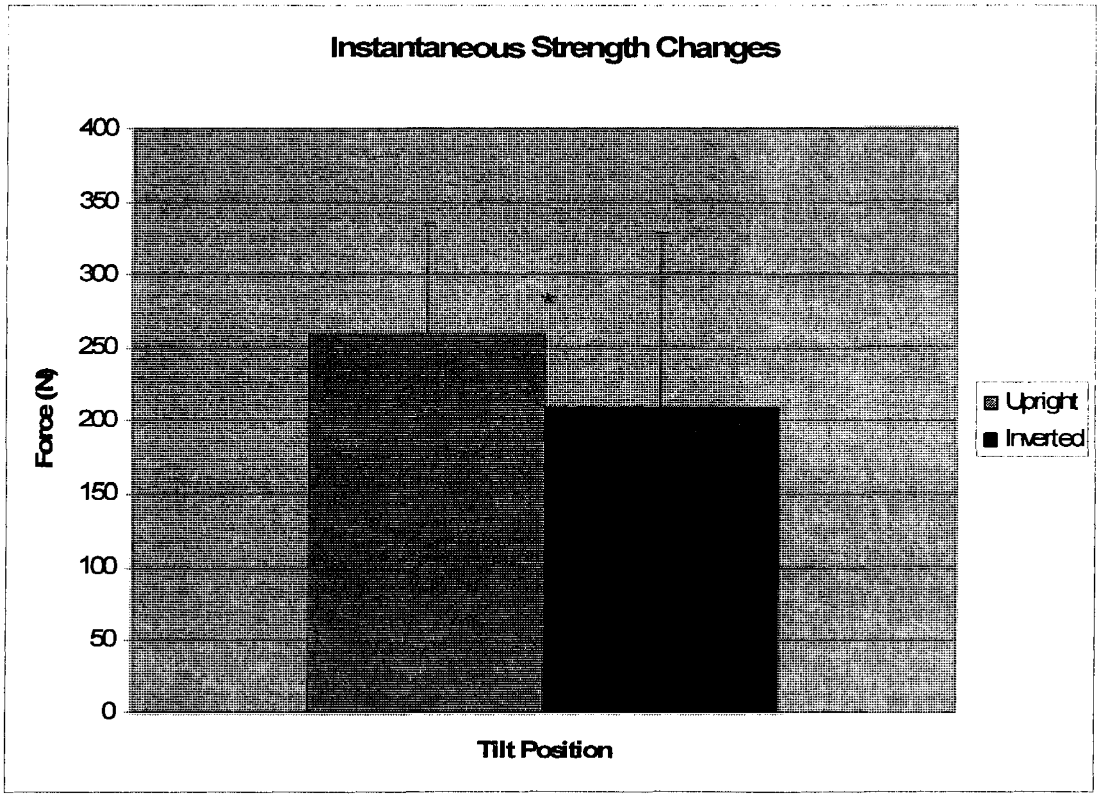

Figure 5: The mean force (in Newtons) during the first 100ms of a MVC. Vertical bars represent SD.