POSTURAL THREAT MODULATES HUMAN PERCEPTIONS OF BALANCE-RELATED MOVEMENT

by

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M.Sc., The University of British Columbia, 2013

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

(Kinesiology)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

September 2018

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Postural Threat Modulates Human Perceptions of Balance-Related Movement

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Abstract

Height-induced postural threat affects emotional state and upright feet-in-place standing balance behaviour during static, voluntary and dynamic tasks. Facing a threat to balance also affects sensory and cortical processes during balance tasks. As sensory and cognitive functions are crucial in forming perceptions of movement, balance-related changes during threatening conditions might be associated with changes in conscious perceptions. Therefore, the purpose of this thesis was to examine the changes and potential mechanisms underlying conscious perceptions of balance-relevant information during height-induced postural threat.

A combination of five experimental procedures utilized height-induced postural threat to manipulate emotional state, balance behaviour, and/or conscious perceptions of sensory stimuli involved in balance. The first three studies assessed conscious perception of body position during static stance, voluntary leaning, and dynamic stance, respectively. During quasi-static balance, height-induced threat increased gain between actual and perceived movement as postural sway decreased in amplitude while perceived movement amplitude remained the same in the HIGH (3.2 m, at the edge) compared to LOW (1.1 m, away from edge) height condition. During voluntary leaning, perceived whole-body position in a voluntary leaning task was larger at height across ten different leaning positions (within the limits of stability). During continuous mediolateral pseudorandom support surface rotations, perceived movement of the trunk was larger while actual lateral movement of the upper trunk did not change in the HIGH compared to LOW height conditions. The continuity of results across these three studies illustrate height-induced postural threat increases the amplitude of perceived movement during balance tasks

independent of behavioural changes. The final study included two experiments to determine how changes in somatosensory perceptual thresholds change with increased threat. Perceptual thresholds for ankle rotations were elevated while foot sole vibrations thresholds remained unchanged in the HIGH compared to LOW condition.

These studies further our understanding of the relationship between emotional state, perceived risk, and balance performance. Taken together, postural threat can affect emotional state and conscious perceptions of balance-related movement. These results highlight the effect of postural threat influences on neurophysiological and cognitive components of balance control, and provide insight into clinical balance assessment and intervention.

Lay Summary

Researchers use postural threat to study the direct effect of perceived fall risk on balance performance. Standing at the edge of an elevated support surface induces emotional state changes, including increased fear, anxiety and arousal, and decreased balance confidence and perceived stability, and cause young and older adults to employ a stiffening strategy when standing. Physiological and cognitive processes during conscious perceptions of movement are potential mechanisms underlying these behavioural changes. This thesis used novel applications of established psychophysical techniques to examine how threat influences human perceptions of stance. Collectively, the results of this thesis demonstrated height-induced postural threat amplifies the perception of different movement types during standing balance tasks. These results provide important insight into how fear may modify balance, and lead to the development of new assessment and treatment tools to reduce the likelihood and impact of falls.

Preface

All data presented in this thesis was collected by Taylor Cleworth (Cleworth TW), with assistance where noted, in the Neural Control of Posture and Movement Lab within the School of Kinesiology at the Vancouver-Point Grey campus of The University of British Columbia (UBC), Canada. All text and figures in this thesis were created by Cleworth TW under the supervision of Carpenter MG, with guidance from Inglis JT and Chua R. The UBC Clinical Research Ethics Board reviewed and approved all methodologies used throughout this thesis (combination of ID: H17-03282; Title: Threat effects on balance perceptions; and ID: H06-70316, Title: Central and peripheral mechanisms to human balance control).

A version of Chapter 2 was published in Neuroscience Letters [Cleworth, T. W., & Carpenter, M. G. (2016). Postural threat influences conscious perception of postural sway. *Neuroscience Letters*, 620, 127-131]. Cleworth TW was the lead investigator on the project and was responsible for conceptualizing the study, designing experimental procedures, data collection and analysis, interpretation of results, and drafting and revising the manuscript, figures, and tables. Carpenter MG was the supervisory author and contributed to the project conception and design, interpretation of results, as well as providing critical review of the manuscripts, figures, and tables.

A version of Chapter 3 was published in Gait and Posture [Cleworth, T. W., Inglis, J. T., & Carpenter, M. G. Postural threat influences the conscious perception of body position during voluntary leaning. *Gait & Posture*, 21-25]. Cleworth TW was the lead investigator on the project responsible for conceptualizing the study, designing experimental procedures, data collecting and analyzing, and drafting and revising the manuscripts and figures. Carpenter MG was the supervisory author and contributed to the project conception and design, as well as providing critical review of the manuscripts, figures, and tables.

Chapter 4 is being prepared for submission to a peer-reviewed journal [Cleworth, T. W., Adkin, A. L., Alum, H. J., Chua, R., Inglis, J. T., & Carpenter, M. G.]. Cleworth TW was the lead investigator on the project responsible for conceptualizing the study, designing experimental procedures, data collecting and analyzing, and drafting and revising the manuscripts and figures. Adkin AL contributed to the conception of the experiment, interpretation of the data, and critical review of written content and figures. Allum HJ contributed to conception of the experiment and critical review of the written document. Inglis JT and Chua R contributed to data analysis techniques, interpretation of the data, and provided critical review of the written document and figures. Carpenter MG was the supervisory author and contributed to the project conception and design, data analysis techniques, as well as providing critical review of the manuscripts, figures.

Chapter 5 is being prepared for submission to a peer-reviewed journal [Cleworth, T. W., Peters, R. M., Chua, R., Inglis, J. T., & Carpenter, M. G.]. Cleworth TW was the lead investigator on the project responsible for conceptualizing the study, designing experimental procedures, data collecting and analyzing, and drafting and revising the manuscripts and figures. Peter RM provided valuable assistance with study design, data analysis assistance, and critically reviewed written content and figures. Inglis JT and Chua R contributed to data analysis techniques, interpretation of the data, and provided critical review of the written document and figures. Carpenter MG was the supervisory author and contributed to the project conception and design, data analysis techniques, as well as providing critical review of the manuscripts, figures.

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List of Abbreviations

$\boldsymbol{\eta_p^2}$ – Partial Eta Squared – Statistic of effect size
1b – Muscle afferent nerve classification
Aβ – Cutaneous afferent nerve classification
AP – Anterior-Posterior body axis
BGA – Background Muscle Activity
BOS – Base of Support
COG Centre of Gravity
COM – Centre of (body) Mass
Conf – balance Confidence
COP – Centre of (foot) Pressure
CNS – Central Nervous System
d – Cohens D – Statistic of effect size
EC – Eyes Closed
EDA – Electrodermal activity
EEG - Electroencephalography
EMG – Electromyography
EO – Eyes Open
FA1 – Fast Adapting cutaneous mechanoreceptor classification type 1
FA2 – Fast Adapting cutaneous mechanoreceptor classification type 2
GTO – Golgi Tendon Organ
HIGH – High height-induced postural threat condition
IRED – InfraRED emitting diodes
LOW – Low height-induced postural threat condition
ML - Medio-lateral body axis
MP – Mean Position
MPF – Mean Power Frequency – frequency measure
POT – Potentiometer data – perceived movement measures
PM – Perceived Movement
QRMS – Quotient of Root Mean Square – gain measure for perceived to actual movement
RMS – Root Mean Square – amplitude measure
SD – Standard Deviation
SE – Standard Error
SEP – Somatosensory-Evoked cortical Potential
S1 – Primary Somatosensory cortex
S2 – Secondary Somatosensory cortex
SA1 – Slowly Adapting cutaneous mechanoreceptor classification type 1
SA2 – Slowly Adapting cutaneous mechanoreceptor classification type 2
SOL – Soleus muscle
TA – Tibialis Anterior muscle

Acknowledgements

I would like to acknowledge my supervisor Professor Mark Carpenter for the exemplar dedication and commitment put forward to high-quality science and graduate student mentorship. I owe a great deal of gratitude to his patience and support throughout my time as a graduate student. I am thankful for the opportunity to train and develop as a researcher under the supervision of Professor Carpenter.

I am grateful for the continued support and training provided by my committee members Professors J. Timothy Inglis and Romeo Chua, who have guided me throughout my time as a graduate student with compassion and devotion to research. I would also like to thank Professors John Allum and Allan Adkin for their support throughout my degree, in addition to Dr. Craig Tokuno and Dr. Ryan Peters for their time and knowledge that have guided my research. I would not be where I am today without this network of excellent researchers.

I would like to thank my examination committee, Professors Mark Redfern, Anthony Herdman and Peter Crocker for the constructive feedback and stimulating questions throughout the defense. It was a pleasure to work with you during the final moments of my degree.

I would like to thank the past and present members affiliated with the Neural Control of Posture and Movement Lab who have assisted me throughout my degree. I thank you for your support, feedback, and mentorship throughout each and every aspect associated with life as a graduate student.

A special thank you goes to my family and friends who have supported me throughout my academic career. I am truly grateful for their encouragement and never-ending support.

Finally, I would like to thank the School of Kinesiology and The University of British Columbia for their financial and administrative support throughout my degree.

Chapter 1: Introduction

1.1 Fear of falling influences on balance

Falling is of major concern in populations with balance deficits, specifically in the elderly as falling is the number one cause of injuries, and are experienced by more than one third of individuals 65 years or older (Accreditation Canada, 2014). The mortality rates and financial costs associated with falls, and related injuries, are on the rise in Canada. The number of deaths due to falls in Canada increased 65% from 2003 to 2008 (Public Health Agency of Canada, 2014) with the economic burden costing $8.7 billion in 2010 (Parachute Canada, 2014). Physiological deficits are not the only cause of a fall as psychological factors such as fear or confidence can affect balance. A fear of falling is a direct consequence of a fall, and is prevalent in over 50% of fallers (Legters, 2002). Fear of falling leads to inactivity through avoidance behaviours (Lachman et al., 1998; Howland et al., 1998), as well as increased fall risk (Legters, 2002). However, a fear of falling is also a predictor of future falls (Friedman et al., 2002). Fear of falling has been shown to alter balance performance in older adults (Maki et al., 1991; Okada et al., 2001), and young healthy adults (Davis et al., 2009). Therefore, there is a need to examine the relationship between fear, in addition to other possible emotional state changes, and standing balance.

1.2 Standing balance

Humans maintain standing balance by keeping the Centre of Mass (COM) within the base of support (BOS). The goal of a postural control system is to support the body against gravity, stabilize body segments during internal and external forces, and balance the body within the BOS, specifically during feet in place stance (Rothwell, 1994). COM, defined as an average position representing the position of equal mass distribution, and Centre of Pressure (COP), a point representing the sum of all forces acting on the feet thought to represent the net neuromuscular control of sway, are quantified during balance assessments. Three main tasks categorize balance control, maintenance of the COM within the BOS during unperturbed quiescent standing, voluntary movement of the COM, and reactive balance in preparation of and in response to destabilizing forces. The ability to perform these complex tasks is dependent on the integration of sensory feedback from multiple sources about the relative position, velocity and acceleration of individual body segments in relation to each other, to gravitational vertical, and to the support surface (Rothwell, 1994; Akram et al., 2008).

The vestibular, somatosensory, and visual sensory systems provide the central nervous system (CNS) with critical information to balance. The vestibular sensory system, thought to play more of a significant role in dynamic postural control, provides the CNS with information regarding head angular and linear acceleration from semicircular canals and otoliths, respectively. During quiet standing, vestibular information was once considered less relevant as the amplitude of movement required for perceptual sensory thresholds from the vestibular system is much greater than the movement amplitudes observed during quiet standing (Fitzpatrick &

McCloskey, 1994). However, patients with a vestibular loss have increased sway amplitudes compared to age-matched healthy controls (prior to the development of compensatory strategies typically observed over time, Allum et al., 2001), and reduced triggered balance reactions when exposed to support surface perturbations (Allum, et al., 1994). When combined with other sensory disturbances such as closing their eyes, standing on foam or a sway-referenced platform, participants with a vestibular loss may even experience a fall (Dichgans & Diener, 1989). Therefore, while the role of vestibular information in quiet stance is less clear, during more unstable conditions, vestibular information provides adequate and useful information about body orientation and head acceleration.

Multiple receptors in the somatosensory system, including cutaneous, muscle spindle, Golgi Tendon Organs (GTOs), and joint receptors, provide afferent feedback to the CNS during normal standing. Each receptor responds to unique forms of stimuli during standing balance. Cutaneous receptors located in the epidermal and dermal layers of the skin sense pressures underneath the foot and stretching of the skin across the ankle joint. The feedback from these receptors contributes to postural control. Tactile sensitivity decreases associated with ischemic block, hypothermic anaesthesia, age or diabetic neuropathies can alter foot sole cutaneous afferent firing rates (Lowrey et al., 2013), increase postural sway (McKeon & Hertel 2007; Patel et al., 2009; Stål et al., 2003; Wang & Lin 2008) and alter stepping responses to postural perturbations (Perry et al., 2000). Muscle spindles located in the ankle musculature (as well as other areas such as the trunk or neck) are involved in postural control as they indicate changes in muscle length. Age- or disease-related decline in muscle spindle afferent feedback is related to increased sway during unperturbed stance (Nardone et al., 2006), while increased activation of muscle spindles through tendon vibration causes a whole-body shift or lean during stance (Thompson et al., 2007). GTOs located at the musculotendinous junction in series with skeletal muscle fibers provide feedback related to muscle load. GTOs, in combination with other load bearing receptors, are thought to promote anti-gravity muscle loading (Duysens et al., 2000; Van Doornik et al., 2011) and are used to regulate muscle activity during standing balance (Faist et al., 2006; Horslen, 2016). Joint receptors may also contribute to postural control, indicating joint position and range of motion limits (Proske et al., 1988). While there is limited evidence to support the role of joint receptors during feet in place standing, joint receptors of the ankle have the potential to relay information regarding ankle angle and changes in pressure within the joint capsule (Refshauge & Fitzpatrick, 1995; Burke et al., 1988). Finally, the visual sensory system also plays a role in standing balance as removal of visual input increases sway amplitude (Kolleger et al., 1989; Carpenter et al., 2001), and linear motions of visual scenes can induce leaning behaviours (Lestienne et al., 1977). Removal of any one of these systems (vestibular, somatosensory, or visual) does not directly result in a fall; however, the removal of all three (or the reduction in reliable sensory information) will result in the inability to stand upright without assistance. The integration of these sensory systems are critical for the detection of postural sway during normal standing (Fitzpatrick & McCloskey, 1994). In addition, this integration is utilized when detecting stimuli and triggering postural responses (Allum et al., 1998; Inglis et al., 1994), and in developing an internal representation of the COM relative to any functional limits of stability and the external world (Young, 1982).

Postural stability has historically been considered a subcortically controlled task (Magnus, 1926; Bolton, 2015), and supported recently given that animal preparations retain the ability to remain upright during balance tasks (Honeycutt & Nichols, 2010) and sensorimotor processing delays associated with cortically-derived responses are potentially too long in duration to influence automated balance reactions (Diener et al., 1984; Bolton, 2015). However, indirect and direct evidence suggests a broadened neural network including the cerebral cortex is responsible for controlling balance, at least in the later stages of compensatory balance responses. Indirect support of a cortical component in balance control was demonstrated by examining disturbances in postural performance when the cerebral cortex was injured (abnormal balance responses in stroke patients, Geurts et al., 2005) or preoccupied by dual tasks (interference from cognitively demanding tasks impairs performance on posture, the cognitive task, or both, Andersson et al., 1998; Maki & McIlroy, 2007; Redfern et al., 2007; Woollacott & Shumway-Cook, 2001). More recently, temporally coupled neural activity (electroencephalography, EEG) to postural instability during quiet stance (Varghese et al., 2015; Slobounov et al., 2005) or larger balance reactions (Adkin et al., 2006; Dietz et al., 1984; Jacobs et al., 2008) have illustrated the direct involvement of the cerebral cortex across different standing balance tasks.

1.3 Objective measures of standing balance

Posturography is used as a diagnostic tool to assess postural instability. It uses objective measures of postural responses as a means to overcome subjective drawbacks currently used in clinical assessments (Visser et al., 2008). Balance assessment occurs during static, relatively unperturbed stance, or dynamic externally (platform rotations) or internally (weight shift) perturbed stance (Bloem et al., 2003). During dynamic stance, rapid perturbations can be used to assess defensive postural reactions (Allum et al., 1994; Carpenter et al., 2004; Cleworth et al., 2016), while continuous slow moving oscillatory perturbations can be used to assess anticipatory feed-forward and reactive feedback postural control (Diener et al., 1982; Dietz et al., 1993). Measures used to quantify postural control typically include kinetic (vertical and shear forces, and reactive torques), kinematic (individual segment or whole-body motion) and electromyography (EMG; muscle activity) recordings. More global measures of movement can be used to simplify the assessment of postural control, such as calculating the COM and COP (Winter, 1995). Descriptive measures in the time or frequency domain are then used to characterize postural sway. Amplitude, speed, and frequency based outcome measures of these assessments allow for researchers and clinicians to diagnose potential declines in balance, develop targeted intervention strategies, and to monitor long-term balance ability.

1.4 Differentiating fear, anxiety, arousal and vigilance (Sylvers et al., 2011)

Aversive stimuli, which are considered to be threatening, elicit emotions of fear and anxiety. Both these negative emotional states increase levels of vigilance and arousal. Arousal is a physiological and psychological state of excitement, whereas vigilance is a state of alertness and wakefulness typically associate with anticipation of dangerous stimuli. While generally considered being of similar cause, fear and anxiety can be classified as different emotions. Fear is generally associated with avoidance behaviours, including freezing, and is linked to the fight or flight response. When fearful, individuals attempt to escape the specific imminent threat. Anxiety on the other hand, is associated with a sustained level of hypervigilance and arousal in anticipation of an event or situation. Instead of avoiding scenarios evoking increased aversive emotional states, individuals remain within anxiety-evoking scenarios but are hyper-aroused and vigilant while threatened. In addition, moments of worry and uncertainty are more prevalent during anxiety provoking situations.

1.5 Indirect evidence linking fear and balance

Fear of falling has been linked to an increased risk of falls (Freidman et al., 2002), specifically in elderly individuals (Tinetti et al., 1988). Older adults with a fear of falling have an increase in postural sway (Maki et al., 1991), decrease in functional reach (Li et al., 2003) and an increased amplitude of balance reactions (Okada et al., 2001). Fear of falling can also lead to a number of adverse consequences including reduced muscle strength and decreased activity (Tinetti et al., 1994; Howland et al., 1998; Nevitt et al., 1989) and is associated with further aversive psychological states including anxiety and depression (Burker et al., 1995). There is also an association between anxiety and instability, where highly anxious individuals have larger sway profiles (Bolmont et al., 2002). While beneficial, it is difficult to illustrate a direct and/or causal relationship between the state of these participants and the behavioural outcomes. It is therefore important to induce state changes, as observed in those with a fear of falling, within otherwise healthy controls to examine fear-related changes in postural control strategies.

1.6 Postural threat influences on balance

Assessing the effect of fear of falling on balance, by comparing fearful and non-fearful groups, can be confounded by co-variables such as muscle strength, and makes it difficult to determine any causal relationship between fear of falling and balance deficits. Postural threat can be used to induce a perceived risk to balance, manipulate feelings of fearfulness and/or anxiety, and increase levels of arousal in otherwise healthy individuals (Brown & Frank, 1997; Carpenter et al., 2001; Horslen et al., 2013; 2014; Naranjo et al., 2015; 2016; Cleworth et al., 2012; 2016; Adkin et al., 2000; 2010; Hauck et al., 2008; Huffman et al., 2009; Davis et al., 2011). Elevation of a support surface is a common method used to induce postural threat during balance tasks (Brown & Frank, 1997). However, other forms of postural threat can be used, including the use of virtual reality scenes resembling real world heights (Cleworth et al., 2012; 2016; Simeonov et al., 2005) or the threat of an impending postural perturbation (Shaw et al., 2012; Horslen et al., 2013; Lim et al., 2017; Johnson et al., 2017). Psychological changes with postural threat include increases in perceived levels of fear and anxiety, and decreases in levels of stability and balance-related confidence (Adkin et al., 2008; Hauck et al., 2008; Huffman et al., 2009; Cleworth et al., 2012; Zaback et al., 2015; Naranjo et al., 2015). Consequently, balance-related behaviours change with postural threat. During moments of quiet standing at the edge of a hydraulic lift, individuals will lean away from the edge and adopt a stiffening strategy, evidenced by an increase in frequency and decrease in amplitude of COP (Carpenter et al., 1999; 2001; Cleworth et al., 2012) and COM displacements (Carpenter et al., 2001). In addition, changes in lower leg co-contraction occur, where increased levels of tibialis anterior (TA) and decreased soleus (SOL) activity is observed (Cleworth et al., 2016; Zaback et al., 2017). Postural threat also influences voluntary balance tasks. Anticipatory postural adjustments prior to a ‘rise to toes’ task decrease in amplitude, as evidenced by decreases in COP displacement and TA EMG activity, when standing at the edge of an elevated support surface (Adkin et al., 2002), but increase in amplitude with the threat of an impending perturbation (Phanthanourak et al., 2016). In addition, functional reach tasks decrease in amplitude when participants stand at the edge of a hydraulic lift (Hauck et al., 2008). Finally, postural threat also influences dynamic balance control. When individuals are perturbed, either through upper body pushes or support surface displacements, balance correcting responses are larger (Carpenter et al., 2004; Cleworth et al., 2016) and COM displacements are directed away from the threat (Brown & Frank, 1997; Carpenter et al., 2004).

1.7 Mechanisms involved in stance that may change with threat

While the mechanism underlying behavioural changes associated with threat remains in question, recent evidence has suggested changes in balance-related sensory function and cognitive demands may contribute to the threat-related effects on balance. Specific sensory systems and cognitive function have been explored to help understand behavioural modifications related to threat-induced states (Horlsen et al., 2013; 2014; Lim et al., 2017; Naranjo et al., 2015; 2016; Davis et al., 2011; Huffman et al., 2009; Zaback et al., 2015).

1.7.1 Somatosensory changes with postural threat

Postural threat adapts multiple sensory processes related to muscle spindle, cutaneous receptors and GTOs during standing balance tasks. Prochazka, Hulliger, Zangger and Appenteng(1985) originally observed increased muscle spindle sensitivity in cats, and proposed gamma motor neuron activity could increase independent of alpha motor neuron activity, which was dependent on the motor tasks completed (Prochazka et al., 1985). Increased spindle sensitivity has since been proposed to occur in humans using indirect evidence when standing under threatening conditions. Stretch reflexes, evoked by a tendon tap, increase in amplitude when standing under threatening conditions (Horslen et al., 2013). These results were unlikely mediated by changes in the reflex pathway outside of spindle sensitivity, such as the motor neuron pool, as Hoffman reflexes, an electrical substitute to the tendon reflex bypassing the muscle spindle, remain unchanged at height. In support of muscle spindle sensitivity changes, ramp and hold perturbations of the ankle elicited larger stretch reflex amplitude and gain relationships (between stretch velocity and reflex amplitude) with postural threat (Horslen, 2016). GTO-related 1b inhibition was also modulated with threat, where decreased inhibition was observed in high compared to low threat conditions. Finally, cutaneous reflexes elicited from electrical stimuli of the sural nerve only appear to increase in amplitude with threat when background activity increased as well, although cutaneous reflexes do change with arousal during gait (Haridas et al., 2008; Zaback et al., 2018). When controlling for background activity, cutaneous reflexes do not appear to be influenced directly by threat during standing. However, arousal can change blood flow to the skin, which may subsequently modulate cutaneous receptors (Elam et al., 2004; Roberts, 1997).

1.7.2 Vestibular changes with postural threat

Early anatomical evidence suggested a direct influence of anxiety on the vestibular network. Reciprocal connections exist between supraspinal centres involved in postural control and threat assessment, including the dorsal raphe and locus coeruleus, thalamus, amygdala, basal ganglia, hypothalamus, parabrachial nucleus, and vestibular nuclei (Balaban, 2002; 2004; Staab et al., 2013). Expanding on anatomical work, threat-related increases in fear, arousal, and anxiety occur in parallel to changes in vestibular-evoked responses. Vestibular-evoked balance responses in ground reaction forces increase while standing on elevated support surfaces (Horslen et al., 2014), and responses in muscle activity of the lower leg increase while standing under threat of perturbations (Lim et al., 2017). The gain of vestibular ocular reflexes and vestibular evoked myogenic potentials also increase when standing at the edge of a hydraulic lift (Naranjo et al., 2015; 2016).In combination, there appears a direct relationship between postural threat and vestibular function in humans, likely affecting the vestibular nuclei and not the vestibular apparatus.

1.7.3 Cortical-related changes with postural threat

Postural threat modifies some of the neurological correlates and cortical areas involved in postural orientation and equilibrium, as evidenced using EEG. Cortical potentials associated with unexpected balance perturbations have a large N1 (or termed N100) component which are thought to involve somatosensory inputs from the balance disturbance (Adkin et al., 2006; Quant et al., 2004). These N1 responses increase in amplitude, but do not change in latency, with postural threat (Adkin et al, 2008; Sibley et al, 2010). Early components of cutaneous evoked cortical potentials remain unchanged when there is a threat to balance (Davis et al., 2011; Horslen, 2016). However, later components, specifically P110-N140, which are thought to represent the neural activity in secondary somatosensory cortex (S2) and the posterior parietal cortex (Libet et al., 1967; Schubert et al., 2006), increase in amplitude when standing at the edge of an elevated support surface (Horslen, 2016).

1.7.4 Cognitive processes change with postural threat

Postural threat changes the focus of attention, and may be related to threat-related changes in balance performance (Huffman et al., 2009; Zaback et al., 2015; 2016). Individuals become more conscious about the appearance of their balance-related movements (Huffman et al., 2009; Zaback et al., 2015), become preoccupied with threat-related stimuli and movement processes, and attempt to use various coping strategies to regulate anxiety (Zaback et al., 2016). Shifting body position away from the edge of an elevated support surface has been associated with increased conscious monitoring of postural control (Huffman et al., 2009), while conscious appraisals of movement appearance are related to a decrease in sway amplitude (Zaback et al., 2015). Broadly shifting attention in threatening conditions can influence attentional processes associated with postural control and lead to significant changes in balance behaviour.

1.8 Additional views to explain threat effects on standing behavior

Previous literature has used a common approach of attributing these changes in sensory and cortical processes, and cognitive function to explain some of the behavioural changes observed during postural threat. However, these changes individually or in combination may influence balance by changing the way in which movements related to balance are perceived (Llewellyn et al., 1990; Horslen et al., 2013). This is a reasonable assumption given perceptual interpretations shape postural responses (Mergner & Rosemeier, 1998) and these perceptions not only rely on the afferent information received by the CNS, but also relies on the higher order cortical processing of sensory information. There is indirect evidence of an incongruence between perceived and actual balance performance, such as when decreased feelings of stability occur despite no changes in actual sway amplitude (Huffman et al., 2009), and anecdotal evidence from subjective reports of increased perceived sway amplitude during standing despite decreased sway (height-induced postural threat studies). Therefore, it is reasonable to suspect a change in conscious perceptions related to movements can influence balance behaviour during threatening tasks, and these may be as problematic as actual physiological deficits.

1.9 Perception during standing behavior

Perception is the conscious awareness of accessible stimuli or environmental features through interpretation and understanding of sensory information. Perception is not merely a copy of the physical world conveyed through the passive influx of sensory information, but is shaped by cognition to make inferences about the world (stimulus). Studying perception involves the investigation of the numerous sensory receptors independently or in combination with other receptors, the afferent pathways that relay information from the receptor to the cerebral cortex, and the processes involved in interpreting those signals. Perceptions have been studied in individual sensory systems, such as vision (Posner, 1980; Verghese, 2001), but are also thought to play a significant role in balance. Detecting moments of sway during balance tasks is critical for the maintenance of stable posture. Moments of instability or during responses that decrease the likelihood of a fall (Slobounov et al., 2005) evoke cortical potentials that are related to the processing of sensory information (Adkin et al., 2006). Sensory information from vestibular, visual and somatosensory systems provide information of body orientation and body position relative to the environment and other body segments. Integrating sensory information into a body in space representation can be further shaped by cognitive factors during postural tasks (Mergner & Rosemeier, 1998).

General forms of perceptions during stance are measured clinically and experimentally. Perceived stability is used as a qualitative measure of perceived balance performance in conjunction with, or independent from, objective measures of balance (Schiepatti et al., 1999). Prior studies assessing perceived stability show young healthy adults can accurately detect changes in objective stability across increased postural task complexity using a subjective stability scale (Schieppatti et al., 1999). However, increased perceptions of instability occur without concomitant changes in sway amplitude in patients with Parkinson's disease (Horak et al., 1992; Schieppati et al., 1993), orthostatic tremor (Fung et al., 2001) or visual height intolerance (Huppert et al., 2013), and in young healthy adults while standing under threatening conditions (Huffman et al., 2009).

1.10 Perception relies on sensory systems

Developing an understanding of our environment and our position in it occurs through the senses. As explained by Fitzpatrick and McCloskey (1994), perceived movement and sensory acuity begins with stimulus detection, followed by neural mechanisms involved in sensory processing, and ends with a report indicating stimulus characteristics. Sensory information originates from stimulus transduction, where energy collected from specialized receptors is converted into electrical signals and propagated into the CNS (Kandel et al., 2013). The electrical signal is a common signaling mechanism across all forms of sensory systems, whereas the specialized receptors are specific to a form of stimulus. Skin deformation, motion, stretch and vibration activate mechanoreceptors, which give rise to the sense of touch. Muscle spindles signal for changes in muscle length and the speed of muscle length changes. Hair cells in the vestibular system activate when the head accelerates in an angular or linear direction (depending on the component). Characteristics of the stimulus transfer through the nervous system by changes in the number and firing rate of afferent fibers. Larger stimuli activate more sensory receptors thus activating more afferent fibers, and/or discharge action potentials at a higher frequency. These sensory neurons synapse onto structures of the CNS, which typically relate to a single sensory modality, and terminate within multiple designated cortical areas. This link is the first step in central processing of sensory information.

In order to understand the complexity of a sensory pathway, consider one form of sensory information. When there is a tactile stimulus delivered to the sole of the foot, the class of skin receptors innervated by large diameter Aβ fibers relay information via action potentials up through the dorsal horn of the first sacral neural foramen into the spinal cord. This sensory nerve fiber ascends medially in the fasciculus gracilis and synapses onto the nucleus gracilis within the medulla (for upper limb, afferent fibers ascend in the fasciculus cuneatus and synapse onto the nucleus cuneatus). Secondary neurons cross the midline in the medulla and project to the thalamus terminating in the ventral posterior nucleus (lateral zone) and synapsing onto tertiary neurons. These tertiary neurons then project to the somatotopically organized primary somatosensory cortex, specifically area 3b deep within the central sulcus. From here, higher order neural processes receive and interpret the sensory information.

1.11 Perception relies on cortical processing

Recent evidence suggests both parallel and serial sensory processing in later cortical stages using animal preparations (Inui et al., 2004; Palva et al., 2005). A complex neural network involving numerous cortical regions pull together information from numerous sensory systems to formulate perceptions, which can be related to whole-body position or individual sensory modalities. These percepts have been illustrated not to resemble mirror images of a given stimuli, but rather are creations within the mind influenced by prior experience and central states of the individual. Specifically, perceptions related to specific characteristics of physical stimuli can be enhanced while others are ignored.

Physiological evidence has suggested the neural activity in primary somatosensory cortex (S1) may not be enough to elicit the conscious perception of a stimulus. Serial processing of sensory information through higher cortical areas involved in cognition occurs during unimodal sensory stimuli (Inui et al., 2004) and may influence the conscious perception of a stimulus. Event-related potentials from subdural (Libet et al., 1967), scalp (Schubert et al., 2006), and magnetoencephalography recordings (Preissl et al., 2001), as well as cortico-cortical coherence (Palva et al., 2005) revealed early components (ranging from 30 to 80ms) were strongly correlated with tactile stimuli in S1 independent of conscious awareness. When stimuli escaped awareness, there were little to no activity in later components. Sensory information relays from S1 to a number of cortical areas including a unimodal association cortex S2. Direct links between S1 and S2 are unlikely involved in consciousness (Gallace & Spence, 2008). Instead, the conscious perception of stimuli comes from higher order association areas, including the posterior parietal cortex, which receives information from, and provides feedback to S2. The neural correlates to perceptual awareness stems from the synchronization of neural activity between S2 and higher order association areas (Palva et al., 2005). Thus, it is not surprising that later components of the cortically evoked responses explained above strongly correlate with tactile consciousness (Libet et al., 1967; Preissl et al., 2001; Schubert et al., 2006).

1.12 How is perception measured? The field of psychophysics

While sensory physiology examines the neural consequences of a stimulus, the study of psychophysics quantifies the relationships between physical stimuli and the perceived sensations they evoke (Kandel et al., 2013). Participants typically rate their perceived sensation to a specific physical attribute of a stimulus using verbal reports, subjective scales, or individualized devices. As previously described, each specific sensory system involves a distinct neural network with multiple components, starting with the receptor and ascending into the spinal cord, brainstem, thalamus and cortical levels. These ‘perceptual systems’ are used to make inferences about the world and interactions within it by transforming sensory ‘code’ into a conscious perception. However, often the perception on directionality, amplitude and timing of stimuli are necessary to be functionally relevant. For example, if an ankle is dorsi-flexed during a simple kinaesthetic joint matching task, the basic perception that a movement has occurred will not allow participants to interpret direction, and lead to incorrect responses when trying to indicate where the ankle is positioned.

There are a few methodological techniques available for use in psychophysical experiments. Testing sensory sensitivity involves the application of a range of stimuli above and below sensory thresholds. Experimenters can use a) forced choice, where participants are presented with two intervals and are asked to indicate where the target stimuli occurred; b) magnitude estimation, where a single stimulus is given and participants must report using a known scale; c) reaction time; d) just noticeable differences, where participants are asked to report when two stimuli are different; and e) a method of limits, stimuli are presented in ascending and descending steps until the smallest amplitude of a stimulus can be perceived. Using a method of limits, or adapted staircase method, can assess perceptual thresholds. Perceptual thresholds to sensory stimuli provide valuable information regarding sensory function. For example, elevated tactile thresholds have been linked to somatosensory deficits and age (Peters et al., 2016), while cognitive processes such as fear and attention can simply alter sensory perceptual thresholds (vision: Posner, 1980; Verghese, 2001; audition: Jones & Yee, 1993; Haykin & Chen, 2005; touch: Craig & Evans, 1995; and proprioception: Yasuda et al., 2014).

Subjective reporting is typically used to quantify the sensations participants perceive. These reports are grounded by some form of normalization (Kandel et al., 2013), thus making it acceptable to compare responses across participants. In relation to upright stance, continuous integration of sensory information from multiple sources is likely utilized to formulate a single perception of body orientation and position. Thus, it is beneficial to understand transient components (for example, discriminatory thresholds), as well as more continuous global perceptions during moments of upright stance.

1.13 Threat-related neurophysiological changes can alter perceptions of balance-related movement

Conscious perceptions related to balance-relevant sensory information have the potential to be influenced by postural threat due to the recent evidence suggesting threat-related changes in sensory systems (Horslen et al., 2013; Naranjo et al., 2015; 2016; Lim et al., 2017), cortical activity (Adkin et al., 2008; Sibley et al., 2010; Horslen, 2016), and cognitive function (Huffman et al. 2009; Zaback et al., 2015; 2016; Johnson et al., 2017). Previous studies have already established threat-related changes in conscious perceptions across a range of sensory modalities. By increasing the aversive emotional state, it appears that perceptions of unpleasant stimuli characteristics amplify, while perceptions of pleasant or calming features, if present, weaken. In addition, arousal can modulate perception based on stimulus priority (Mather et al., 2016). Fear and anxiety may bias attention toward threatening stimuli (MacLeod & Mathews, 1988), or amplify sensory processing through neurophysiological changes (Mather et al., 2016; Zadra & Clore, 2011). Fear (or similar emotional states) can change the visual perception of environmental features. Slopes are perceived as steeper (Stefanucci et al., 2008), heights are perceived to be higher (Clerkin et al., 2009), while target size (Teachman et al., 2008) and insects (Vasey et al., 2012) are perceived to be bigger when fearful. Fear also amplifies aversive components of auditory stimuli, where auditory tones are perceived as louder (Siegel & Steffanucci, 2011; Asutay & Västfjäll, 2012), closer (Gagnon et al., 2013) and more annoying (Borsky, 1979). Stressful or aversive states also influence the perception of taste. Weaker perceptions of the pleasant aspects of tastes, such as sweet or savory, occur with stress (Al'absi et al., 2012) whereas negative moods lead to stronger perceptions of unpleasant bitter and sour tastes (Platte et al., 2013). It is unknown whether these threat-related changes in perception occur in balance-related sensory systems, specifically those involved in postural control, but it may explain why perceptions of balance stability decrease without concomitant changes in sway amplitude (Huffman et al., 2009).

1.14 Aims of thesis

The overall aim of this thesis was to understand how height-induced postural threat, and the concomitant changes in emotional state, sensory function, and attentional processes, influence the perceptions of balance-related movement. Three studies were used to examine the effect of height-induced threat on conscious perceptions of whole-body movement across different balance tasks, including quiet standing, volitional leaning, and externally perturbed stance. A final study investigated the effect of height-induced postural threat on lower leg somatosensory acuity to further examine the potential mechanisms underlying threat-related changes in perceived movement.

Chapter 2: Postural threat influences conscious perception of postural sway

2.1 Introduction

Postural control, in addition to fear and anxiety, is altered when under the threat of a balance perturbation or fall from an elevated surface (Carpenter et al., 2001; Shaw et al., 2012; Horslen et al., 2013). With threat, healthy young and older adults typically adopt a postural stiffening strategy characterized by decreased amplitude and increased frequency of sway; they also lean away from the direction of the threat (Huffman et al., 2009; Cleworth et al., 2012; Carpenter et al., 2006). Threat-related postural changes are accompanied by changes in sensory function; the gain of proprioceptive and vestibular reflexes are increased (Horslen et al., 2013; Horslen et al., 2014; Davis et al., 2011; Naranjo et al., 2015) and the amplitude of cortical sensory processes are also magnified with threat (Adkin et al., 2008). However, what is currently unknown is how these changes in postural control and altered sensory systems may influence the conscious perception of balance-related sensory information under threatening conditions.

Negative or aversive emotions, such as fear or anxiety, have been linked to changes in perception of auditory, visual and physical stimuli. Visual perceptions of the magnitude/size of an observed height (Clerkin et al., 2009), slope (Stefanucci et al., 2008), physical object (Teachman et al., 2008) or insect (Vasey et al., 2012), are greater with fear. Likewise, with increases in fear, auditory tones are perceived to be louder (Siegel & Stefanucci, 2011; Asutay & Västfjäll, 2012), closer (Gagnon et al., 2013), and more annoying (Borsky, 1979); tactile stimuli are perceived to last longer (Shi et al., 2012); and perceived pain is increased (Rhudy &

Meagher, 2000). Finally, stimuli are perceived as more aversive, or more threatening, when individuals are in a state of increased anxiety or fear (Asutay & Västfjäll, 2012). With this in mind, an altered perception of sway could explain why participants report feeling more unstable (Huffman et al., 2009; Cleworth et al., 2012), despite the fact that the amplitude of sway decreases (Cleworth et al., 2012), or remains unchanged (Huffman et al., 2009) when standing at high heights.

Therefore, the purpose of this study was to examine how changes in threat can influence conscious perceptions of postural sway. The study was designed to test the hypothesis that the threat-related changes in actual sway amplitude and frequency will be different from measures of perceived sway recorded using a novel online tracking device and retrospective report.

2.2 Methods

Twenty young healthy adults (age 20.9 ± 2.1 years) volunteered for the study from the University of British Columbia and surrounding area. All participants reported no known neurological or orthopedic disorders that could affect their balance, and gave written consent prior to participation in accordance with the University of British Columbia Clinical Research Ethics Board.

2.2.1 Procedure

Participants stood on a force plate (#K00407, Bertec, USA) mounted at the edge of a hydraulic lift (2.13 m × 1.52 m, M419-207B10H01D, Penta-lift, Canada) at simulated ground level (LOW) and at 3.2 m above ground level (HIGH; Figure 2-1 A-B) (Davis et al., 2009). In the LOW condition, a table was placed in front of the platform, level with the support surface, to simulate ground level (standing away from an edge). Platform heights were presented in an ascending order to maximize the effect of height (Adkin et al., 2000). Participants stood barefoot, with their hands at their side in all trials. Feet were placed at a width equal to the length of their feet, and the position was marked and kept constant throughout all experimental trials. A harness was fitted to the participants and attached to the ceiling with a rope that had enough slack to ensure it provided no weight bearing or feedback during experimental trials. Participants were instructed to stand normal or to stand normal while tracking their movements in real-time in the anterior-posterior plane using a hand-held potentiometer (POT; Figure 2-1C). In all trials, the POT was held in the right hand, but only in the tracking conditions was the POT manipulated with the thumb. Both standing tasks were performed with eyes open (EO) and closed (EC). For each participant, trial order was randomly presented in the LOW condition, and then the order was matched in the HIGH condition. Prior to the first experimental condition, participants practiced standing under three different conditions with their eyes open to become familiar with the experimental tasks: 1) mentally track sway during quiet standing, 2) use the POT to track large amplitude sinusoidal voluntary sway, and 3) use the POT to track sway during quiet standing. Each practice trial was performed until participants felt comfortable with the task, and the experimenter visually confirmed that the participants were able to track their sway using the POT (2nd and 3rd practice trial); each practice trial lasted approximately 15-30 seconds.

2.2.2 Measurements

3D Motion capture data was collected (100 Hz; Optotrak, Northern Digital Inc.) to estimate Centre of Mass (COM) position. Due to the large recording area, and line of site issues, associated with capturing motion analysis data at both low and high heights, kinematic data recordings were limited to from 5 infrared emitting diodes (IREDs) placed over the following bony landmarks on the left side of the body: acromion process, greater trochanter, lateral epicondyle of the knee, lateral malleolus, and base of the 5th metatarsal. Periods of missing data (< 500 ms) were interpolated using a cubic spline, otherwise the trial was truncated to the longest duration with usable data for COM only (2 trials at 45 seconds and 58 seconds, respectively). In accordance with Brown and Frank (1997), the Anterior-Posterior (AP) horizontal COM displacement was calculated by using a 4 segment model from 2-dimensional coordinates defining the foot, shank, thigh and head/arms/trunk segments in conjunction with anthropometric data (Winter, 2004), and filtered offline using a 1.5 Hz dual-pass Butterworth filter (Gage et al., 2004).

POT voltages and ground reaction forces and moments were collected at 100 Hz (Power 1401 with Spike 5 software, CED, UK). Centre of Pressure (COP) was calculated from ground reaction forces low-pass filtered at 3 Hz (Gage et al., 2004), and POT was filtered at 1.5Hz (similar to COM), using dual-pass Butterworth filters. For each COP, COM, and POT data, the mean position was calculated and subtracted from each respective trace to remove any bias. Root mean square (RMS) and mean power frequency (MPF) were calculated from COP, COM, and POT data in the AP direction from the unbiased signal to quantify the amplitude and frequency, respectively, of actual and perceived sway during quiet standing trials:

$$MPF = \frac{\sum f \cdot P(f)}{\sum P(f)}$$

where f represents frequencies within the signal and P is the power amplitude at each frequency; and:

$$RMS = \sqrt{\frac{1}{n}\sum_{i=1}^{n} x_i^2}$$

where x is individual sample and n is the number of data points. In order to determine how well the participants could use the POT to track sway under normal conditions, cross-correlations were calculated between the POT signal, and COP and COM signals respectively, at the LOW height condition (averaged across visual conditions).

Mean electrodermal activity (EDA) was calculated for each trial by averaging the level of EDA (sampled at 100 Hz) collected during the task from two electrodes placed on the thenar and hypothenar eminences of the left hand (Skin Conductance Module 2502, Cambridge Electronic Design, UK). Prior to each experimental task, participants rated their confidence on a scale from

0 (not confident at all) to 100 (completely confident) that they could remain upright and avoid a fall in the upcoming condition. After each condition, participants reported their level of fear on a scale from 0 (I did not feel fearful at all) to 100 (I felt completely fearful), perceived stability on a scale from 0 (I did not feel stable at all) to 100 (I felt completely stable), as well as rated their perceived movement from 0 (I did not move at all) to 100 (I moved as much as possible). In addition, participants rated their state anxiety using a contextually modified version of the Sport Anxiety Scale (Geh et al., 2011) with 10 questions related to their somatic anxiety and worry in reference to the condition previously performed. All questions were on a 9-point Likert scale ranging from 1 (I did not feel this at all) to 9 (I felt this extremely).

2.2.3 Statistical Analysis

A 2 x 2 repeated measures ANOVA was used to examine the effects of height (LOW vs HIGH) and vision (eyes open vs closed) on all POT measures. All other measures were analyzed using a 2 x 2 x 2 repeated measures ANOVA to examine the effects of task (Normal vs tracking), height, and Vision. Significant interactions were explored post-hoc using paired t-tests. Significance was set at $p=0.05$.

2.3 Results

At LOW height, moderate cross-correlations coefficients were observed between the POT and COP signals (mean ± standard error of $r = 0.47 \pm 0.03$) and the POT and COM signals ($r = 0.48 \pm 0.04$). The POT signal had an average phase-lag of 197 ± 58.5 ms relative to the COP signal and 352.2 ± 57.5 ms relative to the COM signal. There were no main or interaction effects of height or vision on POT RMS or POT MPF (Figure 2-2C and Table 2-1, $\eta_p^2 < 0.168$). However, main effects of height were observed for COP and COM measures, with a significant shift in mean COP (41.9 ± 3.9 mm LOW and 29.3 ± 3.8 mm HIGH) and COM (30.5 ± 6.5 mm LOW and 19.5 ± 6.9 mm HIGH) away from the edge (Table 2.1, $\eta_p^2 > 0.66$), significant decreases in the RMS of COP (4.8 ± 0.4 mm LOW and 3.9 ± 0.3 mm HIGH) and COM (4.6 ± 0.3 mm LOW and 3.8 ± 0.3 mm HIGH), and significant increases in MPF of COP (0.18 ± 0.01 Hz LOW and 0.24 ± 0.02 Hz HIGH) in the HIGH compared to LOW conditions (Figure 2-2 A-B and Table 2-1, $\eta_p^2 > 0.45$). There was a significant effect of vision on MPF of COP (0.19 ± 0.02 Hz LOW and 0.24 ± 0.02 Hz HIGH) and COM (0.10 ± 0.01 Hz LOW and 0.13 ± 0.01 Hz HIGH) with higher MPF observed in EC compared to EO conditions. Likewise, there was a significant effect of task on RMS of COP (3.7 ± 0.3mm LOW and 5.0 ± 0.5mm HIGH) and COM (3.7 ± 0.3mm LOW and 4.7 ± 0.4mm HIGH), with larger COP and COM RMS observed in tracking compared to normal conditions. All other effects (main or interaction) on COP and COM were non-significant (see Table 2-1).

Increased height significantly decreased balance confidence and stability, and increased fear, anxiety and EDA (see Table 2-1 and 2-2, $\eta_p^2 > 0.35$). No main effects of, or interactions with, height were observed for rated perceived movement. Vision significantly influenced rated perceived movement and EDA, with larger movement and lower arousal observed in eyes closed compared to eyes open conditions (see Table 2-1, $\eta_p^2 > 0.29$). Greater rated perceived movement was reported in the tracking compared to normal standing condition (see Table 2-1, $\eta_p^2 = 0.228$).

2.4 Discussion

The current study was the first to demonstrate conscious perceptions of movement associated with sway do not change in accordance with decreases in actual sway amplitude when a threat to posture is present. As shown previously, sway amplitude decreases, and frequency increases with threat (Carpenter et al., 2001; Huffman et al., 2009; Cleworth et al., 2012). However, the amount of perceived sway, recorded with online tracking and self-reported measures, did not change between height conditions (Figure 2-2).

The ability to record online tracking of participants' perception of sway during stance was also unique to this study. The POT provided reasonable estimates of actual sway behavior, as indicated by the degree to which the tracked sway matched the actual COP and COM displacements (Figure 2-1D) and moderate cross-correlation co-efficients observed between the POT and COP and COM signals at LOW height conditions. Increases in sway with tracking, compared to non-tracking conditions were observed and expected, based on prior reports of increased sway amplitude during dual-task conditions (Anderson et al., 1998; Dault et al., 2001). However, the tracking task did not influence the effect of height, with amplitude and frequency changes with height found to be independent of tracking condition.

The observed disconnect between conscious perception of sway and actual changes in posture with threat could be explained by an increased focus of attention toward conscious motor processing (conscious monitoring and control of movement processes). Studies have shown that while the attention to conscious motor processing is increased with threat, it is not associated with decreases in sway amplitude (Huffman et al., 2009; Zaback et al., 2016). Alternatively, the lack of change in conscious perception of sway could be linked to altered sensory changes known to occur when standing under threatening conditions. Increases in proprioceptive, and vestibular reflex gains have been shown with threat (Horslen et al., 2013; 2014; Davis et al., 2011; Naranjo et al., 2015), which in some cases, may be facilitated by changes in muscles length and increased tonic activity in TA if backward leaning is not controlled. While the proprioceptive changes seen at the spinal level are not evident in early cortical responses (Davis et al., 2011), later cortical changes associated with sensory processing (Dietz et al., 1984), are found to increase significantly when standing at height (Adkin et al., 2008). As a result, while participants reduce the amount of sway at height, a concomitant increase in sensory gain (Horslen et al., 2013; 2014; Naranjo et al., 2015) may allow the CNS to acquire a greater amount of afferent information comparable to a normal state (Llewellyn et al., 1990) and lead to an altered perception, in which they perceive themselves to be swaying more than what is actually happening at height. These results corroborate with studies showing fear-related distortions in perceptions, where threatening features are accentuated (Rachman & Cuk, 1992). Perceiving a spider to be more active or increasing sensitivity to loudness can enhance (i.e. amplify or facilitate) coping mechanisms when necessary (Asutay & Västfjäll, 2012; Rachman & Cuk, 1992). Similarly perceiving more movement may allow for the improved detection of destabilizing stimuli, consequently improving postural stability.

How such a disconnect between perceived sway and actual performance may contribute to balance deficits and falls in participants with underlying fear and anxiety is currently unknown. Future research should investigate how perceptions of more dynamic balance tasks may be influenced by threat, and how the changes may be linked to specific sources of sensory modulation.

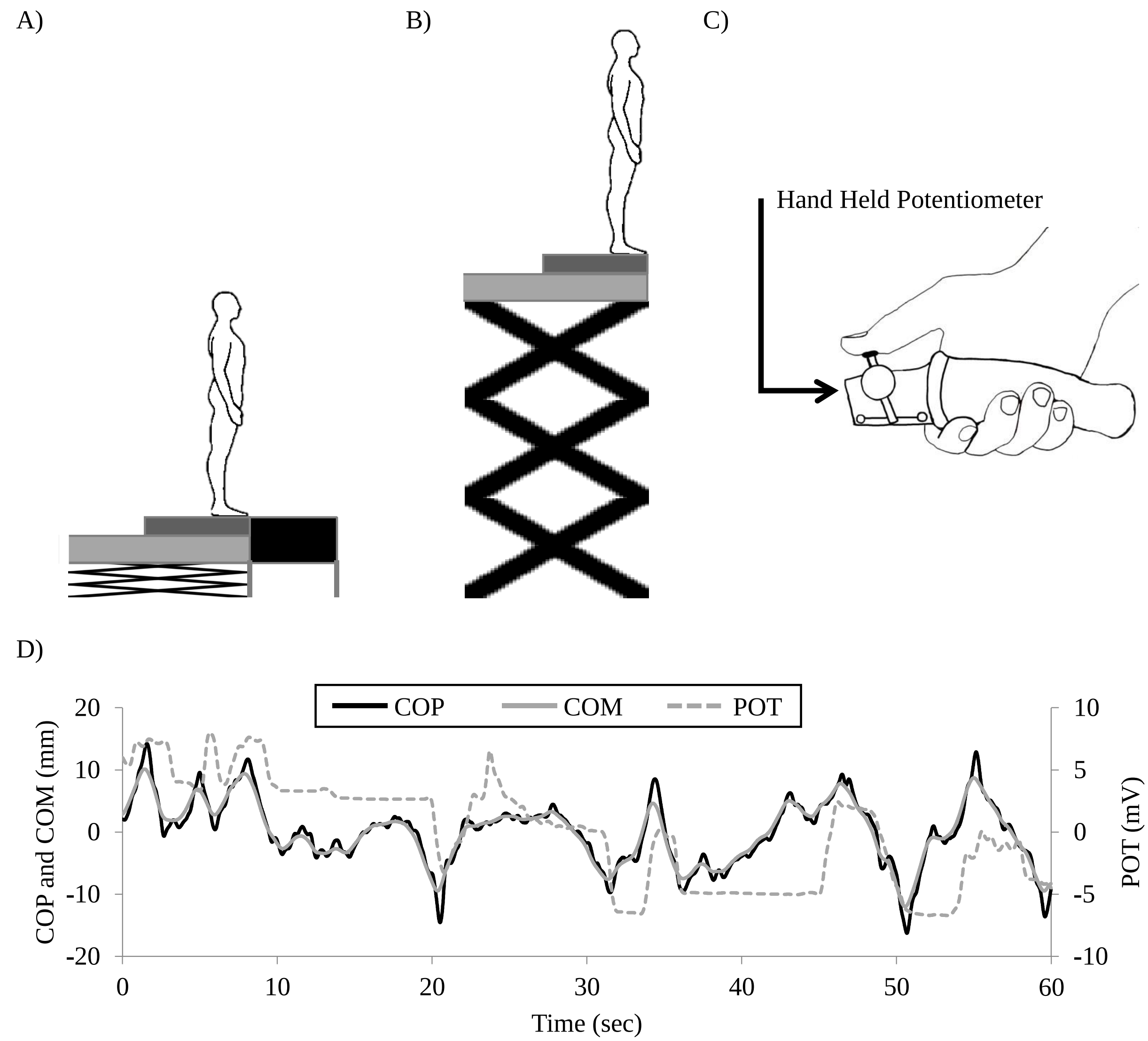

Figure 2-1 Experimental setup for Study 1

Experimental setup for (A) LOW height, (B) HIGH height, and (C) position of hand held potentiometer during tracking conditions. D) Validation data from single trial traces for COM (solid grey line), COP (solid black line) and POT (dashed grey line).

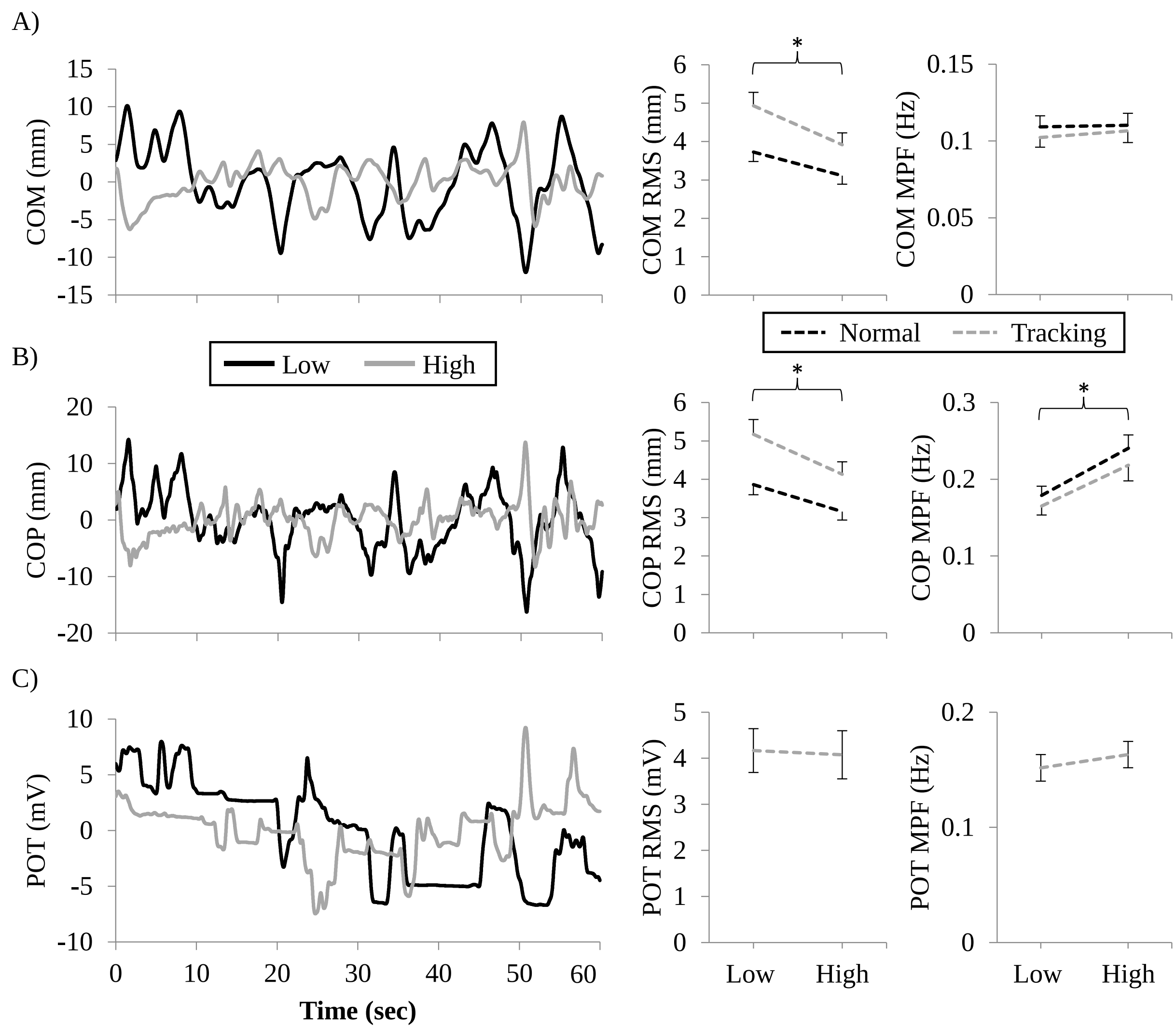

Figure 2-2 Representative and summary data

Representative and summary data for COM (A), COP (B) and POT (C) traces. Representative participant traces (left column) for LOW (solid black lines) and HIGH (solid grey lines) conditions. Group mean and SE (collapsed across vision) for RMS (middle column) and MPF (right column) for normal (dashed black line) and tracking (dashed grey line) conditions. * indicates significance at $p < 0.05$.

		Height (H)		Vision (V)		H×V		Task (T)		H×T		V×T		H×V×T	
		$F_{(1,19)}$	p	$F_{(1,19)}$	p	$F_{(1,19)}$	p	$F_{(1,19)}$	p	$F_{(1,19)}$	p	$F_{(1,19)}$	p	$F_{(1,19)}$	p
COP	MP	**38.86**	**<0.001**	3.58	0.074	0.08	0.783	0.08	0.785	0.17	0.688	0.02	0.904	0.77	0.393
	RMS	**16.98**	**<0.001**	1.10	0.307	0.97	0.337	**11.86**	**0.003**	1.06	0.316	1.31	0.266	1.00	0.329
	MPF	**15.73**	**0.001**	**21.43**	**<0.001**	0.97	0.336	2.29	0.147	0.14	0.712	0.02	0.895	0.70	0.412
COM	MP	**37.75**	**<0.001**	3.19	0.090	0.04	0.843	0.16	0.694	0.14	0.717	0.99	0.333	0.23	0.639
	RMS	**16.51**	**0.001**	3.42	0.080	1.75	0.202	**12.03**	**0.003**	1.19	0.289	1.67	0.211	0.62	0.439
	MPF	0.35	0.561	**32.87**	**<0.001**	<0.01	0.968	0.66	0.427	0.06	0.807	1.55	0.228	1.54	0.229
POT	RMS	0.19	0.667	0.36	0.558	1.91	0.184	-	-	-	-	-	-	-	-
	MPF	0.58	0.455	3.85	0.065	0.94	0.345	-	-	-	-	-	-	-	-
	EDA	**43.64**	**<0.001**	**8.03**	**0.011**	1.71	0.206	0.37	0.553	0.01	0.907	4.26	0.053	0.24	0.630
	Anxiety	**12.92**	**0.002**	0.51	0.486	1.01	0.328	0.01	0.923	2.20	0.154	0.44	0.513	0.06	0.807
	Fear	**16.55**	**0.001**	2.17	0.157	<0.01	0.993	1.58	0.224	1.14	0.299	3.10	0.094	4.02	0.060
	Stability	**10.31**	**0.005**	3.341	0.083	1.245	0.278	0.202	0.658	0.46	0.506	0.36	0.559	0.04	0.837
	Conf	**32.41**	**<0.001**	4.00	0.060	0.04	0.850	0.42	0.523	0.95	0.343	1.15	0.296	1.74	0.203
	PM	2.82	0.109	**15.96**	**0.001**	1.05	0.320	**5.60**	**0.029**	0.33	0.573	0.06	0.807	0.24	0.632

Table 2-1 ANOVA results for height, vision and task effects

COP=centre of pressure; COM=centre of mass; POT=perceived sway; RMS=root mean square; MPF=mean power frequency; MP=mean position; EDA=electrodermal activity; Conf=balance confidence; PM=perceived movement. Bold values indicates significance at the $p < 0.05$ level.

	Eyes Open				Eyes Closed			
	Normal		Tracking		Normal		Tracking	
	LOW	HIGH	LOW	HIGH	LOW	HIGH	LOW	HIGH
EDA	11.11 (1.71)	18.73 (2.73)	9.87 (1.88)	16.79 (2.45)	9.05 (1.85)	14.81 (2.33)	9.73 (1.85)	16.03 (2.80)
Anxiety	12.40 (0.79)	22.45 (3.34)	12.20 (0.48)	21.20 (2.97)	11.40 (0.66)	22.85 (3.29)	12.95 (0.76)	22.50 (3.18)
Fear	0.30 (0.25)	27.55 (6.40)	0.60 (0.50)	15.55 (5.40)	2.85 (1.61)	21.40 (6.48)	2.35 (1.57)	26.05 (6.26)
Conf	95.25 (1.83)	83.75 (4.21)	96.25 (1.30)	86.25 (3.82)	92.25 (2.87)	84.00 (4.07)	92.00 (2.58)	78.00 (3.95)
Stability	90.40 (3.89)	76.70 (4.60)	89.25 (4.27)	78.90 (5.13)	85.40 (4.03)	76.50 (4.68)	82.25 (5.08)	75.75 (4.86)
PM	26.25 (3.58)	31.45 (4.18)	30.90 (4.18)	36.45 (4.10)	36.25 (3.97)	37.05 (4.20)	38.90 (4.73)	42.55 (4.23)

Table 2-2 Mean (SE) for questionnaire and EDA data.

EDA=electrodermal activity; Conf=balance confidence; PM=perceived movement.

Chapter 3: Postural threat influences the conscious perception of body position during voluntary leaning

3.1 Introduction

Balance tasks can be generally divided into three functional categories: 1) maintaining equilibrium during quiescent standing; 2) remaining upright during voluntary movements of the Centre of Mass (COM) and body segments; and 3) reactive balance responses during destabilizing forces. Within these tasks, reports suggest falls occur more often during routine daily activities or tasks, most of which involve voluntarily transferring or shifting the Centre of Gravity (COG) within or outside the base of support (Robinovitch et al., 2013). These falls occur if no compensatory strategies, such as stepping or grasping, are evoked to prevent the COG from being displaced outside the boundaries or functional limits of stability, an area typically smaller than the total base of support used in normal upright stance. A decrease in functional limits of stability can affect the performance of voluntary leaning tasks, as well as influence balance reactions triggered when the COG is moved towards/outside these limits of stability. It is therefore important to investigate contributions to functional limits of stability (King et al., 1994).

Functional limits during voluntary leaning tasks have been shown to be influenced by fear and anxiety. Fearful older adults have a lower level of functional ability during leaning tasks (Li et al., 2003). When at the edge of an elevated support surface, emotional state changes and participants reduce the amount of maximum lean (Hauck et al., 2008). Meanwhile, in the presence of an evaluator, which increases social anxiety, older and younger adults increase their maximum lean position (Geh et al., 2011). Fear may influence functional limits through changes in biomechanical strategies and/or changes in perceptions of functional limits. Discrepancies between studies may be the result of contextual influences on one or both components. By constraining the biomechanical strategy, there can be further examination into how height-related postural threat influences the perceived positon during leaning tasks.

Fear has been shown to influence perceptions of a number of sensory stimuli, with larger or more threatening perceptions evoked during fearful states (MacLeod & Mathews, 1988; Zadra & Clore, 2011). Furthermore, changes in balance perceptions have been observed during quiet standing tasks under height-related threat conditions known to induce fear, anxiety and arousal. For example, participants report increased instability despite decreases in sway amplitude when standing at the edge of an elevated support surface (Hauck et al., 2008). In addition, the results from Study 1 provides evidence of a disconnect between actual and perceived balance performance when standing at height; while participants decreased their actual sway amplitude at height, their perceived sway recorded with an online tracking device and self-reported measures remained unchanged. The differences in actual and perceived movement at height may be mediated by a change peripheral mechanisms, such as sensory receptors (Horsen et al., 2013; Naranjo et al., 2016) or afferent/efferent nerves, or central mechanisms, such as sensory processing and attention (Huffman et al., 2009; Zaback et al., 2015) involved in postural control.

The purpose of this study was to examine the effect of height-related postural threat on conscious perceptions of body position during a voluntary leaning task. It was hypothesized a) participants would perceive a proportional increase in lean position as movement amplitude increased; b) height-related threat would significantly increase the perceived body position during voluntary leaning tasks; and c) the effect of height-related threat would be greatest for larger amplitude movements.

3.2 Methods

Twenty young healthy adults (age 22.1 ± 4.5 years, 10 males) volunteered for this study. All participants self-reported having no known neurological or orthopedic disorders that may have affected their balance. In addition, all participants gave written informed consent prior to participation in accordance with the University of British Columbia Clinical Research Ethics Board.

3.2.1 Procedure

Participants stood on a force plate (40 x 60 cm, model BP400600-1000, AMTI, USA) mounted on a hydraulic lift (2.13 × 1.52 m, M419-207B01H01D, Pentalift, Canada). The support surface was raised to 2 heights, simulated ground (0.8 m, LOW) and 3.2 m above ground (HIGH, Figure 3-1). In the LOW condition, a solid support surface was placed level with, and directly in front of, the hydraulic lift to distance the participant from the edge (Carpenter et al., 2001). In the HIGH condition, there was no additional support surface in front of the participant (similar to previous work, Horslen et al., 2013; 2014). Feet were placed at the anterior edge of the force plate and at a width equal to foot length, and foot position marked on the force plate to ensure a constant foot position across height conditions. A harness was fitted to the participants and attached to the ceiling with a rope that had enough slack to ensure it provided no support or feedback during experimental trials.

3.2.2 Visual feedback

Visual feedback was provided to participants during all practice and experimental conditions (Figure 3-1, Vizard, WorldViz, USA). Participants were facing a 1.4 m x 1 m screen, used to display online feedback of kinematic body position and target locations, located at eye level approximately 2.5 m away. Real time data of marker locations in line with the acromion process (shoulder), greater trochanter (hip) and lateral malleolus (ankle) were used to show the real-time position of the participant. Two segments representing lower body (ankle to hip) and upper body (hip to shoulder) were displayed to help prevent participants from bending at the hip. During the leaning task, participants were asked to keep the two segments aligned (see Figure 3-1) and lean as one ‘straight’ segment. Participants used this feedback to align their body’s to the target location across all experimental conditions.

3.2.3 Setup and practice

Before any experimental conditions were completed, participants performed a series of practice trials at the LOW height to allow the participant to become familiar with the visual feedback, and leaning task. In order to complete the leaning task, participants stood barefoot with their arms crossed across their chest and when instructed, were required to lean as an inverted pendulum, rotating only at the ankle joint (see Figure 3-1) until their body segments matched the target as illustrated by the visual feedback. Participants were seated and raised to 3.2 m upon completion of the practice trials. Participants then stood quietly for 15 seconds while a mean position was calculated for shoulder, hip, ankle and platform locations. This mean position was used to remove any bias in the markers, and used as the baseline position in the visual feedback. Participants were then asked to lean as far forward as possible without bending at the knees or hip, keeping the segments in the visual feedback as straight as possible (see Figure 3-1). Once at a maximum lean position, participants were asked to hold the position for three seconds, which was used to calculate the mean positions of kinematic markers. Participants were then asked to return to baseline and stand normal before beginning the HIGH condition.

3.2.4 Height conditions

During the HIGH and then LOW experimental conditions, participants were instructed to lean forward, keeping the knees and hip straight, until the visual feedback of body position was aligned to the target (see Figure 3-1). Ten amplitudes (10% to 100% of performance based limit of stability, in increments of 10%) were randomly presented in the first ten trials. The same order of 10 targets was repeated two more times for a total of three trials per target amplitude. Across all target amplitudes and tasks, the target and baseline absolute position in the visual scene did not move to ensure participants did not receive any indication of target size. In order to present different target amplitudes, the gain of the visual feedback of body position was altered. For example, if the participant had a shoulder marker target at 15 cm, then in the 100% target trials, the feedback of the participant's position would move at a 1:1 rate and the participant would be on target when body position was 15 cm from baseline. However, if a 50% target was given, the feedback of the participant's position would move at a 2:1 rate and absolute target position was 7.5 cm from baseline but baseline and target positions in the visual feedback did not change. Participants were instructed to wait for the 'Go' signal (the home position would turn green), then lean to the target in a controlled manner. No time constraints were put on the movement as participants leaned at a comfortable pace. Targets were reached when body position was within 5 mm of the target position. Once on target (current position changed colour), a verbal report of how far participants had moved (in percentage) relative to their previous maximum lean was stated by the participant (on a scale from 1% to 100% maximum lean).

3.2.5 Measurements

Prior to each experimental condition, while seated, participants rated how confident they were their ability to remain upright and avoid a fall on a scale from 0 (not confident at all) to 100 (completely confident) for the upcoming balance task. After each condition, a subjective rating of fear (0 = no fear, 100 = fearful) and stability (0 = not stable, 100 = very stable) were given by the participant. Finally, cognitive and somatic anxiety were assessed using a perceived anxiety questionnaire (modified Sport Anxiety Scale, Hauck et al., 2008) where 10 items were quantified and summed for each condition (9 point Likert scale for each item). Electrodermal activity (EDA) was collected during the entire trial from the thenar and hypothenar eminences of the left hand (100 Hz, Skin Conductance Module 2502, Cambridge Electronic Design, UK) and averaged to provide an estimate of physiological arousal.

3D motion capture data sampled at 200 Hz (Optotrak, Northern Digital Inc., Canada) was collected to measure segment displacements, as well as used online to provide visual feedback of body position. Infrared (IRED) markers were placed on bony landmarks of the right side of the body: lateral malleolus, 5th metatarsal, acromion, mastoid process, and zygomatic arch. Three additional IREDs were used in a rigid body to allocate two imaginary marker locations: greater trochanter and lateral epicondyle of the femur. Two markers were also placed on the force plate. Ground reaction forces and moments were collected at 100 Hz (Power 1401 with Spike 2 software, CED, UK). Centre of pressure (COP) was calculated from ground reaction forces and moments low-pass filtered at 3 Hz (Field, 2009). For each height condition (LOW and HIGH), perceived position and actual position were calculated across target stimuli (10% to 100% in increments of 10%). The mean perceived position was calculated by averaging the three verbal reports recorded from like targets, while the mean COP and individual marker positions were calculated from all data when the visual feedback of body position was on target.

3.2.6 Statistical analyses

A 2 x 10 repeated measures ANOVA was used to examine the effect of height (LOW vs HIGH) and target amplitude (10% to 100% of performance-based limit of stability, in 10% increments) on measures of actual and perceived body positions. Mauchly's test of sphericity was used to test the assumption of sphericity, and Greenhouse-Geisser corrections were used if the sphericity assumption was violated. Normality was determined by examining the skewness statistics for each variable (standardized z-score: skewness divided by standard error of skewness). Any value greater or less than ± 3.29 was considered significantly skewed and corrected for by replacing outliers (z-score greater or less than ± 3.29, one value in the current dataset) with a value ± 2 standard deviations of the mean (Field, 2009). In addition, a power law fit was used to examine the relationship between perceived and actual body position. The exponent was then used to compare height conditions. Paired sample t-tests were used to compare power law exponent, physiological arousal and psychological data. Significance was set at $p = 0.05$.

3.3 Results

In the LOW condition, both perceived and actual body position increase with target amplitude (see Figure 3-2A and B, Black; and 3-3B Black). As expected with magnitude estimations, the relationship between actual and perceived body position in the LOW condition is better fit with a power law ($r^2 = 0.91$) than a linear fit ($r^2 = 0.88$). One outlier was removed from all analyses due to their inability to accurately perceive body position as demonstrated by a significantly reduced correlation between perceived and actual body position (LOW: $r^2 = 0.57$, HIGH: $r^2 = 0.34$).

There was a significant main effect of height on all physiological and psychological indicators of emotional state. Specifically, balance confidence and stability significantly decreased, while fear, anxiety, and EDA increased in the HIGH compared to LOW condition (p-values < 0.05, $d > 1.05$).

As shown in Figure 3-2, there was a main effect of target amplitude observed for COP, hip and shoulder displacements, with linear scaling of actual body movement across all target locations incrementing from 10% to 100 % maximum lean (p-values < 0.001, $\eta_p^2 > 0.91$). The scaling of COP, hip and shoulder displacement across target positions was not influenced by height, with no significant main effects or interactions observed (p-values > 0.05, $\eta_p^2 < 0.14$). This confirms that actual body leaning was kept constant for all target locations across height conditions as intended in the study design.

Similar to the actual body position, perceived body position was influenced by target location. Participants scaled their perceived position incrementally from 10% to 100% maximum lean ($F(3.57,64.18) = 168.131$, $p < 0.001$, $\eta_p^2 = 0.903$). Independent of height condition, a strong power law fit was observed between perceived body position and target locations (LOW: $r^2 = 0.93$, HIGH: $r^2 = 0.95$). Although actual leaning amplitude was constant across height conditions, there was a significant effect of height on perceived position (collapsed across target amplitudes, mean difference HIGH-LOW ± standard deviation: 4.9 ± 2.6%; range: 1.9% to 9.7%, $F(1,18) = 8.991$, $p = 0.008$, $\eta_p^2 = 0.328$, see Figure 3-3 C). There was no significant interaction observed between height and target for actual or perceived body positions (p-value > 0.05, $\eta_p^2 = 0.11$). In general, independent of target amplitude, participants perceived themselves to be leaning further forward in the HIGH compared to the LOW condition (see Figure 3-3 A and B). To note, there was no difference in the exponent for the power law relationships observed between perceived and actual body position across height conditions. ($t(18) = 1.077$, $p = 0.296$, $d = 0.25$).

3.4 Discussion

The current study was designed to assess the height-related changes in perceived body position during a voluntary leaning task. A psychometric technique was used to investigate the relationship between actual and perceived body position while controlling for body position. Following previous psychophysical relationships (Bromm & Treede, 1980), perceived body positon relative to maximum lean followed a power law relationship across target locations. When young healthy adults were asked to lean to the same targets while standing at the edge of an elevated support surface, they perceived themselves to be at a further position relative to their functional limits of stability.

These results are consistent with prior reports of height-related decreases in functional reach observed in healthy young adults (Hauck et al., 2008), and fearful compared to non-fearful elderly (Li et al., 2003). The effects of height-related threat to reduce leaning amplitude could be explained by individuals perceiving themselves to be leaning farther than their actual position, and thus will have reached their functional limit of stability at a reduced range. Threat has been shown to influence perception across a wide range of senses. For example, fear (or similar emotional states) can change the visual perception of environmental features. Slopes are perceived as steeper (Stefanucci et al., 2008), heights are perceived to be higher (Clerkin et al., 2009), and target sizes (Teachman et al., 2008) are perceived to be bigger when fearful. Fear also amplifies aversive components of auditory stimuli, where auditory tones are perceived as louder (Siegel & Stefanucci, 2011), closer (Gagnon et al., 2013) and more annoying (Borsky, 1979). The perception of taste is also influenced by stressful or aversive stimuli. The pleasant aspects of tastes, such as sweet or savory, are perceived as weaker (Al'absi et al., 2012) whereas unpleasant bitter and sour tastes are stronger (Platte et al., 2013). Thus, it is not surprising threat-related changes in perception occur during postural stability tasks; first demonstrated during quiet stance when perceptions of balance-related movement remain unchanged despite decreases in actual sway (Study 1) and now demonstrated during voluntary leaning tasks with amplified perceived leaning positions.

Height-induced postural threat has the potential to influence the dynamics of the postural control system. Based on common theories of movement, postural control involves both feedback and feedforward mechanisms utilizing sensory information (Peterka, 2000) which can be shaped by cognition (Mergner & Rosemeier, 1998). These mechanisms of control rely on the sum of proportional error, the derivative of error, and the integral of the error between predicted and actual movements (Botaro et al., 2005; Peterka, 2000). Changes in feedforward control (reliant on the proportional and derivative error) or in feedback control (reliant on the integral of the error) can significantly influence perceived and subsequently actual balance performance. Changes to postural control mechanisms from modulated sensory and cognitive components can affect the feedforward predictive control, which is based on position and velocity sensory information, or the feedback control due to a change in sensitivity to the error between predicted and actual movements. Sensory systems that convey position and velocity information are augmented when standing under threat, including muscle spindles (Horslen et al., 2013; Horslen, 2016); and vestibular pathways (Naranjo et al., 2015; 2016; Lim et al., 2017; Horslen et al., 2014). Furthermore, height-induced threat shifts attention to movement-related processes (Huffman et al., 2009; Zaback et al., 2015) which can shape the interpretation of those sensory signals. As it is difficult in this experiment to distinguish the mechanisms of postural control affected by height-induced threat influencing perceptions of body position during leaning tasks, future studies should examine the effects of height-induced threat on different components used in postural control.

The results of this study suggest the psychological state of an individual can significantly affect perceived body position during postural tasks. While measures of postural stability do not take into account boundaries of stability (van Wegen et al., 2002), implementing this psychometric technique to assess perceived functional limits of stability may be useful in determining balance deficits within those individuals with a fear of falling. An increase in perceived body position relative to the limits of stability in addition to the stiffening strategy typically observed with height-induced threat can reduce postural sway movements putting individuals at a further risk of falls during activities of daily life. Further research should examine the associations between fear of falling and decreased functional ability in populations with balance deficits. Given that social motivation has been shown to have the opposite effect on functional leaning (Geh et al., 2011), there is also the potential to determine if diminished aversive psychological state can attenuate the negative outcomes associated with a fear of falling.

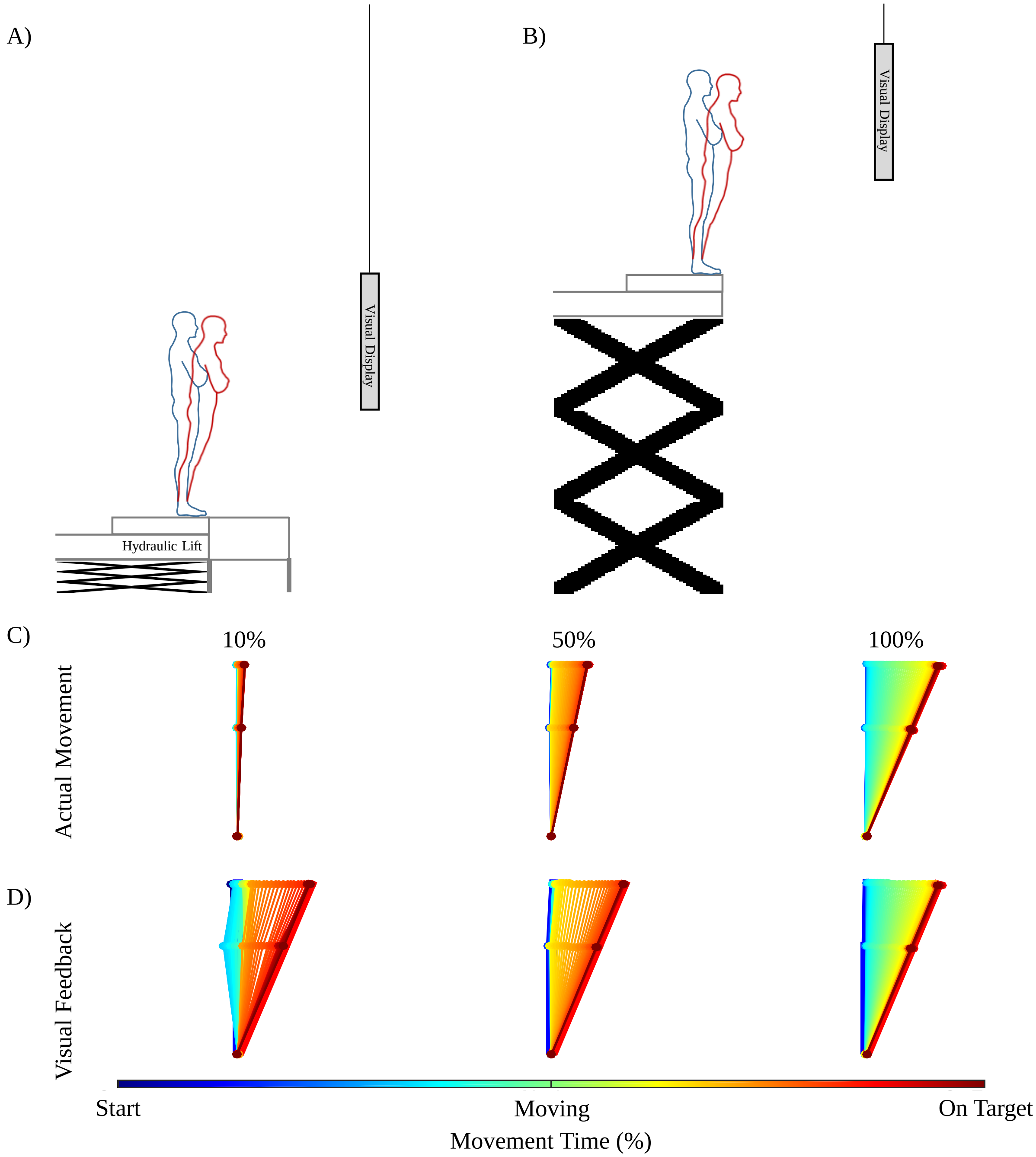

Figure 3-1 Experimental setup for Study 2

Illustration of experimental setup with a participant standing (blue) and leaning (red) for LOW (A) and HIGH (B) conditions facing a screen with the visual feedback displayed. Visual feedback: (C) Actual marker displacement and (D) the visual feedback image observed during

10% (left), 50% (middle), and 100% (right) target movements. Baseline (blue) and target (red) locations never change in the visual feedback image, whereas actual displacements increase as target amplitude increases.

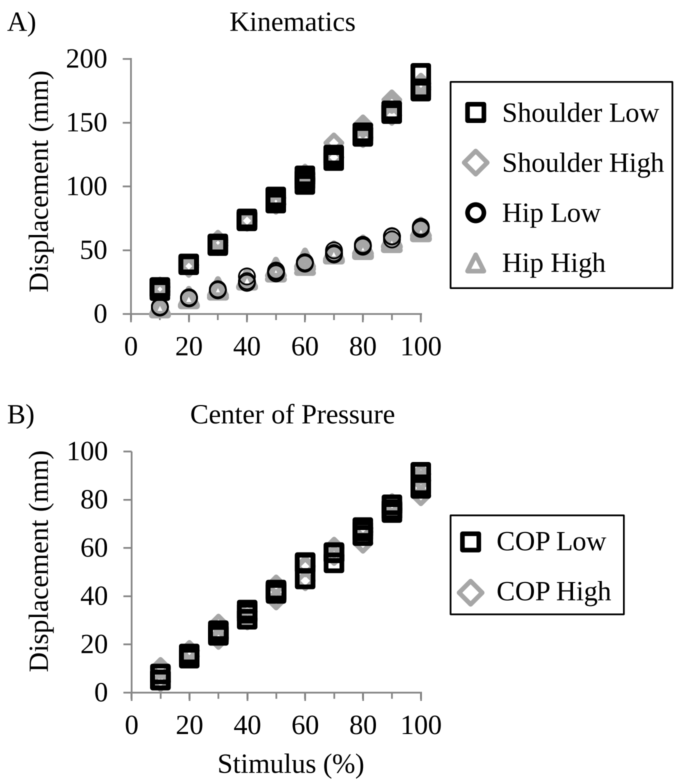

Figure 3-2 COP, shoulder, and hip movement data

Actual movement from a representative participant comparing LOW (black) and HIGH (grey) conditions. Data illustrate shoulder and hip (A), and COP (B) displacements during the time when the participant was on target for each trial. Displacements linearly increased from 10% to 100% of maximum lean for all postural measures.

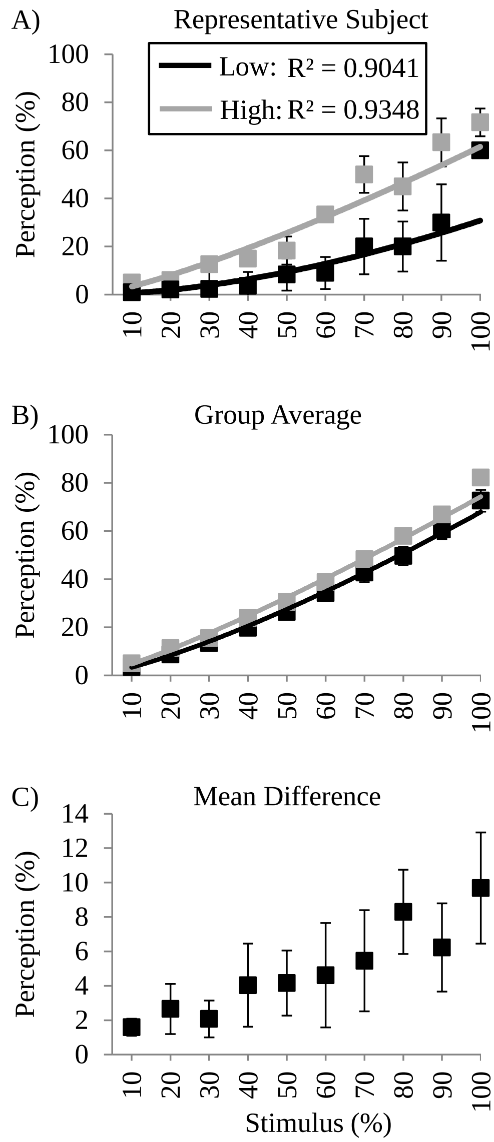

Figure 3-3 Representative and group data for subjective reports on body position.

Subjective reports of perceived body position from a representative participant and group data. Individual and group average data (fitted with a power law function) indicating the increase in perceived position for HIGH (grey) compared to LOW (black) conditions across target amplitudes. (A) Representative participant mean (standard error) for perceived lean (referenced to maximum lean) across three trials at each target amplitude. (B) Group mean (standard error) data from 20 participants for each stimulus. (C) Mean (standard error) difference (HIGH – LOW) in perception of lean amplitude between HIGH and LOW conditions. All error bars represent standard error

Chapter 4: Postural threat modulates perceptions of balance-related movement during support surface rotations

4.1 Introduction

Postural threat, implemented using elevated support surfaces or impending postural perturbations, can be used to evoke fear and/or anxiety. These are associated with increased levels of arousal and decreased perceived stability and balance-related confidence. As such, elevated support surfaces provide a useful tool to examine the direct effects of threatening situations on emotional state and postural control (Brown & Frank, 1997; Carpenter et al., 2001; Horslen et al., 2013; Hauck et al., 2008; Cleworth et al., 2012; Zaback et al., 2015; Naranjo et al., 2016; Lim et al., 2017). During periods of quiet standing at the edge of a hydraulic lift, individuals lean away from the edge and adopt a stiffening strategy, evidenced by an increase in frequency and decrease in amplitude of Centre of Pressure (COP) (Carpenter et al., 1999; 2001; Cleworth et al., 2012) and Centre of Mass (COM) displacements (Carpenter et al., 2001). In addition, changes in lower leg co-contraction has been observed through increased tibialis anterior (TA) activity and decreased soleus (SOL) activity (Cleworth et al., 2016; Zaback et al., 2017).

Voluntary balance tasks are also influenced by postural threat. Anticipatory postural adjustments prior to a rise-to-toes task decrease in amplitude (as evidenced by decreases in AP-COP displacement and ankle dorsi-flexion activity) when standing at height (Adkin et al., 2002).

Height-induced postural threat has further been shown to influence dynamic balance control tasks. When individuals are perturbed, either through upper body pushes or support surface displacements, balance-correcting responses are larger (Carpenter et al., 2004; Cleworth et al., 2016) and COM displacements are directed away from the threat (Brown & Frank, 1997; Carpenter et al., 2004).

Postural threat-related changes in standing behaviour have been attributed to physiological adaptations in sensory and cognitive function (Naranjo et al., 2016; Davis et al., 2011, Adkin et al., 2008; Sibley et al., 2010). Alternatively, changes in behaviour during threatening conditions may be related to modulated perceptions of balance-related movements (Llewellyn et al., 1990; Horslen et al., 2013), which relies on the afferent information being received, as well as higher order cortical processing of sensory information.

Indirect evidence of incongruent perceived and actual balance performance has been observed in the form of decreased feelings of stability during postural threat conditions when postural sway is actually reduced (Hauck et al., 2008; Cleworth et al., 2012); a reduction in postural sway is typically interpreted as an indicator of increased stability (Lord et al., 1991). Recent evidence has demonstrated a clear discrepancy between perceived and actual balance performance. When young healthy adults are placed at the edge of a hydraulic lift, there is no change in the amount of perceived sway despite a significant reduction in sway amplitude (Cleworth & Carpenter, 2016: Study 1). Previous work has been limited to quiet standing tasks, where small amplitude, sometimes imperceptible, sway occurs and the risk of a fall is minor (Cleworth & Carpenter, 2016: Study 1). There is a need to further examine balance-related perceived movements during tasks involving larger amplitude sway across a spectrum of frequencies related to balance, such as dynamic or induced sway standing tasks.

Continuous support surface perturbations have been used to examine dynamic postural control, which involves both reactive and anticipatory postural responses (Diener et al., 1982; Corna et al., 1999; Dietz et al., 1993; van Ooteghem et al., 2008; Akram et al., 2008; Horak et al., 1989). At low frequencies (< 0.5 Hz), participants tend to adopt an in-phase relationship where participants ‘ride’ the platform to allow the body segments to move with the platform (Buchanan & Horak, 2001). This frequency range (0 – 0.5 Hz), coincides with the frequency spectrum of quiet standing, where 99% of sway has been observed at frequencies below 0.68 Hz (Gage et al., 2004). In contrast, at higher frequencies (> 0.5 Hz), there is a shift in strategy where participants counteract the movement of the support surface in an attempt to stabilize the head in space (Buchanan & Horak, 2001).

In order to remain upright during induced sway, sensory information from vestibular, visual and somatosensory systems are integrated by the CNS to control muscle force and joint position, and therefore whole-body position. While sensory signals are relayed to the CNS during balance tasks, it has been suggested the perceptual interpretation of these signals evoke compensatory behaviours (Mergner & Rosemeier, 1998). Utilizing a global and local reference system, individuals can use this sensory information to orient their body to vertical and to other body segments. Any change in afferent information relayed to the CNS has the potential to influence the perception of body orientation and affect postural stability. Numerous methods have been used to illustrate this effect, including posturography, subjective visual vertical and subjective horizontal with support surface rotations. Specifically, muscle tendon vibration, electrical vestibular stimulation, and visual scene motion induce illusions of movement or changes in perceived vertical and cause a behavioural outcome that is associated with leaning (Thompson et al., 2007; Fitzpatrick & Day, 2004; Berthoz et al, 1975). In this respect, accurate perception of whole-body position relative to vertical and base of support limits is important for the postural control system to maintain upright stability.

The purpose of this study was to examine how postural threat influences both whole-body movements and conscious perception of these movements during continuous pseudo-random support surface rotations. It was hypothesized that increased postural threat would cause actual body movement to decrease (Carpenter et al., 2004) or remain constant (Maki et al., 1991) relative to platform movement. Independent of the changes in actual body movement with threat, it was hypothesized postural threat would cause larger perceived movement relative to actual movement (Cleworth & Carpenter, 2016: Study 1).

4.2 Methods

Sixteen young healthy adults (age 24.9 ± 3.3 years, 5 males) volunteered to participate in this study. All participants self-reported having no known neurological or orthopedic disorders that may affect their balance. In addition, all participants gave informed written consent prior to participation in accordance with the University of British Columbia Clinical Research Ethics Board.

4.2.1 Procedures

Participants stood barefoot on a force plate (50.8 x 46.4 cm, model OR6-7-1000, AMTI, USA) mounted on top of a custom-built servo-controlled tilting platform with their hands at their sides while holding a rotary encoder (1/4″ shaft, model E14102402302, Dynapar, USA) in their right hand (Figure 4-1 A and B). The tilting platform was surrounded by a stable support surface, and mounted on top of a hydraulic lift (M419-207B01H01D, Pentalift, Canada). The support surface was raised to two different heights, 1.1 meters (LOW, Figure 4-1 C) and 3.2 meters (HIGH, Figure 4-1D). The LOW condition had an extended support surface 0.6 meters in front of the hydraulic lift level with the top of the force plate, thereby increasing the distance of the participant from the edge to simulate ground level. In the HIGH condition, there was no additional support surface in front of the participant (see also Horslen et al., 2013; 2014). Feet were placed at a width equal to their foot length, and kept in constant position on the force plate throughout all experimental trials. A harness was fitted to the participant and attached to the ceiling with a rope that had enough slack to ensure it provided no support or tactile feedback during the task.

During experimental conditions, participants were instructed to remain upright and avoid a fall while accurately tracking their ML upper trunk position in real-time using the rotary encoder. Participants were asked to focus on the movements of the upper trunk only, independent of what the platform was doing. Two weak springs, one on either side of the point of contact with the thumb (Figure 4-1B), were used to limit the amount of drift that could occur using the tracking device (Cleworth & Carpenter, 2016: Study 1), and provide minimal feedback of the encoder's neutral (vertical) position. Participants performed a minimum of two practice trials, lasting 30 seconds each, to become familiar with the platform movements and practice using the device. Participants completed the practice trials first with eyes open and then eyes closed. The experimenter ensured proper use of the device by comparing trunk linear displacement, platform angular displacement, and tracked position (rotary encoder voltage). If trunk movement and tracked movement were congruent in amplitude and direction (visual inspection for similar patterns), and participants reported ease of use, the experiment continued (all participants correctly performed the task within two eyes open and one eyes closed condition). Participants then performed two seven minute trials in the LOW condition (the first to control for first trial effects, the second used in the analysis), and one in the HIGH condition with their eyes closed. One participant took a step in the second LOW condition shifting the position of the markers and therefore the first LOW trial was used in the analysis.

4.2.2 Tilting perturbations

The tilting platform was servo-controlled with an analog input voltage (Power 1401 with Spike2 software, Cambridge Electronic Designs, UK). During the practice trials, the platform movement followed a sinusoidal waveform with an amplitude of ± 4° at 0.1 Hz. During the seven minute experimental trials, the tilting platform was pseudo-randomly oscillated with a maximum amplitude of ± 4.5°. The tilting platform was oscillated using two bands of frequencies, a sum of sines waveform was created with six independent frequencies, three below 0.2 Hz (low frequencies: 0.08, 0.12, and 0.16 Hz) and three between 0.25 and 0.5 Hz (high frequencies: 0.28, 0.32, and 0.36 Hz, see Figure 4-2).

4.2.3 Data collection and processing

3D motion capture data were collected (250 Hz; Optotrak, Northern Digital Inc.) to monitor actual body position. A total of 6 markers within two individual clusters of three markers each, were placed in line with the manubrium (upper trunk) and between left and right iliac crests (pelvis) to capture movement of the upper trunk and hips, respectively. Data were averaged between the three markers within each of the clusters to obtain a position for each of the two body landmarks. Data were bias-corrected by subtracting the mean of the entire seven minute trial, and then band-pass filtered using a 0.005 Hz (consistent with the rotary encoder) to 2 Hz dual-pass Butterworth filter. Due to the task requiring participants to track their upper trunk movements, only the markers of the upper trunk are used in subsequent analyses.

The rotary encoder voltages and ground reaction forces and moments were collected and exported at 2000 Hz (Power 1401 with Spike2 software, CED, UK). Tracked sway was determined from the voltage of the rotary encoder, and was band-pass filtered using a 0.005 Hz (to remove any drift) to 2 Hz dual-pass Butterworth filter (similar to trunk displacement data). For trunk and tracked data, the mean position was calculated and subtracted from each respective trace to remove any bias. Due to the tracked sway data having a 'unitless' quantity, data were normalized to the LOW condition and expressed as a percentage of this movement. This is in line with previous work as values of perception are typically normalized to allow comparisons of stimulus ratings between participants (Kandel et al., 2013). Normalization was calculated by dividing each data point by the maximum value in the LOW condition. Both the LOW and HIGH condition data were normalized to the maximum amplitude from the LOW condition.

4.2.4 Measurements

Prior to each experimental condition, while the participant was seated at the height of the upcoming condition, participants rated how confident they were that they could remain upright and avoid a fall, on a scale from 0 (not confident at all) to 100 (completely confident). After each condition, subjective ratings of fear (0 = no fear, 100 = fearful) and overall stability (0 = not stable, 100 = very stable) were reported by the participant. Finally, state anxiety was assessed by summing the answers from a modified Sport Anxiety scale (Hauck et al., 2008) with 15 items (9 point Likert scale for each item). Electrodermal activity was collected and averaged from the full seven minutes during each condition from the thenar and hypothenar eminences of the left hand (2000 Hz, Skin Conductance Module 2502, Cambridge Electronic Design, UK).

Root mean square (RMS) and mean power frequency (MPF) were calculated from trunk and tracked data in the ML direction from the unbiased normalized signal to quantify the amplitude and mean frequency of actual and perceived movement. In addition, a quotient (QRMS) was calculated between perceived and actual movement (tracked RMS was divided by actual RMS) to signify the relative changes in perceived movement related to actual movement within a condition.

In addition, the coherence and gain of movement were analyzed by examining the mean-squared coherence and spectral gain. Two separate relationships were analyzed. Trunk displacements were analyzed with respect to platform movement, and perceived movements were analyzed with respect to trunk displacements. In accordance with Jeka et al. (1998), spectral analyses were used to determine coherence and gain between pairs of movement. Only data at the stimulus frequencies (refer to perturbation section above, Figure 4-2B) were examined, as these were the only frequencies with systematic peaks, and combined into low and high frequency bandwidths for analysis. Coherence was calculated using the *mscohere* function (MATLAB, MathWorks) which calculates an estimate of how strong two signals are coupled (with 1 being the maximum strength). Gain was defined as the ratio of the amplitude spectrum (at the driving frequencies) of trunk movement to the platform, and perceived movement amplitude spectrum to trunk movement. For each coherence and gain, in addition to height effects, the mean of the low frequencies (< 0.2 Hz) were compared with the mean of the high frequencies (0.25 to 0.5 Hz).

4.2.5 Statistical analysis

Paired sample t-tests were used to examine the effects of threat on EDA and self-report measures of fear, anxiety, confidence and stability. Paired sample t-tests were also used to compare RMS, MPF and quotient measures of actual and perceived movement. In the case where data were not normally distributed as determined by the Shapiro Wilks test, a non-parametric Wilcoxon Signed Ranks Test was used to compare height effects.

A 2 (height) x 2 (frequency bandwidth) repeated measures ANOVA was used to test the effects of height (LOW, HIGH) and frequency bandwidth (low frequencies, high frequencies) for all coherence and gain measures. Approximate normality was observed in all dependent measures, while normality tests illustrated a violation of normality for a number of variables in the repeated measures ANOVA. Log and square root transformations did not correct for normality, nor did removal of outliers based on z-score normalization (Field, 2009); therefore, due to the robust nature of repeated measures ANOVA and approximate normality (Field, 2009), no normality corrections were used. The criteria for a significant result was set at $p < 0.05$.

4.3 Results

4.3.1 Ability to track

Participants were accurate in tracking their movements in the medial-lateral plane for both LOW and HIGH threat conditions, which were tightly coupled to the rotations of the support surface (Figure 4-5 and 4-6). Similar patterns, changes in amplitude (Figure 4-2A and 4-6A) and frequencies (Figure 4-2 and 4-6) were observed between the platform displacement, trunk displacement and tracked movement across participants. Furthermore, there were similar peaks in spectra (at the stimulus frequencies, Figure 4-2B), and strong coherence between tracked movement and trunk displacement. There were stronger levels of coherence for the high compared to the low frequency range for platform to trunk movement relationship, and trunk to perceived movement relationship (Figure 4-5C and 4-6C).

4.3.2 Physiological and psychological measures

There was a significant effect of threat on measures of physiological arousal and self-reported psychological state. Specifically, anxiety ($t(15) = 3.688$, $p = 0.002$, $d = 0.92$), fear ($t(15)$

= 4.892, $p < 0.001$, $d = 1.2$) and EDA ($t(15) = 3.888$, $p = 0.001$, $d = 0.97$) increased, while balance confidence ($Z = 3.434$, $p = 0.001$, $d = 1.26$) and stability perceptions ($t(15) = 2.924$, $p = 0.010$, $d = 0.73$) decreased in the HIGH compared to LOW threat condition (Figure 4-3).

4.3.3 Mean amplitude and frequency of perceived and actual trunk movement

Trunk displacement RMS was not statistically different between height conditions (29.0 ± 1% LOW and 27.8 ± 1.6% HIGH; $t(15) = 0.920$, $p = 0.372$, $d = 0.23$). In contrast, tracked displacement RMS significantly increased in the HIGH (32.7 ± 1.8%) compared to LOW (28.5 ± 1.5%) condition ($t(15) = 2.788$, $p = 0.014$, $d = 0.70$, Figure 4-4A). As expected with the contrasting effects of height on perceived and actual displacement, QRMS was significantly influenced by threat. QRMS increased in the HIGH (1.25 ± 0.1) compared to LOW (1.00 ± 0.1) condition, indicating more movement was perceived for the movement that occurred ($t(15) = 3.111$, $p = 0.007$, $d = 0.78$).

Platform MPF was 0.28 Hz across all conditions. Trunk movement MPF was larger than platform movement ($p < 0.001$), but was not different between height conditions (LOW: 0.31 ± 0.01 Hz; HIGH: 0.31 ± 0.01 Hz, $Z = 0.155$, $p = 0.877$, $d = 0.07$). Perceived movement MPF was further increased compared to platform and trunk movement MPF ($p < 0.001$), and significantly decreased in the HIGH compared to LOW condition (LOW: 0.39 ± 0.01 Hz and HIGH: 0.37 ± 0.01 Hz, $t(15) = 2.454$, $p = 0.027$, $d = 0.61$; Figure 4-4B).

4.3.4 Coherence and gain analysis

4.3.4.1 Coherence

As expected, participants exhibited a very strong coherence between trunk movements and platform movements (collapsed across height conditions: low frequencies = 0.95 ± 0.01, high frequencies = 0.97 ± 0.01). There was a significant main effect of frequency range, where the high frequency range had a stronger coherence than the low frequency range ($F(1,15) = 12.73$, $p = 0.003$, $\eta_p^2 = 0.46$, Figure 4-5C). There was no effect of height ($F(1,15) = 0.441$, $p = 0.517$, $\eta_p^2 = 0.03$, collapsed across frequency bands: LOW 0.96 ± 0.01 vs HIGH 0.96 ± 0.01) or interaction between height and frequency range ($F(1,15) = 0.517$, $p = 0.483$, $\eta_p^2 = 0.03$) for coherence between trunk displacement and platform movement (Figure 4-5).

Participants also showed a strong coherence between perceived movements and trunk movements (Figure 4-6C); however, this was less than that observed for the trunk to platform coherence. Similar to the platform-trunk relationship, there was a significant main effect of frequency range, where the high frequency (0.889 ± 0.018) range had a stronger coherence than the low frequency (0.744 ± 0.038) range ($F(1,15) = 23.531$, $p < 0.001$, $\eta_p^2 = 0.61$). There was no effect of height ($F(1,15) = 1.487$, $p = 0.241$, $\eta_p^2 = 0.09$, collapsed across frequency bands: LOW 0.806 ± 0.029 vs HIGH 0.826 ± 0.025) or interaction between height and frequency range ($F(1,15) = 0.834$, $p = 0.376$, $\eta_p^2 = 0.05$) for coherence between perceived movement and trunk displacement (Figure 4-6A and C).

4.3.4.2 Gain

The gain calculated between trunk movements and platform movement was significantly affected by frequency range. Gain increased from low to high frequency range ($F(1,15) = 6.704$, $p = 0.02$, $\eta_p^2 = 0.31$, independent of height conditions: low frequency = 0. 402 ± 0.058, high frequency = 0.577 ± 0.054). There was no significant effect of height ($F(1,15) = 0.744$, $p = 0.402$, $\eta_p^2 = 0.05$, collapsed across frequency bands: LOW 0.506 ± 0.0407, HIGH 0.473 ± 0.050) or interaction between frequency range and height ($F(1,15) = 0.150$, $p = 0.704$, $\eta_p^2 = 0.01$) for platform to trunk displacement gain (Figure 4-5B and D).

Gain calculated between trunk and perceived movement was affected by frequency range and height (Figure 4-6D). The significant main effect of height for mean gain indicated larger gains were observed in the HIGH (collapsed across frequency bands: 1.254 ± 0.349) compared to LOW (0.629 ± 0.130) condition ($F(1,15) = 4.571$, $p = 0.049$, $\eta_p^2 = 0.23$). The significant main effect of frequency range for mean gain indicated larger gains were observed in the high frequency (collapsed across height conditions: 1.119 ± 0.289) compared to low (0.764 ± 0.158) frequency range ($F(1,15) = 4.778$, $p = 0.045$, $\eta_p^2 = 0.24$, Figure 4-6B and D). There was no significant interaction between height and frequency range ($F(1,15) = 2.150$, $p = 0.163$, $\eta_p^2 = 0.13$).

4.4 Discussion

Postural threat can significantly influence how young healthy adults perceive whole-body movements during feet in place stance. While standing on a support surface that was continuously and pseudo-randomly oscillated in the ML direction, participants were accurate in tracking their upper trunk movements, yet increased the amplitude of their perceived movement when standing at the edge of an elevated support surface. Furthermore, perceived stability decreased in conjunction with increased perceived movement despite no change in actual movement.

The movement of the upper trunk was highly correlated with the movement of the support surface, which oscillated at frequencies below 0.5 Hz. Strong correlations between platform and trunk movements supports previous work showing participants tend to ride the platform at the frequencies between 0 – 0.5 Hz (Buchanan & Horak, 2001). The lack of threat-related changes in amplitude, and relationship between actual trunk movements and platform displacements observed in the current study corresponds with prior work. For example, Young et al. (2012) examined balance performance in vestibular loss patients and aged-matched controls while standing on an oscillating translational platform placed at low and high (0.6 m) heights. They found that all participants used the same “body over feet” strategy when standing with eyes closed independent of height (Young et al., 2012). Likewise, no significant differences in the amplitude of postural responses induced by an oscillating platform were observed between fearful and non-fearful older adults (Maki et al., 1991).

The ability to perceive body movement was not affected by height, as evidenced by similar levels of coherence between actual and perceived movement across height conditions. However, despite no change in actual trunk movement with threat, the perceived trunk movement amplitude was significantly increased in the HIGH compared to LOW condition. As a result, there was a 25% increase in the amplitude ratio (QRMS) between perceived and actual movement, and increases in the gain calculated from power spectrum ratios of perceived and actual trunk movement in both the low frequency (121 ± 31%) and high frequency (150 ± 48%) range. Overall, this evidence suggests that threat contributes to larger estimates of perceived movement relative to actual body movement in dynamic balance conditions. This is consistent with prior observations of larger perceptions during quiet stance, where threat-related decreases in actual sway amplitude were accompanied by no change in perceived sway amplitude (Study 1). Furthermore, participants performing a voluntary whole-body forward leaning task reported larger perceptions of forward leaning when standing under threatening conditions despite no changes in actual body position (Study 2).

Conscious perceptions of different sensory stimuli have been shown to be modulated by aversive emotional state, where unpleasant characteristics of stimuli tend to be amplified, while pleasant or calming features, if present, tend to be attenuated. Fear (or similar emotional states) can change the visual perception of environmental features (Stefanucci et al., 2008; Clerkin et al., 2009; Teachman et al., 2008; Vasey et al., 2012), and can amplify aversive components of auditory stimuli (Siegel & Steffanucci, 2011; Asutay & Västfjäll, 2013) and taste (Al'absi et al., 2012; Platte et al., 2013). This may result from fear and anxiety biasing attention toward threatening stimuli (MacLeod & Mathews, 1988), and/or amplification of sensory processing typically observed with emotion (Vuilleumier, 2005). Our evidence suggests these factors also apply to the perception of whole-body, balance-related movement, and thus may rely on similar mechanisms integrating threat evaluation, conscious control and awareness of motion, and postural control (Staab et al., 2013). This includes reciprocal connections between the amygdala and a complex network involving the parietal, limbic, and vestibular cortices, thalamus, and brainstem structures that can modulate the sensitivity of sensory and cognitive processes involved in the perceptual awareness of body motion (Balaban 2002; 2004; Dieterich & Brandt, 2008; Staab et el., 2013).

Postural threat-related influences on perceived movement may be mediated through changes in the acquisition and/or processing of sensory information. The acquisition of sensory information at the receptor or spinal level is potentially influenced by threat, as evidenced by increases in proprioceptive and vestibular sensitivity in young healthy adults when standing at the edge of an elevated platform (Horslen et al., 2013; 2014; Naranjo et al., 2015; 2016; Lim et al., 2017). Processing of sensory information also appears to be affected by postural threat, although this occurs in later periods of cortical activity. Cortical potentials related to whole-body perturbations, such as the N100 (Adkin et al., 2008; Sibley et al., 2010), and later P110 and N140 components following cutaneous nerve stimulation (Horslen, 2016) were found to increase when young healthy adults stood at the edge of an elevated support surface. In contrast, early-evoked cortical potentials related to tendon taps, or cutaneous stimulation were found to remain unaffected when standing at height (Davis et al., 2011; Horslen, 2016).

Changes in perceived movement with increased threat could also be related to a change in selective attention, as the ability to perceive a stimulus increases with directed attention (Bradshaw et al., 1992; Post & Chapman, 1991; Craig & Rollman, 1999). A shift in attention has been known to occur with threat-related stimuli as they bias attention more so than neutral stimuli (Mathews & MacLeod, 1994). Likewise, postural threat during quiet stance has been shown to increase attention toward movement-related processes, threat-related stimuli, and self-regulatory strategies (Zaback et al., 2016; Johnson et al. 2017), and increase perceived conscious control and monitoring of movement (Huffman et al., 2009). However, the extent to which threat-related changes in attention may contribute to the current results during dynamic balance tasks is uncertain, particularly when participants were instructed to focus directly on movement in order to consciously track perceived sway across LOW and HIGH height conditions.

4.5 Limitations

A potential limitation to this study is the orientation of the postural threat relative to the balance task. Standing at the edge of an elevated support surface places the postural threat in the anterior direction, while platform rotations and subsequent trunk and perceived movements were in the lateral direction. While only limited studies have examined AP and ML responses during continuous perturbations, there is no evidence to suggest an effect of direction on threat-related changes. Young healthy adults standing at the edge of a support surface showed no directional effects on the change in height-related responses to vestibular perturbations (Horslen et al., 2014) and a fear of falling had no effect on balance responses to both AP and ML continuous support surface translations (Maki et al., 1991). Furthermore, technical limitations of an AP sway design limited the ability to sufficiently test the effects of height-induced postural threat on perceived sway. Orienting the rotating platform in the AP direction would increase the distance between the edge of the support surface and the participant, thus reducing postural threat effects (Carpenter et al., 1999). Future work should examine the postural threat effects on perceived and actual postural sway during continuous rotations with congruent orientations.

4.6 Conclusions

Threat-related changes in the perception of static and dynamic balance may be an important mediator in the known relationship between fear of falling, balance deficits and falls (Hadjistavropoulos et al., 2011). For example, if fearful individuals misperceive the actual magnitudes of balance-related movements or the amplitude of internal and external perturbations, they may inaccurately scale a postural response, and/or utilize inappropriate compensatory strategies that could increase the chance of a fall. This may explain why anxious individuals with a high perceived falls risk but a low physiological falls risk have almost twice as many falls as their low perceived falls risk counterparts (Delbaere et al., 2010), or why anxious individuals abort one-legged stance tasks early at the slightest risk of losing balance (Maki et al., 1991). However, more research is needed to understand the potential mechanisms through which threat-related changes in fear, anxiety and arousal may contribute to changes in balance perception, and the extent to which of these factors may relate to balance deficits in populations with high levels of fear-related falls-risk.

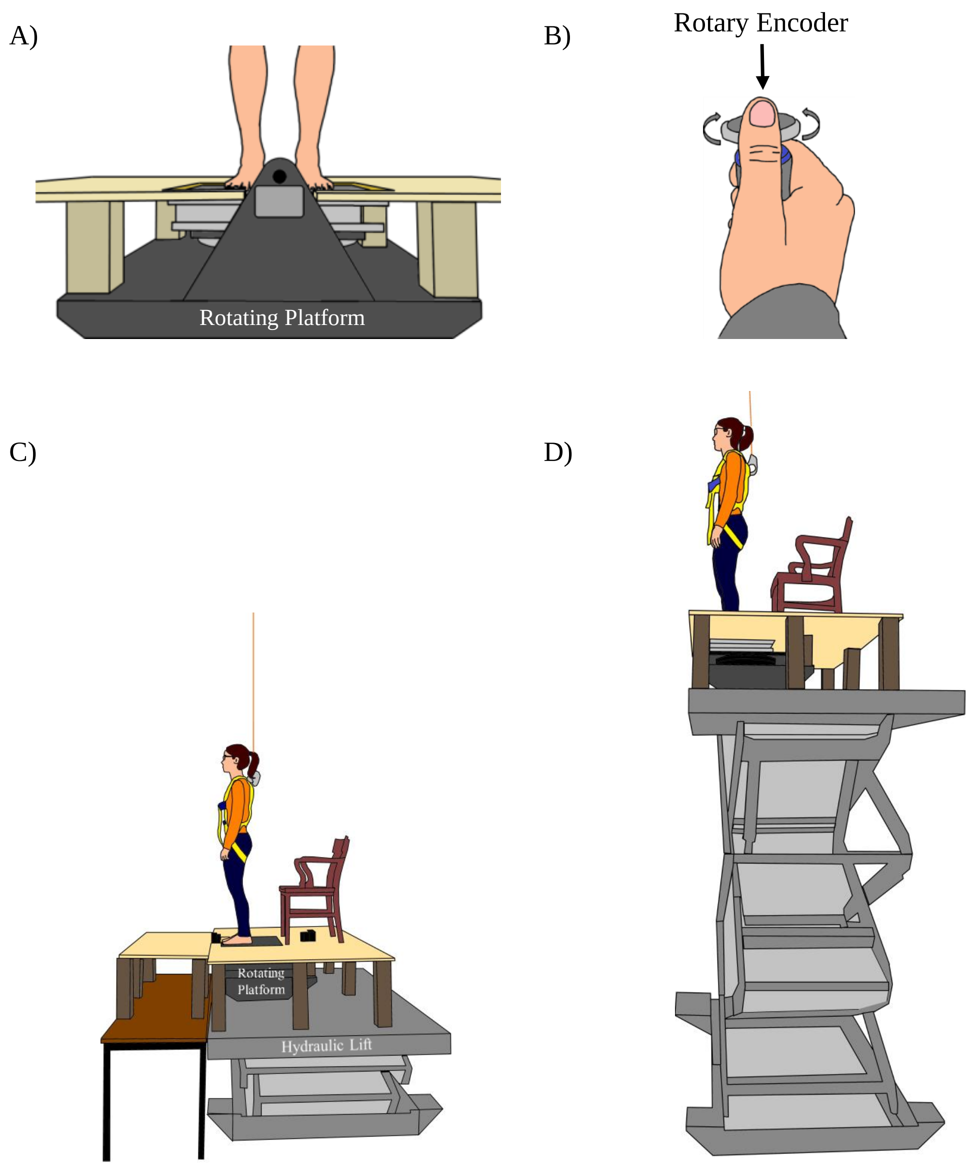

Figure 4-1 Experimental setup for Study 3

Illustration of experimental setup with a participant standing on a rotating platform (A) while holding a rotary encoder (B) in their right hand for LOW (C) and HIGH (D) conditions.

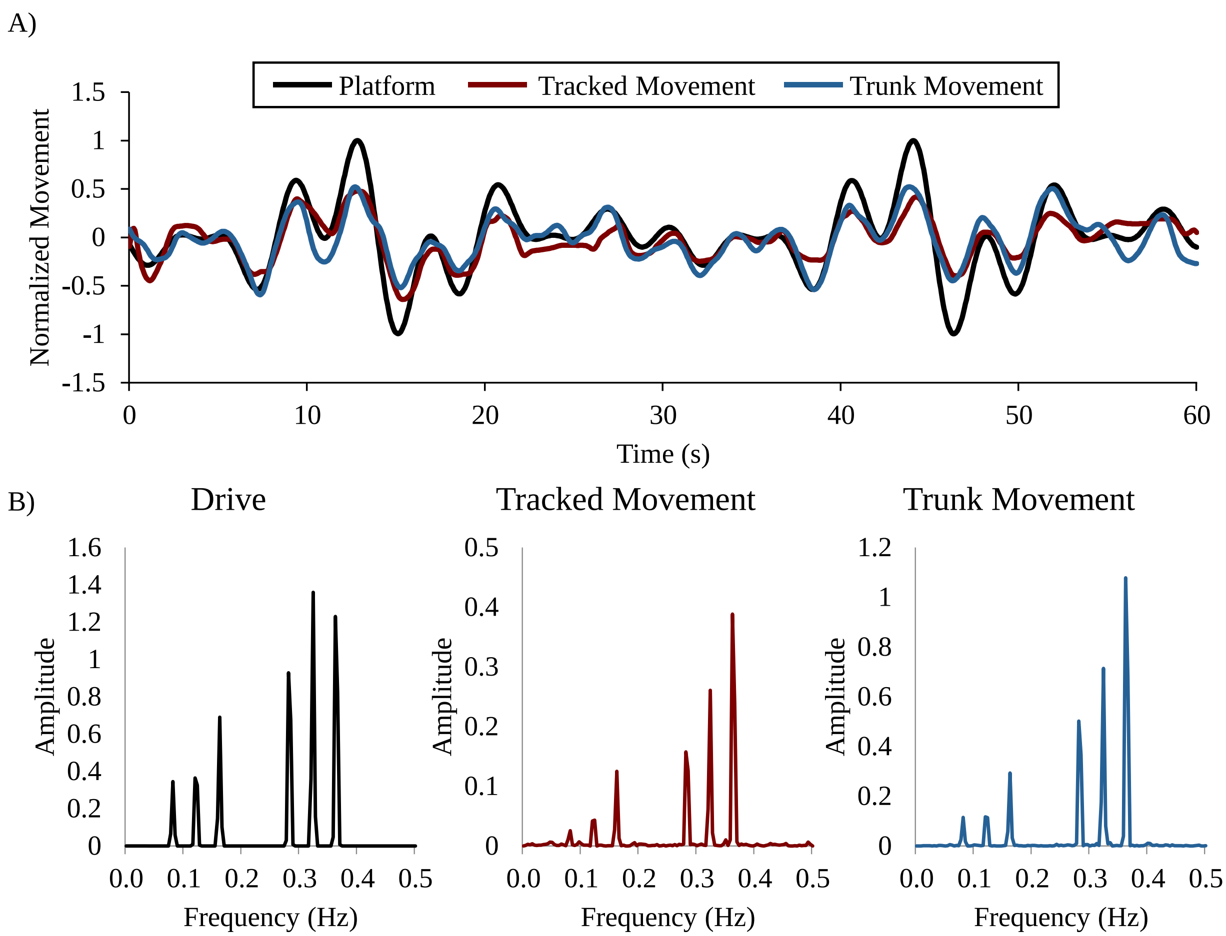

Figure 4-2 Representative data for tracking actual movement

(A) Representative participant data (A) traces and (B) power spectrum during the LOW condition for platform rotations (black), tracked movement (dark red) and actual trunk movement (dark blue).

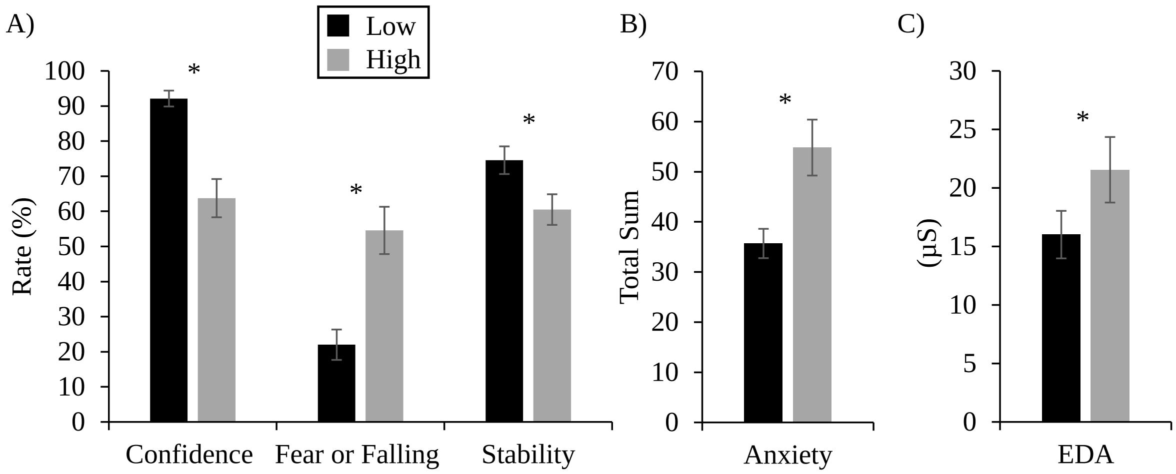

Figure 4-3 Psychological and physiological measures

Group mean (standard error) psychological (anxiety, fear, balance confidence, and stability) and physiological (electrodermal activity, EDA) data for LOW (black) and HIGH (grey) conditions. * indicates a significant difference ($p < 0.05$).

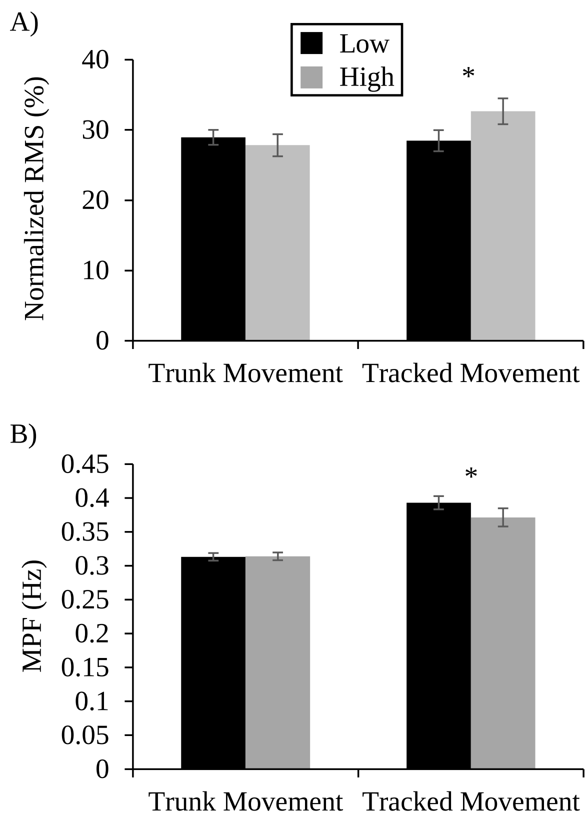

Figure 4-4 Amplitude and frequency measures

Group mean (standard error) for (A) normalized root mean square (RMS) and (B) mean power frequency (MPF) of trunk movements and tracked movement for LOW (black) and HIGH (grey) conditions. * indicates a significant difference ($p < 0.05$).

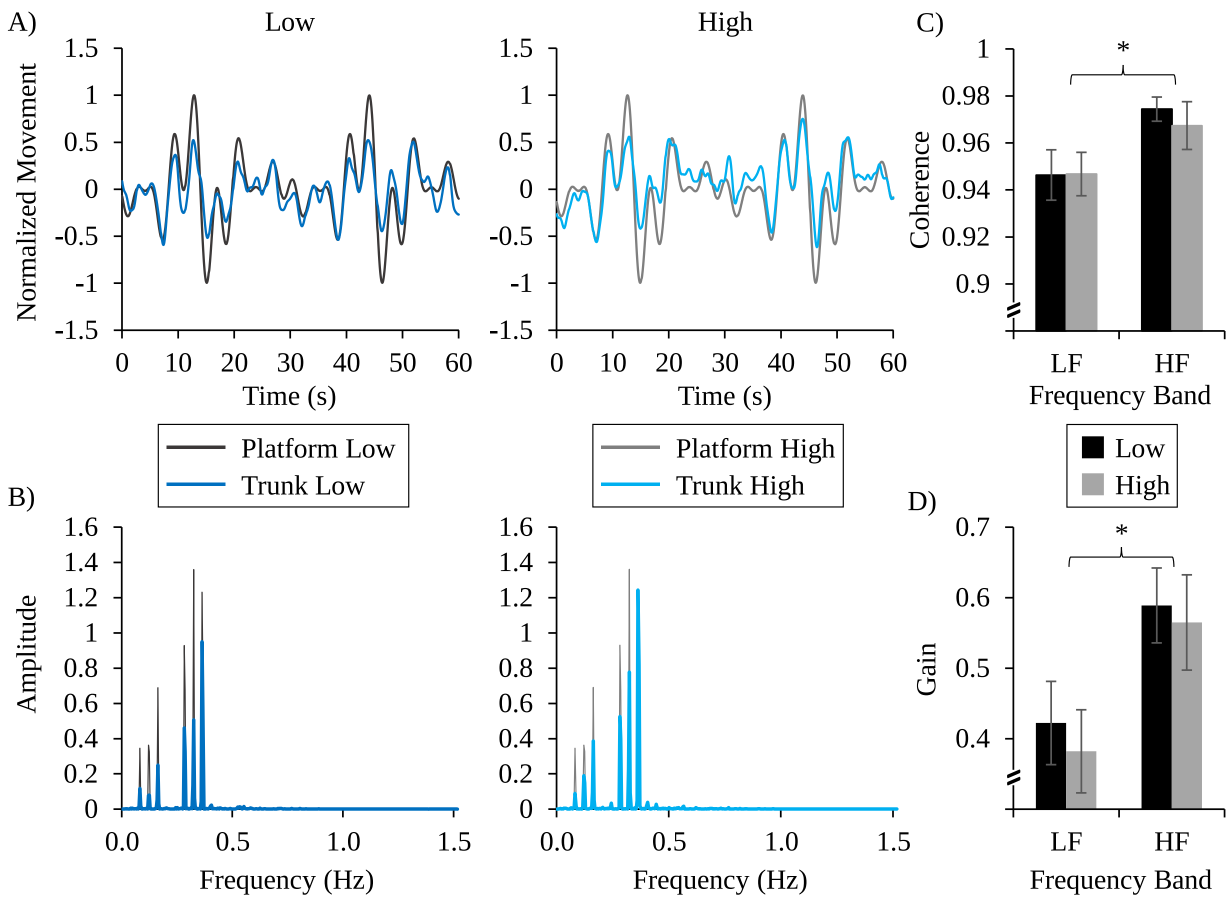

Figure 4-5 Representative and group data for movement relative to platform

Representative participant (A) trace and (B) power spectrum comparing platform movement (grey) and trunk movement (blue) for LOW (left column) and HIGH (middle column) conditions. LOW platform: dark grey; LOW trunk: dark blue; HIGH platform: light grey; HIGH trunk: light blue. Group mean (standard error) for (C) coherence and (D) gain between platform and trunk movement comparing LOW (black) and HIGH (grey) conditions across low frequency (LF) and high frequency (HF) bandwidths. * indicates a significant difference ($p < 0.05$).

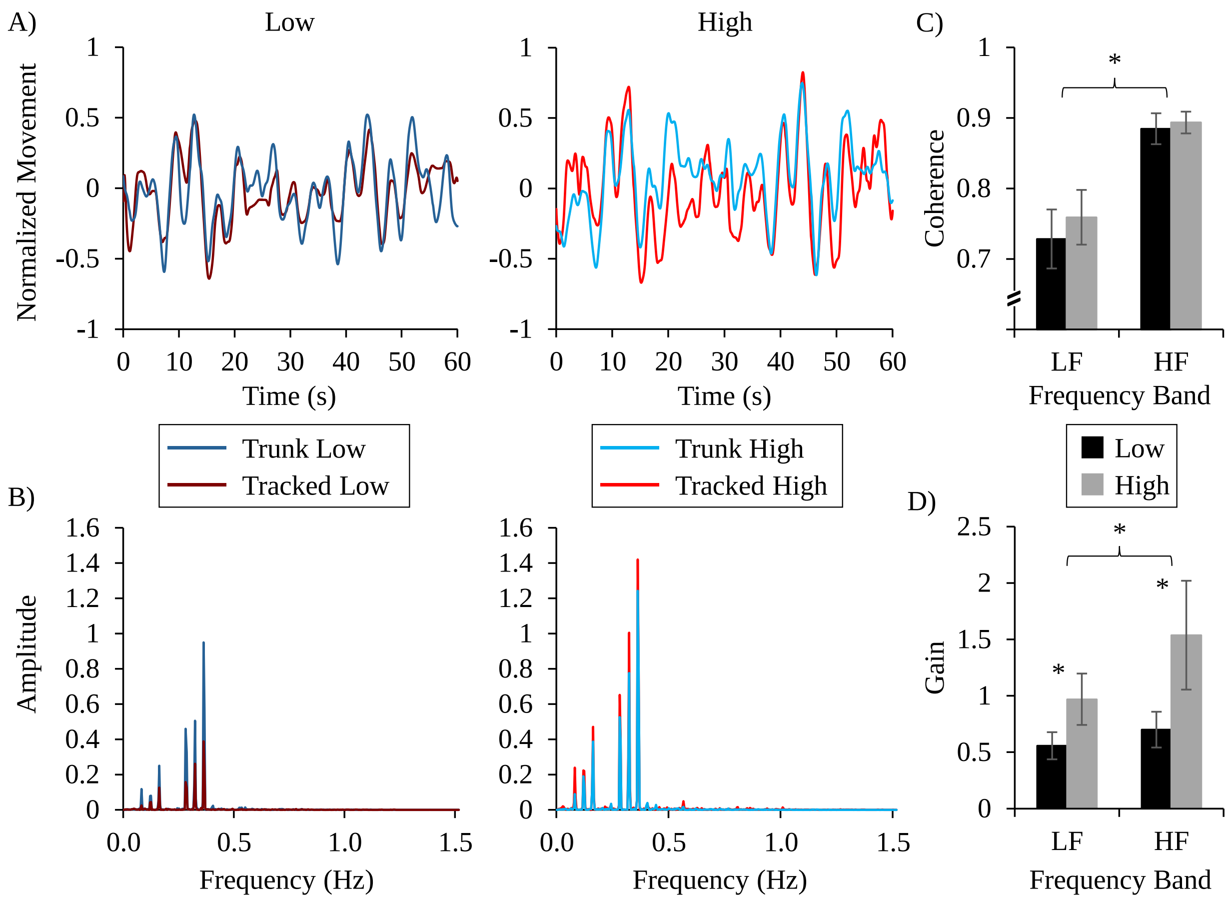

Figure 4-6 Representative and group data for tracking relative to actual movement

Representative participant (A) trace and (B) power spectrum comparing trunk movement (blue) and tracked movement (red) for LOW (left column) and HIGH (middle column) conditions. LOW trunk: dark blue; LOW tracked: dark red; HIGH trunk: light blue; HIGH tracked: light red. Group mean (standard error) for (C) coherence and (D) gain between trunk and tracked movement comparing LOW (black) and HIGH (grey) conditions across low frequency (LF) and high frequency (HF) bandwidths. * indicates a significant difference ($p < 0.05$).

Chapter 5: Postural threat effects on perceptions of lower leg somatosensory stimuli during standing

5.1 Introduction

Threatening conditions eliciting aversive emotional states, such as standing at the edge of an elevated support surface, can modify behavioural responses and sensory perceptions. When threatened, anxiety, fear and arousal increase and are accompanied with altered sensory processing and related perceptions of different sensory stimuli. For example, visual perceptions of spiders (Vasey et al., 2012) and the steepness of hills (Stefanucci et al., 2008) are magnified during increased levels of fear when threatened with a phobic stimulus or potentially dangerous action, respectively. Likewise, during stressful conditions, auditory stimuli are perceived as louder (Siegel & Stefanucci, 2011; Asutay & Västfjäll, 2013) or closer (Gagnon et al., 2013), and unpleasant bitter and sour tastes are perceived as stronger (Platte et al., 2013). Multi-sensory perceptions of standing balance have also been shown to be amplified under threatening conditions such as when standing at the edge of an elevated support surface (Studies 1 – 3). During quiet standing, voluntary leaning, and dynamic stance, height-induced threat significantly increases the amplitude of perceived whole-body movement. However, the mechanisms through which height-induced threat affects these perceptions of whole-body movement are not known.

Changes in amplitude of perceived movements (or any other form of sensation) may be mediated by: a) a decrease in the detectable threshold (stimulus/contrast gain), b) an amplification of the response proportional to stimulus intensity (response gain), or c) a combination of the two (Horak & Diener, 1994; Lim et al., 2014). Decreasing the threshold for detectable movements will allow smaller movements to be perceived, thus affecting all subsequent perceptions (see Figure 5-1A). Alternatively, the response to a detectable stimulus may be multiplied by a constant gain factor resulting in an increased response strength proportional to stimulus intensity without any change in detectable thresholds for movement (see Figure 5-1B). Thus, one way of discriminating the underlying mechanisms involved in perceptual gain changes observed with height-induced postural threat is to assess detection thresholds within a balance-relevant sensory system.

Perceptual thresholds have been assessed within a number of balance-relevant sensory systems, which includes vestibular, visual, and somatosensory systems. Whole-body sway is thought to be heavily reliant on afferent information from somatosensory receptors in the ankle (Thelen et al., 1998), as the majority of sway occurs about the ankle joint in the sagittal plane (Gage et al., 2004), and movement detection thresholds are lowest for somatosensory-related movements compared to visual or vestibular systems (Fitzpatrick & McCloskey, 1994). It is therefore important to consider the somatosensory system as a potential contributor to height-related effects on perception.

Perceptions of somatosensory stimuli are derived from physical stimulation of various sense organs, and central processing and interpretation of sensory information (Fitzpatrick & McCloskey, 1994). Peripheral (Simoneau et al., 1994) and central (Dannenbaum & Jones, 1993) somatosensory deficits can cause significant changes in perceptual acuity as evidenced by elevated perceptual thresholds for somatosensory stimuli. Perceptions of somatosensory stimuli have the potential to be influenced by threat as both the acquisition and cortical-related sensory processing of afferent information have been shown to be affected by a height-induced postural threat (Horslen, 2016; Davis et al., 2011; Adkin et al., 2008; Sibley et al., 2010).

The aim of this study was to investigate the effect of height-induced postural threat on lower leg somatosensory acuity using an ankle kinaesthetic task. Since ankle kinaesthesia relies on different classes of somatosensory receptors including muscle spindles and cutaneous mechanoreceptors (Refshauge & Fitzpatrick, 1995), multiple experiments were needed to determine how different classes of somatosensory receptors contribute to any height-related changes. The purpose of Experiment 1 was to determine the effects of postural threat on ankle movement discrimination thresholds, tested using ankle rotations during normal upright stance. The purpose of Experiment 2 was to determine the effects of height-induced postural threat on foot sole vibrotactile discrimination thresholds. Due to known changes in somatosensory processes (Horslen et al., 2013; Davis et al., 2011; Adkin et al., 2008; Sibley et al., 2010), it was hypothesized that perceptual thresholds across experiments would decrease to promote the detection of smaller ankle movements and foot sole vibrations with height-induced threat.

5.2 Methods

A total of 33 young healthy adults volunteered to participate in this study; 15 (age 26.5±3.8 years, 9 females) participated in Experiment 1 and 18 (age 27.2 ± 5.2 years, 10 females) in Experiment 2. All participants self-reported having no known neurological, orthopedic, or cognitive disorders that may affect their balance performance, or perception of ankle rotations or foot sole vibrations. All participants gave informed written consent prior to participation in accordance with the University of British Columbia Clinical Research Ethics Board.

5.2.1 Experimental setup for experiment 1

Participants stood barefoot, held a bi-directional toggle switch in their right hand and looked straight ahead. Participants stood with their stance width equal to a maximum width of 40 cm due to the constraints of the experimental setup, with their left foot positioned on top of a custom built single axis servo-controlled tilting platform, and right foot positioned on an adjacent firm support surface (Figure 5-2). All motor command signals were generated using Spike 2 software (CED, UK) and output from a data acquisition board (Power 1401; CED; UK). The axis of rotation of the participant's subtalar joint was oriented with the axis of rotation of the tilting platform. The entire support surface was mounted at the edge of a hydraulic lift (Figure 5-2; M419-207B01H01D, Pentalift, Canada). Foot position was marked on the force plate and kept constant across trials to ensure a consistent rotation of the ankle. One-legged rotations were used to limit the effect of platform rotations on whole-body movement (Corna et al., 1996; Horslen, 2016). Furthermore, there does not appear to be a difference in sensory acuity when one or both ankles are moved (Refshauge & Fitzpatrick, 1995).

5.2.2 Experimental setup for experiment 2

Participants stood barefoot (stance width 40 cm) on a stable support at the edge of a hydraulic lift (M419-207B01H01D, Pentalift, Canada) (Figure 5-2D). A 6 mm probe protruded through a 7 mm opening in the support surface and made contact with the left foot sole. The left foot was positioned to align to the probe with a location approximately 80% of maximum width from the lateral border near the ball of the foot, and 80% of maximum length from the tip of the big toe to the back of the heel. If the probe aligned with the space between the metatarsal and phalange, where there is little to no skin contact with the support surface, the foot was moved anteriorly until sufficient force (approximately 2 N) on the probe was obtained (no more than 5 mm). Corresponding with previous studies (Peters et al., 2016), this location corresponded to the skin over the anterior aspect of the metatarsal head, which has been reported to be more tightly coupled to balance relative to more posterior areas of skin on the sole of the foot in the elderly (Cruz-Almeida et al., 2014). Foot position was marked on the force plate and kept constant across trials to ensure a consistent contact force of the probe onto the skin surface. The probe was attached to a linear motor (model MT-160; Labworks) in series with a force transducer (model 31; Honeywell). An accelerometer (model 2220-010; X Tronics) was also secured to the back of the motor piston. Acceleration and force from the single force transducer were differentially amplified (×1 and ×100, respectively) and online low-pass filtered at 600 Hz (Brownlee model 440; AutoMate Scientific). All motor command signals were generated using Spike 2 software (CED, UK), output from a data acquisition board (Power 1401; CED; UK) and sent to a motor amplifier (PA-141; Labworks) (Mildren et al., 2016).

5.2.3 Data acquisition

In both experiments, 3D motion capture data were collected to estimate body position (250 Hz; Optotrak, Northern Digital Inc.). Infrared emitting diodes were placed at the front and back of the force plate's top surface, left base of the fifth metatarsal, lateral malleolus, and fibular head.

Electromyography (EMG) was recorded using a bipolar arrangement of 2 surface electrodes placed 2 cm apart over the muscle bellies of the left soleus (SOL) and tibialis anterior (TA). EMG was band-pass filtered between 10 and 500 Hz (Telemyo, 2400R, Noraxon, USA), and sampled at 2000 Hz. Offline, each EMG signal was corrected for bias, low-pass filtered at 100 Hz using a dual-pass Butterworth filter, and full-wave rectified.

Vertical load under the left foot was recorded using a force plate (100 Hz; model OR6-7-1000, AMTI, USA) mounted on the single axis platform (Experiment 1), or 4 load cells (100 Hz; SSB-250 with BSC4A-C14, Interface Advanced Force Measurement, USA) embedded into the support surface (Experiment 2). Electrodermal activity (EDA) was collected from the thenar and hypothenar eminences of the left hand (100 Hz, Skin Conductance Module 2502, Cambridge Electronic Design, UK).

Prior to each experimental condition, while the participant was seated at the height of the upcoming condition, participants rated how confident they were they could remain upright and avoid a fall on a scale from 0 (not confident at all) to 100 (completely confident). After each condition, a subjective rating of fear (0 = no fear, 100 = fearful) and stability (0 = not stable, 100 = very stable) was reported by the participant. Finally, state anxiety was assessed after each condition by summing the answers from a modified Sport Anxiety scale with 16 items (9 point Likert scale for each item) (Hauck et al., 2008).

5.2.4 Threat manipulation

In both experiments, participants stood under conditions of LOW and HIGH threat with gaze directed to a visual target at eye level approximately 1.8 m away. In the LOW threat condition, the top of the standing support surface was 1.1 m above the ground. An extension was added 60 cm beyond the edge of the platform to position the participants further away from the edge of the support surface and further reduce threat in this condition (Figure 5-2; Carpenter et al. 2001). In the HIGH threat condition, the support surface was raised to 3.2 m above the ground, with no additional support surface to the right of the participant to maximize threat effects (Figure 5-2; Carpenter et al., 2001). Prior to the first experimental condition, participants stood quietly for 20 seconds to establish pre-stimulus baseline (neutral) measures. Baseline vertical force level was monitored throughout experimental trials and used to provide verbal feedback from the experimenter if a neutral position was deviated from by two standard deviations. If needed, feedback was delivered only immediately after a stimulus was perceived, to minimize the possibility of shifting attention away from the psychophysical task.

5.2.5 Experimental procedures

When assessing the sensitivity within the proprioceptive system, there are a number of methods that can be used to determine a threshold, including method of limits, constant stimuli, and adaptive staircase methods. Due to the time limitations for maintaining psychological changes with height, an adaptive staircase method was selected because of its relatively short duration (five minutes) compared to approximately twenty minutes needed for a method of limits approach (Berquin et al., 2010).

Prior to any experimental conditions, participants completed two practice trials to familiarize with the experimental procedures, and to remove any first trial effects. At LOW height, participants were asked to identify which of two ankle rotations (Experiment 1) or foot sole vibrations (Experiment 2) they felt (using the correct input device for each stimulus) followed by a verbal report. A minimum of five randomly ordered stimuli were administered using a constant amplitude (all presumed suprathreshold; 1° rotation in Experiment 1; 3 Hz >1 N and 40 Hz > 0.5 N in Experiment 2). This trial was used to ensure proper use of experimental equipment, and that each participant could detect large amplitude stimuli. The second practice trial consisted of 16 stimuli of each direction/frequency, randomly presented using experimental procedures (see below) to ensure participants could sufficiently perform the task.

Experiment 1: While standing in the two postural threat conditions, participants performed an ankle rotation discrimination task using an adaptive staircase procedure. The left ankle was rotated in the anteroposterior direction in a dorsi-flexion and plantar-flexion direction.

Platform rotation speed was kept constant at 0.25°/s while amplitude was varied. Participants were asked to indicate when they felt either an ankle dorsi-flexion by pushing a hand held toggle switch up, or an ankle plantar-flexion by pushing a hand held toggle switch down. The correct detection of an ankle rotation was only accepted if the switch was correctly pushed within platform movement onset up to 2 seconds after platform movement offset. To reduce the likelihood of false-positive responses, participants were specifically instructed to indicate a movement direction only when they were sure they had felt a movement, and to not respond if no movement or an unidentifiable movement was perceived. Stimulus to stimulus, the peak-to-peak amplitude of the voltage command was adjusted using an adapted staircase method (4-2-1-step, modified from Dyck et al., 1993). Briefly, each staircase starts with 0.1 V (approximately 0.2°) steps in stimulus intensity. Steps were halved after four steps to 0.05 V. Stimuli were halved again to 0.025 V after another four steps and kept constant for seven steps. This method provided more accurate thresholds in pilot data than the reduction in step size on reversals previously used (Dyck et al., 1993; Peters et al., 2016). To accommodate the discrimination technique, two staircases were interlaced, one for each of the two stimuli. Furthermore, to accommodate an ascending and descending staircase method (typically seen in a method of limits technique), a new staircase was implemented half way through each experimental condition. Staircase-direction was counterbalanced across participants such that stimulus 17 for each of the movement directions was set at a low or high amplitude depending on whether the start of the experiment started with a high or low amplitude, respectively. The 4-2-1-step algorithm was then reset and continued until the end of the trial (Figure 5-3). Stimulus-direction was randomly presented to avoid any anticipation bias.

Experiment 2: Similar experimental procedures to Experiment 1 were used. Instead of ankle rotations, participants performed a foot sole vibration detection task using the same adaptive staircase procedure. Natural stimuli of the foot sole during standing will most likely activate all cutaneous afferent classes (Inglis et al., 2002; Kennedy & Inglis, 2002). While the perception of different frequency ranges of vibration are thought to be derived from specific afferent classes in the hand (slowly adapting type 1 (SA1) up to 4 Hz, fast adapting type 1 (FAI) between 4 – 40 Hz, and FAII greater than 40 Hz, Bolanowski et al. 1988), recent evidence in the foot suggests sensitivity of cutaneous receptors to frequency ranges overlap making it difficult to attribute perception to specific afferent classes (Strzalkowski, 2015). Vibrotactile perceptual thresholds of lower frequencies (< 4 Hz) may be mediated by a population of afferents, specifically SA but may also include FAI, higher frequencies are mediated by FA afferents alone (> 20 Hz, Strzalkowski, 2015). Therefore, two stimuli were used to possibly dissociate the contribution of possible sub-classes (slow and fast adapting) of cutaneous afferents to the changes in the perception of sway-related movement during threat. During upright stance, vibrations were applied at random intervals (3 to 5 seconds) perpendicular to the skin. Vibration stimuli were applied for 1 second in duration. Participants were asked to indicate when they felt either a 3 Hz vibration by pushing a button in one hand, or a 40 Hz vibration by pushing a button the other hand (participants were able to choose which hand held the 3 and 40 Hz buttons). The correct detection of a vibration was only accepted if the button was pushed between vibration onset and 1 second after vibration offset (2 seconds total). To reduce the likelihood of false-positive responses, participants were specifically instructed to push a button (indicating 3 Hz or 40 Hz felt) only when they were sure they had felt the given vibration, and to not respond if no vibration or unidentifiable vibration was felt. Similar to Experiment 1, the peak-to-peak amplitude of the voltage command was adjusted from stimulus-to-stimulus using an adapted staircase method (4-2-1-step, modified from Dyck et al., 1993), and staircases for both frequencies were interlaced. However, in this experiment, descending staircases were used prior to ascending for all participants (Figure 5-3B). Stimulus frequency was randomly presented to avoid any anticipation bias.

5.2.6 Baseline measures and detection threshold estimates

For both experiments, motion capture data were used to calculate segment displacements of the ankle and foot. Two-dimensional filtered coordinates defining the foot (toe to lateral malleolus) and shank (malleolus to fibular head) were used to calculate the angle of the ankle. In Experiment 1, potentiometer-based feedback from the platform and the voltage supplying the motor was recorded (sampled at 2 KHz, Power 1401 with Spike2 software, CED, UK). In Experiment 2, probe acceleration, contact force and the voltage supplying the motor was recorded (sampled at 5 KHz, Power 1401 with Spike2 software, CED, UK). Mean background EMG activity, vertical force, and foot and ankle position were calculated offline from 1 second prior to onset of platform movement (Experiment 1) or vibration (Experiment 2) for all stimuli in each height condition.

To compute ankle rotation and foot sole vibrotactile discrimination thresholds, data was reanalyzed offline using the peak displacement of the foot calculated from motion capture data (Experiment 1) or peak-to-peak force from the force transducer (Experiment 2). In accordance with previous work (Peters et al., 2016), this method accounted for trial-to-trial variability and inter-individual differences in biomechanical properties of the ankle and/or foot. Thresholds were then calculated as the mean of the smallest step-amplitude reversal points (Figure 5-3). If only one reversal point for a given direction (Experiment 1) or frequency (Experiment 2) was observed in the smallest step-amplitudes, the last two stimuli were averaged and used in the mean calculation. False detection rates were calculated from all 2 second periods where no platform movement (Experiment 1) or vibratory stimulus (Experiment 2) was given within a trial, and reported as a percentage of the number of times a stimulus was perceived during these periods (number of blank stimuli detected divided by total number of 2 second periods with no stimulus). Participants were removed from further analysis if a false detection rate in the LOW condition exceeded 20% (Berquin et al., 2010). As a result, one participant in Experiment 1 and no participants in Experiment 2 were removed due to large false detection rates. One additional outlier in Experiment 1 and one in Experiment 2 was removed due to higher than normal (two times higher than any other participant) thresholds within the LOW condition.

5.2.7 Statistical analysis

Paired sample t-tests were used to examine the effects of threat on EDA and self-report measures of fear, anxiety, confidence and stability. A 2 (height) x 2 (ankle movement direction) x 2 (staircase-direction) repeated measures ANOVA was used to test the effects of height (LOW, HIGH), ankle movement direction (dorsi-flexion, plantar-flexion), and staircase-direction (ascending, descending) for calculated thresholds in Experiment 1. If a significant movement-direction effect was observed, separate 2 (height) by 2 (staircase-direction) repeated measures ANOVA's were used to examine each movement direction independently. A 2 (height) x 2 (staircase-direction) x 2 (frequency) repeated measures ANOVA was used to test the effects of height (LOW, HIGH), staircase-direction (ascending, descending), and stimulus frequency (3 Hz and 40 Hz) on perceptual thresholds. If a significant frequency effect was observed, separate 2 (height) by 2 (staircase-direction) repeated measures ANOVA's were used to examine each frequency independently. The criteria for a significant result was set at $p \leq 0.05$ with trends identified when $p \leq 0.1$.

5.3 Results

5.3.1 Effect of staircase-direction and stimulus

Due to the interlacing of staircases for the two forms of stimuli (Figure 5-3; Berquin et al., 2010), participants reported an inability to predict stimuli for both experiments. In Experiment 1, a negative hysteresis effect was visually observed, where the first reversal point in ascending data was smaller than the first reversal point in descending data. Participants could perceive platform-triggered ankle rotations as small as 0.07°, on average (averages ranged from 0.07° to 0.1° for ankle dorsi-flexion and plantar-flexion across heights, Figure 5-5, while individual thresholds ranged from 0.024° to 0.368°). There was a significant effect of staircase-direction ($F(1,12) = 9.289$, $p = 0.01$, $\eta_p^2 = 0.44$), where ascending stimuli (0.076° ± 0.01°) were significantly larger than descending stimuli (0.108° ± 0.01°) further supporting a negative hysteresis effect (Figure 5-5B). The counterbalance of ascending or descending stimuli resulted in no differences between first block and second block of staircase delivery ($F(1,12) = 0.042$, $p = 0.840$, $\eta_p^2 < 0.01$). There was a non-significant trend ($F(1,12) = 3.902$, $p = 0.07$, $\eta_p^2 = 0.25$; Figure

5-5A) for a decrease in amplitude detection thresholds for toes up (0.08° ± 0.01°) compared to toes down (0.10° ± 0.01°).

In Experiment 2, a perceptual hysteresis effect was visually observed, where the first reversal point in ascending data was larger than the first reversal point in descending data (Figure 5-3C). There was no main effect of staircase-direction (3 Hz: $F(1,16) = 1.378$, $p = 0.258$, $\eta_p^2 = 0.08$; 40 Hz: $F(1,16) = 0.155$, $p = 0.699$, $\eta_p^2 < 0.01$) nor were there any interactions (Figure 5-6B). There were significant differences between the 3 Hz and 40 Hz stimuli ($F(1,16) = 62.986$, $p < 0.001$, $\eta_p^2 = 0.80$) with smaller amplitude vibrations perceived for the 40 Hz compared to the 3 Hz vibration (Figure 5-6A). Subsequent height analyses split 3 and 40 Hz stimuli based on these significant differences.

5.3.2 Effect of height

5.3.2.1 Emotional state

Postural threat had a significant effect on all psychological variables and EDA in both experiments (Figure 5-4). Balance confidence (Experiment 1: $t(12) = 3.672$, $p = 0.003$, $d = 1.02$; Experiment 2: $t(16) = 3.112$, $p = 0.007$, $d = 0.75$) and perceived stability (Experiment 1: $t(12) = 2.403$, $p = 0.033$, $d = 0.66$; Experiment 2: $t(16) = 4.261$, $p = 0.001$, $d = 1.03$) decreased, while fear (Experiment 1: $t(12) = 4.341$, $p = 0.001$, $d = 1.20$; Experiment 2: $t(16) = 5.088$, $p < 0.001$, $d = 1.23$), anxiety (Experiment 1: $t(12) = -2.710$, $p = 0.019$, $d = 0.75$; Experiment 2: $t(16) = 5.270$, $p < 0.001$, $d = 1.28$) and EDA (Experiment 1: $t(12) = 3.420$, $p=0.005$, $d = 0.95$;

Experiment 2: $t(16) = 2.959$, $p = 0.009$, $d = 0.72$) increased when standing in the HIGH compared to LOW threat condition (Figure 5-4).

5.3.2.2 Baseline measures

There was a significant increase in vertical force at height under the stimulated (left) foot in Experiment 1 ($t(12) = 3.587$; $p = 0.004$, $d = 0.99$) and Experiment 2 ($t(16) = 3.722$, $p =0.002$, $d = 0.90$). While significant, this difference was relatively small in both experiments (< 5%). In contrast, there was no evidence in either experiment of any effect of height on the background activity for SOL (Experiment 1: $t(12) = 0.636$, $p = 0.535$, $d = 0.18$; Experiment 2: $t(16) = 0.233$, $p = 0.818$, $d = 0.06$). Similarly, there was no effect of height on the background activity for TA in Experiment 1 ($t(12) = 1.142$, $p = 0.276$, $d = 0.32$); however, there was a non-significant trend for larger TA activity at height in Experiment 2 ($t(16) = 1.87$, $p = 0.08$, $d = 0.45$). There was no effect of height on the pre-stimulus location of the foot segment ($t(12) = 0.388$, $p = 0.705$, $d = 0.11$) or ankle ($t(12) = 0.965$, $p = 0.354$, $d = 0.27$) in Experiment 1, or pre-stimulus probe force ($t(16) = 1.124$, $p = 0.278$, $d = 0.27$) in Experiment 2.

5.3.2.3 Thresholds

In Experiment 1, there was a significant effect of height on perceptual thresholds calculated for ankle rotations (Figure 5-5C; $F(1,12) = 7.285$, $p = 0.018$, $\eta_p^2 = 0.38$). Specifically, higher perceptual thresholds across stimulus and staircase-direction were observed in the HIGH ($0.103° \pm 0.02°$) compared to LOW condition ($0.081° \pm 0.013°$). Nine of thirteen participants had an average increase in threshold amplitude across stimulus-direction by staircase-direction conditions. Twelve of thirteen participants had a higher threshold at height within at least two of the four stimulus-direction by staircase-direction conditions. There were no significant stimulus-direction or staircase-direction by threat interactions, or three-way interaction effects for ankle rotation perceptual thresholds. Representative participant (for one condition) and group average data are shown in Figure 5-5C, D, and E. In Experiment 2, there were no significant height effects on the thresholds calculated for 3 Hz or 40 Hz foot sole vibrations (3 Hz: $F(1,16) = 1.369$, $p = 0.259$, $\eta_p^2 = 0.08$; 40 Hz: $F(1,16) = 0.137$ $p = 0.716$, $\eta_p^2 < 0.01$; Figure 5-6). There were no significant staircase-direction by threat interactions for foot sole vibrations.

5.4 Discussion

The primary aim of this study was to determine the effect of postural threat on detection thresholds for somatosensory stimuli during standing tasks. When young healthy adults stood at the edge of an elevated support surface and experienced either single limb ankle rotations (Experiment 1) or foot sole vibrations (Experiment 2), the ability to perceive and discriminate an ankle rotation was significantly reduced, while detection thresholds for foot sole vibrations did not change.

Detection thresholds for ankle rotations were on average 0.09° ± 0.01°, similar to previous work when taking into account the velocity used in the current study (Fitzpatrick & McCloskey, 1994). The observed trend of lower detection thresholds for dorsi-flexion rotations (0.078°) compared to plantar-flexion rotations (0.105°) is also consistent with prior reports

(Thelen et al., 1998). Comparing foot sole vibrations in this study to previous work is difficult given differences in probe diameter, stimulus location, postural orientation and dependent variables used (displacement or force); however, the observations of lower detection thresholds for 40 Hz (0.154 N) vibrations compared to 3 Hz (0.395 N) vibrations matches prior reports (Strzalkowski, 2015).

In an attempt to shed light on the unknown mechanisms underlying threat-related perceptual gain changes (Study 1 – 3), this study showed perceptual thresholds to somatosensory stimuli remain unchanged or increase when under threatening conditions. Height-induced postural threat increased detection thresholds by 40% and 38% for dorsi- and plantar-flexion of the ankle, respectively. Therefore, threat-related changes in perceptual gain during whole-body movements (Study 1 – 3) are unlikely to be mediated by a decrease in perceptual threshold. As a consequence of this, increased response gain (Figure 5-1B) remains a viable mediator to amplifying perceptual gain observed with height-induced postural threat (Studies 1 – 3).

5.4.1 Confounding effects of height

A number of compensatory actions that occur with postural threat have the potential to explain the observed changes in ankle rotations, including muscle activity, stimulus variability, and weight on stimulated leg. Muscle activity has been shown to increase in ankle dorsi-flexors when standing at height (Carpenter et al., 2001) and can potentially reduce movement-related thresholds (Taylor & McCloskey, 1992). Contradictory to proposed mechanisms, muscle activity has been shown to reduce muscle spindle coding accuracy during ankle rotations (Peter et al., 2017). Increased SOL and TA co-contraction at height (Cleworth et al., 2016; Carpenter et al., 2001) can increase stiffness of the lower leg, thus changing the resulting effect of platform rotation on foot movement (stimulus variability). However, the results of the current study are unlikely to be mediated by a change in the state of the lower limb. EMG activity was not significantly influenced by height possibly due to the ML orientation of the participant to the threat, reducing the need for a backwards lean or increased TA activity. Furthermore, controlling voltage (drive) online but reanalyzing data offline using actual foot displacements or probe force amplitudes accounted for trial-to-trial variability that may have occurred from increased stiffness (mechanical properties) (Peters et al., 2016).

Vertical force on the stimulated leg did increase with height, however this relatively small (< 5%) change is unlikely to explain the observed results, given that previous reports have illustrated no change in ankle angular displacement thresholds when in a standing compared to lying condition effectively removing body weight (Refshauge & Fitzpatrick, 1995). If anything, an increase in vertical force would be expected to increase the articular pressure of the joint and reduce perceptual thresholds (Burke et al., 1988). For foot sole vibrations, a change in posture has been shown to increase vibratory perceptual thresholds (Mildren et al., 2016). These changes were observed under the metatarsals and the heel, and across four different frequencies (3-250 Hz). However, further examination of the results revealed the heel-related stimuli demonstrated a clear increase in threshold, while the 3 Hz and 40 Hz metatarsal-related stimuli did not significantly change with posture (Mildren et al., 2016). Furthermore, Germano et al. (2016) illustrated no change with posture when using a singular small diameter probe (7 mm compared to an array of probes used by Mildren et al., 2016). Therefore, the relatively small increase in vertical force is unlikely to influence vibratory thresholds observed in the current study as a small diameter probe was used to vibrate the foot sole and was located near the base of the first metatarsal (forefoot).

5.4.2 Psychophysical phenomenon: Hysteresis, judgement uncertainty, and task specificity

Hysteresis effects are common in psychophysical experiments; however, different hysteresis phenomena were observed between experiments in the current study. While there was no effect of staircase-direction on thresholds calculated for foot sole vibrations, there was objective evidence showing the consistently reported perceptual hysteresis for the first turning point in Experiment 2 (Hock & Schöner, 2010). Generally, ascending stimuli lead to a perceived stimulus that was larger than the first unperceived stimulus for a descending staircase (Figure 5-2). Perceptual hysteresis was not observed in Experiment 1, instead 'negative hysteresis' (Lopresti-Goodman et al., 2013) was observed as the ascending staircase led to lower thresholds compared to a descending staircase (Figure 5-5A). Similar hysteresis effects have been observed previously in joint position sense studies. When the knee is passively extended from a flexed starting position, participants matched a target position with a flexion error (not extended enough). When the knee was passively flexed from an extended starting position, participants matched the same target position with an extension error (not flexed enough) (Weiler & Awiszus, 2000).

One factor thought to influence hysteresis is judgement uncertainty (Hock & Schöner, 2010). Judgement uncertainty arises when participants cannot clearly separate two perceptual alternatives. During a postural task, it may be difficult to perceive a passive ankle rotation, but not an externally produced foot sole vibration. This is evidenced by lower false identification rates (ease of differentiating 3 Hz and 40 Hz) and the observed perceptual hysteresis in Experiment 2. Participants had higher false identifications with ankle rotations (i.e., when an ankle dorsi-flexion is presented, the participant perceived a plantar-flexion) than vibrotactile sensations (mean 4.4% and 2.9%, respectively). When standing, continuous static pressure is sensed by slowly adapting receptors, which are thought to provide information necessary for controlling COP (Hämäläinen et al., 1992; Kennedy & Inglis, 2002; Magnusson et al., 1990). As 99% of COP displacements occur under 1.21 Hz (Gage et al., 2004), the overlap in pertinent sensory information between the vibrotactile detection task (3 and 40 Hz) and quiet standing balance task (< 2 Hz) is minimal, and would allow for easy discrimination between the two tasks. In addition, a difference of between 6 and 12 Hz is all that is needed in order to discriminate vibratory stimuli (Harris et al., 2006). Further evidence to support the difficulty in perceiving stimuli between experiments is with false alarm rates. In Experiment 2, no participant perceived a vibratory stimulus when there was no stimulus to perceive in the LOW condition. In contrast, in Experiment 1, 9 out of 13 participants (1.6% of all 52 sham trials across participants, on average) indicated an the perception of an externally-produced rotation when in fact the sensation was likely due to sensory noise alone. Therefore, the negative hysteresis observed in Experiment 1 is likely mediated by uncertainty between dorsi- and plantar-flexion rotations intermixed with natural sway movements.

5.4.3 Perceived ankle movements affected by threat

5.4.3.1 Sensory receptor, perceived movement, and postural threat

Height-related changes in detectable thresholds for ankle rotation discrimination may be mediated by a change in the sensory pathway associated with some somatosensory receptors, specifically muscle spindles, joint receptors and GTOs, but unlikely to include cutaneous mechanoreceptors. Ankle rotations are thought to activate different classes of receptors including and specific to muscle spindles of the lower leg musculature, but also including cutaneous and joint receptors, and GTOs. The lack of a change in discriminatory thresholds to foot sole vibrations provides evidence to support the inability of the cutaneous system to be tuned by postural threat, as previously observed using cutaneous reflexes in young healthy adults when standing at height (Horslen, 2016). The changes observed in Experiment 1 are unlikely to be the result of a change in sensitivity from muscle spindles. Thresholds were shown to increase with threat, which could be mediated by a decreased spindle discharge during ankle rotations. However, with postural threat, tendon-tap evoked potentials and short latency stretch reflexes are increased in amplitude (Horslen et al., 2014) while Hoffman-reflexes remain constant (Horslen et al., 2014) or decrease (Sibley et al. 2007). The collective result of these effects indicate increased muscle spindle sensitivity (Horslen et al., 2013; 2016; Davis et al., 2011). Therefore, assuming spindle sensitivity increases with height, the observed changes with ankle movement detections could be related to modulation of the spinal and supra-spinal afferent pathways involved in processing sensory information. These regions are likely to be specific to sensory systems involved in an ankle rotation and not a vibratory stimulus on the foot.

5.4.3.2 Cortical processing, perceived movement, and postural threat

Cortical areas receiving information pertaining to somatosensory stimuli can be modulated across tasks and by threatening conditions (Davis et al., 2011; Staines et al., 1997; McIlroy et al., 2003). The amount and direction of modulation has been shown to be reliant on the somatosensory information required by the task (Staines et al., 1997). Sensory gating occurs during passive movement (Staines et al., 1997) where faster movements increase gating (Rauch et al., 1985). Sensory gating also occurs during balance tasks (McIlroy et al., 2003) and when standing quietly in a threatening condition (Davis et al., 2011). Facilitation of initial cortical activity occur with kinaesthetic task demands (Staines et al., 1997), and with responses to destabilizing perturbations when balancing in threatening conditions (McIlroy et al., 2003; Adkin et al., 2008; Sibley et al., 2010), while later cortical processing is affected by height-induced threat (Horslen, 2016). Although a number of factors influencing sensory gating at cortical levels occur when standing at height, such as the presence of a threat, and increased movement frequency (Carpenter et al., 2001) and subsequent speed (van der Kooij et al., 2011), it does not appear to influence the perception of all sensory signals as cutaneous-related stimuli elicited similar detectable thresholds between conditions.

In addition to modulating the amplitude of cortical activity, threat has the potential to influence correlated spiking activity involved in the perception of a stimulus. Synchronicity within and across specific cortical regions, including the primary and secondary somatosensory cortices, has been shown to be associated with increased performance in consciously detecting stimuli (Melloni et al., 2007). Gamma band (40-80Hz) oscillations are associated with attending to relevant stimuli, while alpha band (8-14 Hz) oscillations are related to the suppression of distracting stimuli (Foxe & Snyder, 2011). With height-related threat and increased anxiety, increased levels of alpha band EEG (Knyazev et al., 2004) mediated through changes in movement reinvestment (Ellmers et al., 2016) may suppress the perception of distracting stimuli, while emotional threat increases perception of stimuli mediated by an increase in gamma band synchronization (Garcia-Garcia et al., 2010). In the current study, participants were asked to perform both the postural task (remain upright) and the perceptual task simultaneously. While speculative, if the balance task was to take precedence under a postural threat, the perceptual task would become distractor stimuli leading to elevated perceptual thresholds. Future work is needed to examine the cortical-related activity associated with perceived somatosensory stimuli during threatening conditions.

5.4.3.3 Signal-to-noise ratio, perceived movement, and postural threat

During postural tasks, the CNS is flooded with sensory information from internal and external sources within somatosensory, vestibular and visual systems. In the current study, balance-related sensory information was also relayed to the represented cortical areas, thus creating a more complex psychophysical discrimination task than when lying prone. The threshold amplitude of perceived ankle rotations from the rotating platform (maximum across participants is 0.36°) were well within the ankle angular displacement from quiet standing postural tasks (1 – 1.5°, Gage et al., 2004; Gatev et al., 1999). Based on signal detection theory (Green & Swets, 1988), the ability to detect ankle rotations or foot sole vibrations depends on the stimulus signal exceeding the current level of noise within the respective sensory modality and

CNS. Improving stimulus detection rates can occur by increasing the signal-to-noise ratio (larger stimuli or decreased background noise).

Traditionally, researchers consider noise to affect detection thresholds negatively by interfering with the identification of a stimulus, a process called masking. However, a number of studies have examined the influence of subthreshold noise as a means to enhance signal detection, termed stochastic resonance. For example, subthreshold vibrations on the bottom of the foot were only perceived when a small level of noise was added to the stimuli (Wells et al., 2005); however, if the noise was too large (at or above threshold) there was a decreased ability to indicate the presence of a stimulus (Wells et al., 2005). Subthreshold noise levels have beneficial effects for postural tasks as well, where vibrations below threshold applied to the entire fool sole decreased postural sway, presumed to indicate increased stability (Priplata et al., 2003).

There is evidence in the current study to indicate increased levels of noise at height. Balance-related sensory information has been thought to be gathered during quiet stance (Carpenter et al., 2010; Murnaghan et al., 2011) leading to accurate perceptions of whole-body movement (Cleworth & Carpenter, 2016: Study 1), but increasing sway-related ‘noise’ with threat. Participants increase sway frequency at height, increase sensitivity of muscle spindle (indirect evidence) and vestibular gain and coupling (Horslen et al., 2013; 2014; Naranjo et al., 2015), leading to a net increase in sensory information relayed to the CNS during quiet stance. Furthermore, false detection rates can indicate the level of noise within the system (Chaudhuri, 2011). False detection rates were increased at height in Experiment 1, and remained constant in Experiment 2, suggesting an increase in sensory-related noise during ankle rotation detections only. Therefore, height-related behaviour could increase sensory noise and mediate the decreased ability to perceive ankle rotations.

5.4.3.4 Attention, perceived movement, and postural threat

Selective attention is another possible mechanism for a threat-related change in ankle movement-related thresholds. Allocation of attentional resources to secondary tasks can directly affect performance during tactile (Lloyd et al., 1999), auditory (Haykin & Chen, 2005), visual (Verghese, 2001) and even ankle-related perceptual tasks (Yasuda et al., 2014). Changes in attention can occur with height-induced threat. During static and anticipatory postural control tasks, height-induced threat increases attention toward movement-related processes, threat-related stimuli, and self-regulatory strategies while decreasing attention toward task-irrelevant information (Zaback et al., 2016). Threat-related changes in attention have also been related to an increased conscious control and monitoring of movement (Huffman et al., 2009). These attentional changes were related to a focus of attention during postural tasks independent of any secondary tasks. It is unclear how attentional focus would change when performing a secondary task to balance in a threatening condition. Interestingly, a null effect of height on foot-sole cutaneous-related thresholds suggest global attentional changes are not influencing height-related changes in perception. It is however possible for the influence of attention to interact differently with varying levels of balance and secondary task complexity (Woollacott & Shumway-Cook, 2001). Future work should examine the specific effects of threat on attention during varying secondary tasks to standing balance.

5.4.4 Clinical applications

An interesting relationship emerges when comparing the effects of age and fear of falling on balance. Age has been known to have a deleterious effect on balance performance across a number of postural tasks (Laughton et al., 2003; Vereeck et al., 2008). More importantly, those who have a fear of falling further decrease postural stability (Maki et al., 1991). Furthermore, older adults have reduced sensitivity to ankle rotations (Thelen et al., 1998) and foot sole vibrations (Peters et al., 2016). The current study illustrates a similar decrease in perceived ankle rotation with postural threat during increased levels of fear and anxiety. The link between reduced stability and fear of falling may be mediated by a decrease in ankle-related acuity during quiet standing.

5.4.5 Limitations

There are two potential limitations in the current study. The first limitation is the effect of rotating the foot and its relationship to changes in ankle angle. Due to movements that occur during normal quiet standing, it was difficult to obtain accurate measurements of movement amplitude for ankle rotations. The normal amount of sway was much larger than the induced rotation of the ankle, and so threshold calculations could not be made off ankle movement, but instead foot movement. The second potential limitation is the observed change in vertical force, and therefore leaning position, with height. Although quite small and potentially functionally irrelevant, a change in vertical force in the rotated ankle would increase joint articular pressure, increase foot sole pressure, and could therefore influence the detection of ankle rotations and foot sole vibrations. For ankle rotations, thresholds decrease in a standing compared to sitting position (Refshauge & Fitzpatrick, 1995), the opposite effect observed here and is therefore unlikely to mediate the results.

5.5 Conclusions

In conclusion, detectable thresholds for ankle rotations increased while thresholds for foot sole vibrations remained unaffected while performing a postural task during threatening conditions. Changes in sensory receptors, afferent inflow and cortical activity are unlikely, yet undetermined, mechanisms to explain these results. Height-related effects in the ankle task are likely mediated by changes in signal-to-noise ratios and changes in pertinent stimuli possibly related to attention. The results of the current study further support previous work (Horslen, 2016) suggesting cutaneous information is unaffected by threat. Since perceptual thresholds in balance-relevant somatosensory systems remain unchanged or increase with postural threat, the height-related changes in perceptual gain of whole-body movements are likely attributed to stimulus gain of other sensory systems not tested in this study (e.g. vestibular or visual), or increases in response gain (increased response strength proportional to stimulus intensity; Horak & Diener, 1994; Lim et al., 2014) of all, or select sensory stimuli associated with balance control.

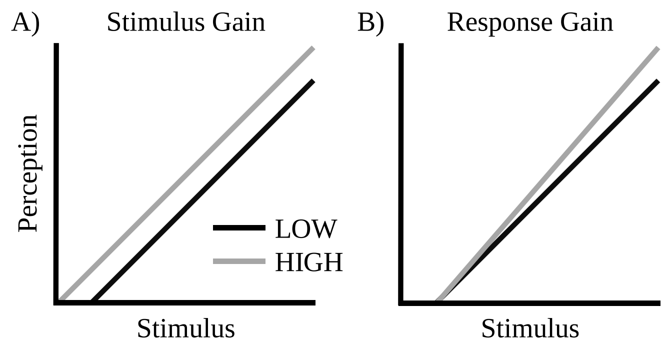

Figure 5-1 Stimulus and response gain.

Schematic representation of two possible mechanisms for increased gain of perceived movement. (A) Stimulus gain: a change in threshold for detectable movement; (B) Response gain: change in slope between stimulus and perception.

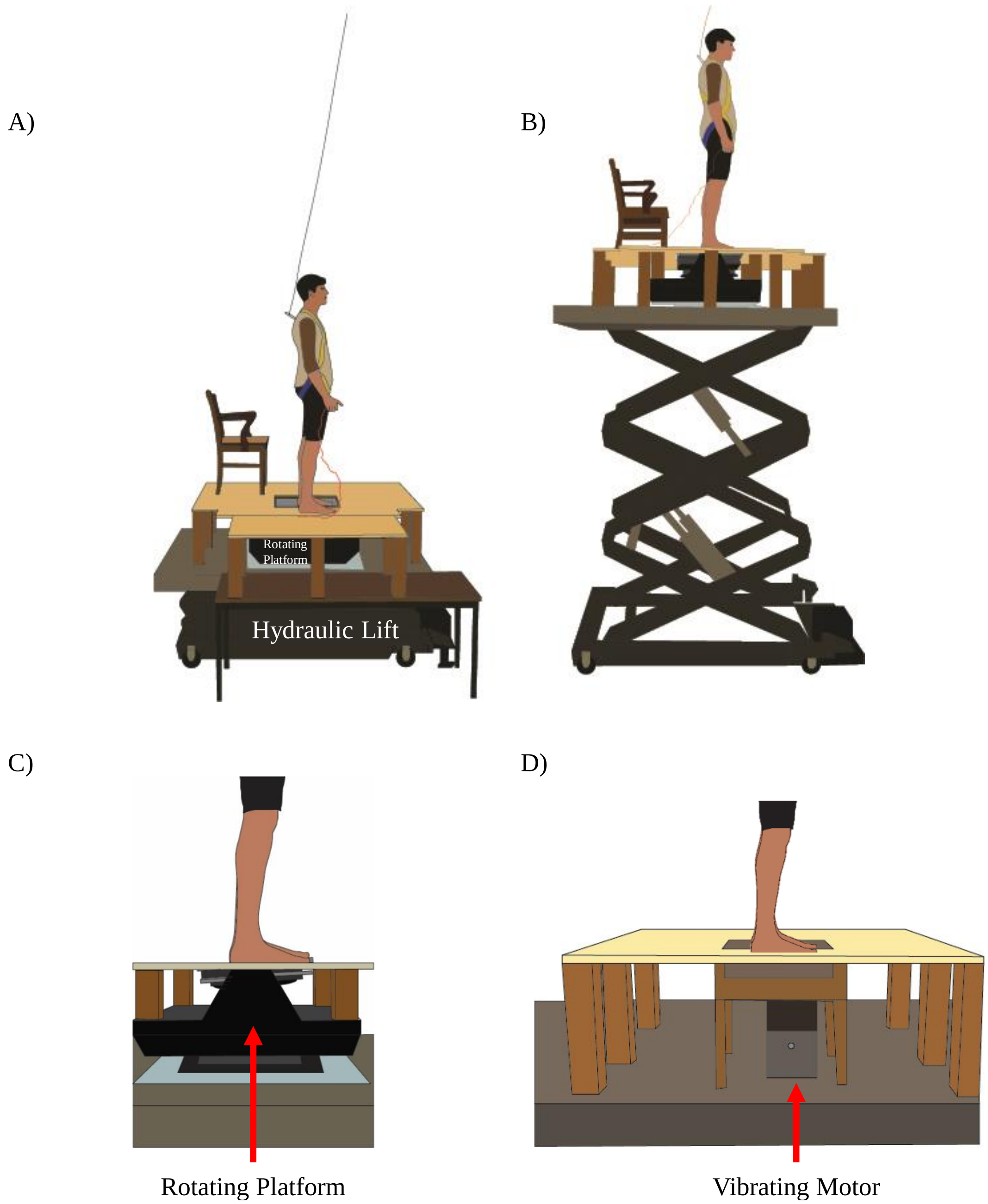

Figure 5-2 Experimental setup for Study 4

Illustration of experimental setup for A) LOW height and B) HIGH height conditions. Participants stood on C) a force plate on top of a rotating platform (Experiment 1) or D) force platform with a vibrating probe protruding through the support surface (Experiment 2).

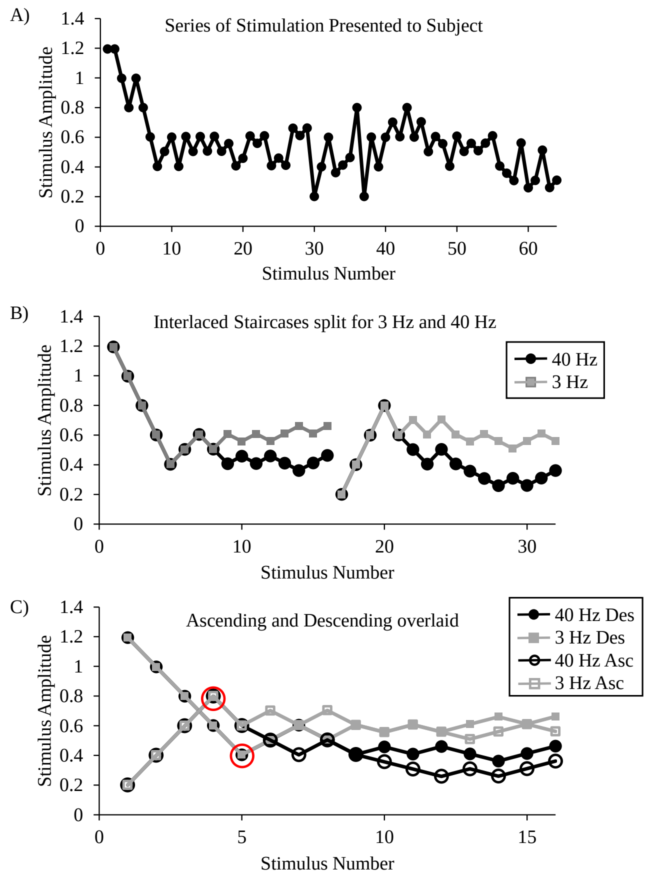

Figure 5-3 Results of experimental session

Representative results of an experimental session for Experiment 2 (similar method used for Experiment 1). A) Series of stimuli as presented to the participant. B) The same series of stimuli split based on the ascending and descending staircases for each stimulus type (frequency for Experiment 2 and rotation direction for Experiment 1). Grey squares represent stimulus amplitude for 3 Hz vibrations, while black circles represent stimulus amplitude for 40 Hz vibrations. C) The same series of data displayed by overlaying ascending (open faced markers) and descending (filled markers) staircase-directions for 40 Hz (Black) and 3 Hz (Grey) vibrations. Red circles illustrate the first turning point and the perceptual hysteresis observed in Experiment 2.

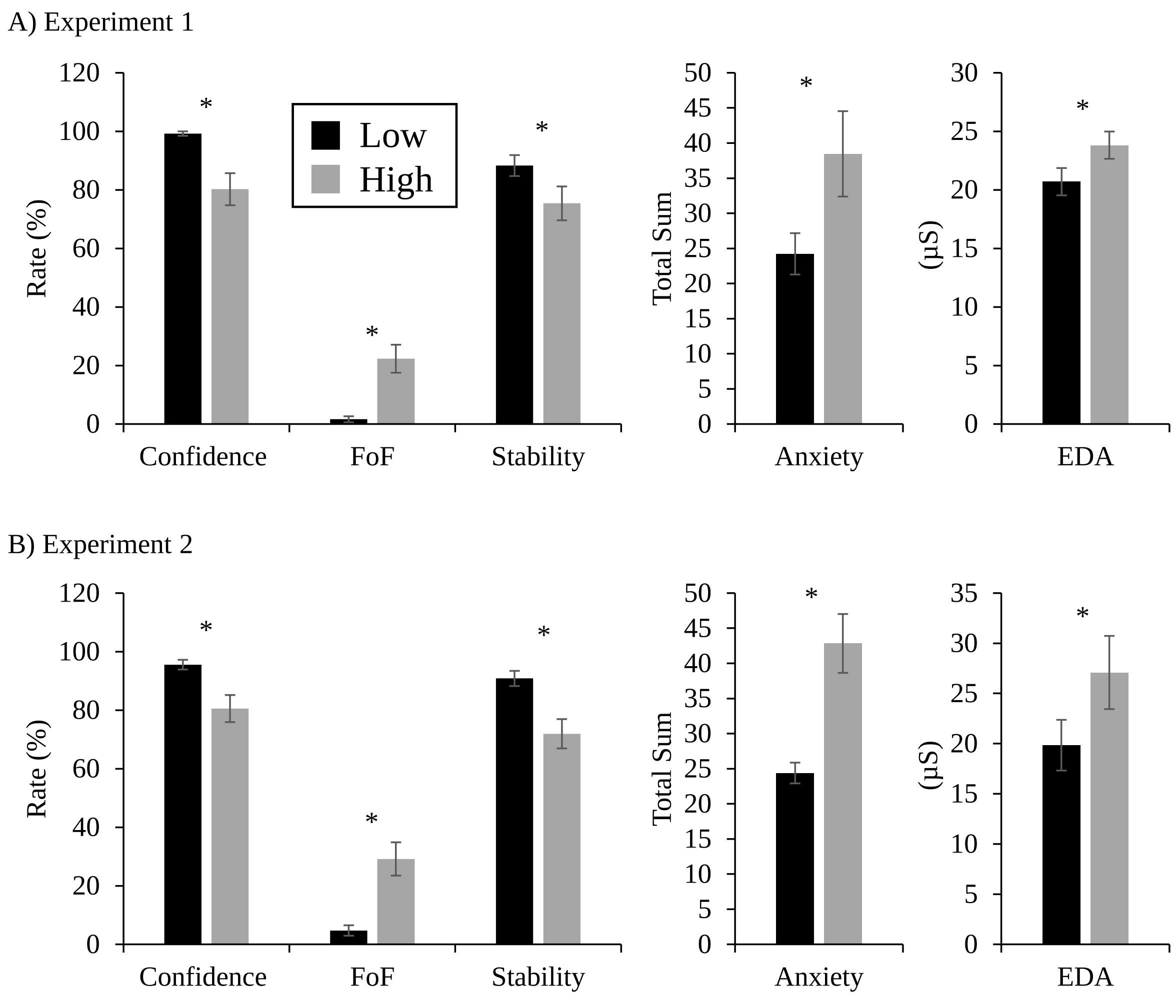

Figure 5-4 Psychological and physiological measures

(A) Experiment 1 and (B) Experiment 2 group mean (standard error) psychological (anxiety, fear, balance confidence, and stability) and physiological (electrodermal activity, EDA) data for LOW (black) and HIGH (grey) conditions. * indicates a significant difference ($p < 0.05$).

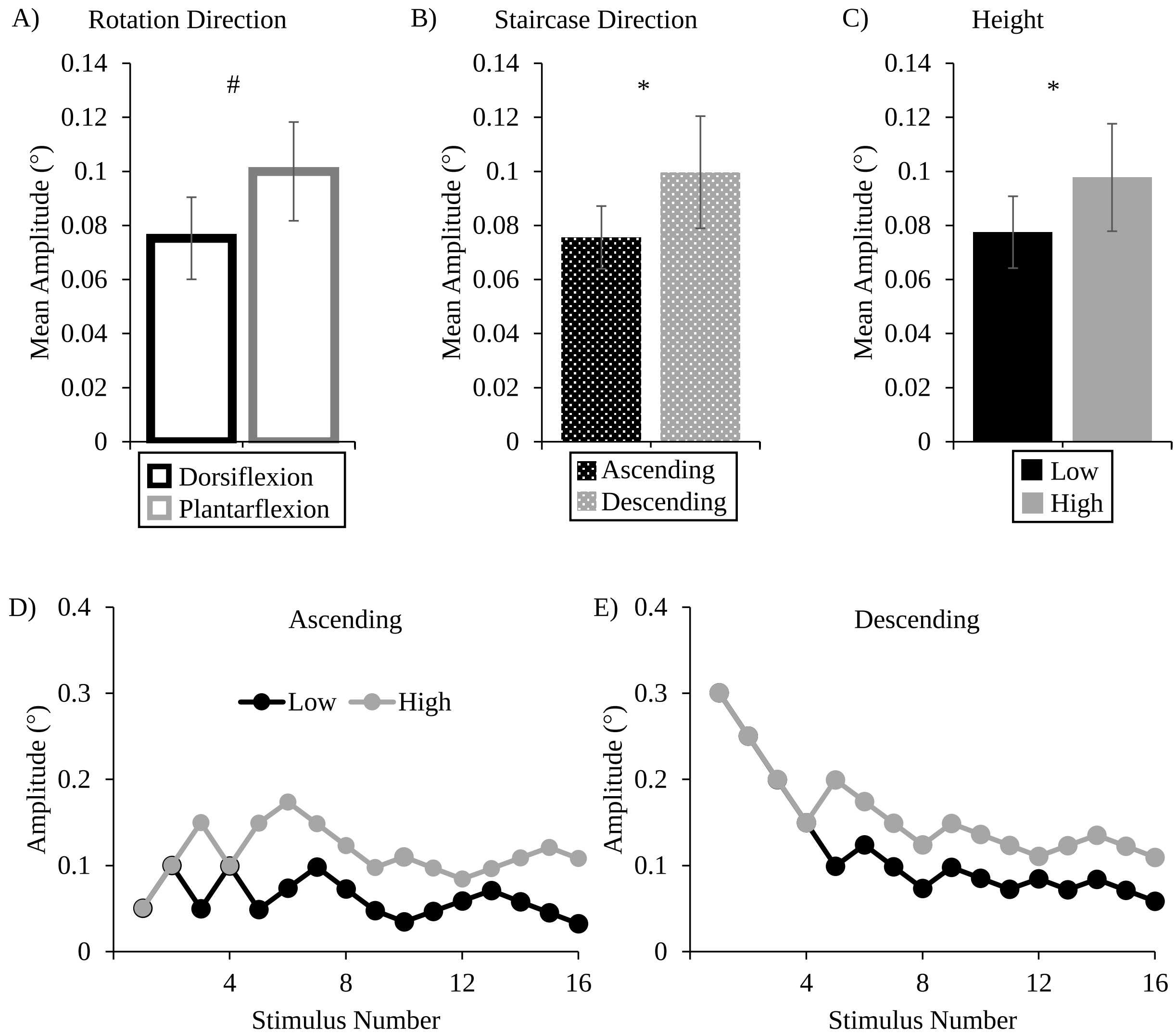

Figure 5-5 Group and representative data for main effects on ankle rotation thresholds

Group mean (standard error) from Experiment 1 for (A) dorsi-flexion (black open bar) and plantar-flexion (grey open bar) stimuli, (B) ascending (black checker) and descending (grey checker) staircases, and (C) LOW (black filled) and HIGH (grey filled) conditions. Representative participant data for (D) ascending staircase and (E) descending staircase for LOW (black) and HIGH (grey) conditions. * indicates a significant difference ($p < 0.05$); # indicates trend towards a significant difference ($0.05 < p < 0.1$).

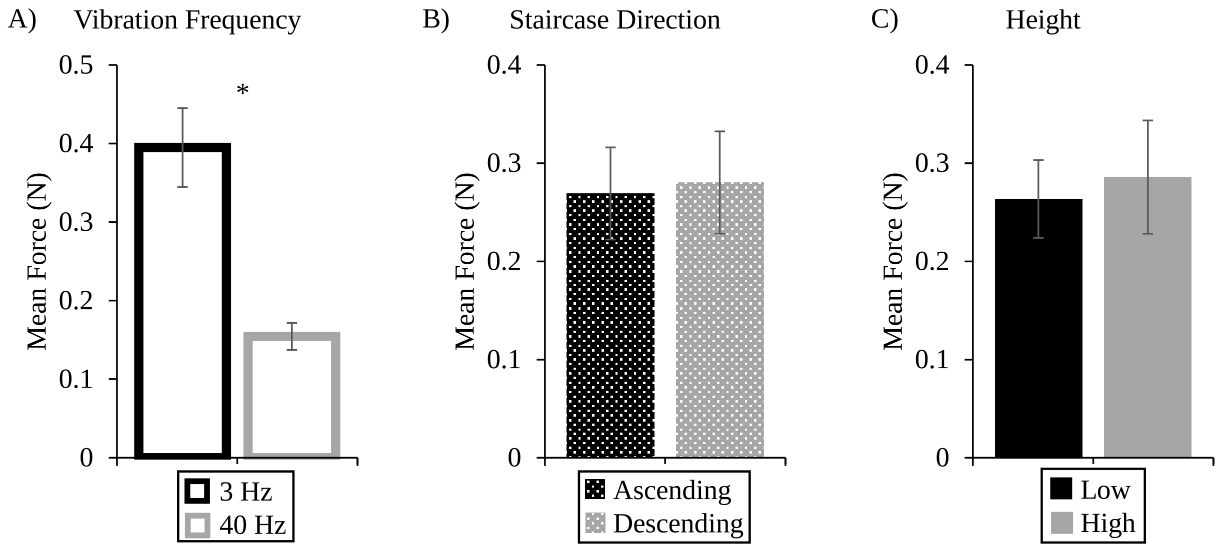

Figure 5-6 Group data for main effects on foot-sole vibration thresholds

Group mean (standard error) from Experiment 2 for (A) 3 Hz (black open bar) and 40 Hz (grey open bar) stimuli, (B) ascending (black checker) and descending (grey checker) staircases, and (C) LOW (black filled) and HIGH (grey filled) conditions. * indicates a significant different ($p < 0.05$).

Chapter 6: Conclusions

6.1 Overall background and aim

A fear of falling can affect balance performance and lead to an increased risk of falls and fall-related injuries (Freidman et al., 2002). Fearful elderly individuals have increased postural sway, decreased functional reach, and increased dynamic balance responses compared to their non-fearful counterparts (Maki et al., 1991; Li et al., 2003; Okada et al., 2001). Environmental constraints elicited through elevated support surfaces (height-induced postural threat) have been used to understand the relationship between balance-related threat, psychological processes and balance performance (Brown & Frank, 1997; Carpenter et al., 2001; Adkin et al., 2008; Davis et al., 2009; Sibley et al., 2010; Horslen et al., 2013; Naranjo et al., 2015; Cleworth et al., 2012; Zaback et al., 2016). Young healthy adults standing at the edge of an elevated support surface adopt a stiffening strategy during quiet stance, with reduced amplitude and increased frequency of postural sway (Carpenter et al., 2001) accompanied by increased co-contraction of the lower leg muscles (Cleworth et al., 2016; Zaback et al., 2017). During dynamic balance, postural reactions increase in amplitude (Carpenter et al., 2004; Cleworth et al., 2016), anticipatory postural responses are reduced (Adkin et al., 2002; Zaback et al., 2015), and there is a decreased range of voluntary leaning towards the edge (Hauck et al., 2008). The mechanism underlying behavioural changes during a height-induced postural threat has been proposed to involve changes in sensory function and/or cognitive processes (Adkin et al., 2008; Sibley et al., 2010; Davis et al., 2011; Horslen et al., 2013; 2014; Zaback et al., 2015; 2016; Naranjo et al., 2015; 2016). A change in perceived motion or position of the body that relies on both sensory and cortical processes may mediate the changes in balance behaviour during height-induced postural threat.

Sensory afferents relay information to the CNS and higher cortical areas for sensory processing during balance tasks (Adkin et al., 2006). Altering sensory feedback or processing from a number of sensory systems has a direct influence on behaviour during a balance task (Kavounoudias et al., 1998; Roll et al., 2002; Thompson et al., 2007; Fitzpatrick & Day, 2004). Direct usage of primary signals from the peripheral receptors is unlikely in postural control (Gurfinkel et al., 1988), while interpreting the sensory signals relayed from the periphery to the CNS is a vital component of postural control (Mergner & Rosemeier, 1998). Interpreting primary afferent signals requires detailed knowledge of the current postural task (Gurfinkel et al., 1988), is used to formulate appropriate direction-specific responses (Oude Nijhuis et al., 2009; MacPherson & Horak, 2012; Puntkattalee et al., 2016), and aids in orienting body segments to the surrounding environment and gravity (Horak, 2006). Sensory signals are processed and integrated into a complex system containing information about the position of body segments relative to one another and environmental impacts (Gurfinkel et al., 1988), and used to derive perceptions of the physical events that affect our bodies in the external world (Mergner & Rosemeier, 1998). In body orientation studies, if the internal representation of verticality is misaligned from true vertical, a leaning or tilting action can persist, resulting in postural instability (Horak, 2006). For example, vibrating the Achilles tendon during quiet stance evokes perceptions of muscle lengthening and causes a lean opposite to the direction of the perceived lengthened muscle (Thompson et al., 2007). Furthermore, during perceptions of postural instability, there may require a higher cortical level of postural control (Solopova et al., 2003), as demonstrated when a link between cortical gamma activity and postural instability was observed (Slobounov et al., 2005). Therefore, the purpose of this thesis was to understand how threat, the concomitant changes in emotional state, sensory function, and cognitive processes influence the perception of balance-relevant sensorimotor-related information during static and dynamic postural tasks. Experimental procedures used novel applications of established psychophysical techniques in a series of four studies to examine how postural threat alters balance-related movement perceptions.

6.2 Summary of results

6.2.1 Emotional state during postural threat

Throughout this thesis, converging evidence from psychological measures of fear, anxiety, and confidence, and physiological measures of arousal (EDA) validate the effectiveness of height-related threat manipulation. Standing at the edge of an elevated support surface significantly modulates the aversive emotional responses independent of the balance task or postural orientation to the height-related threat. Replicating previous findings, height significantly increased fear, anxiety, and physiological arousal, while decreasing balance confidence (Adkin et al., 2002; Carpenter et al., 2006; Cleworth et al., 2012; Davis et al., 2009; Hauck et al., 2008; Huffman et al., 2009).

6.2.2 Perception of whole-body movement during postural threat

The aim of the first three studies was to investigate the effect of height-induced postural threat on conscious perception of whole-body movements across three different balance tasks. The purpose of Study 1 (Chapter 2) was to examine how postural threat can influence conscious perceptions of postural sway during a quiet standing task. Analyses compared perceived and actual sway movement amplitudes during a feet-in-place quiet standing task between a LOW and HIGH height condition. Post-hoc self-reported estimates of perceived movement amplitude and manual tracking of body position using a hand-held potentiometer during continuous AP sway measured sway perception. The amplitude of COP and COM displacements were used to quantify actual movement. As hypothesized, height-induced threat decreased the amplitude, and increased the frequency, of COP (Carpenter et al., 2001; Cleworth et al., 2012; Zaback et al., 2015) and estimated COM (Carpenter et al., 2001) displacements, which was consistent with previous reports. However, height-induced postural threat had no effect on perceived movement amplitude despite a significant reduction in COP and COM movement amplitude. The results of this study indicate an increase in perceptual gain with height-induced postural threat.

While postural threat influences perceptions of movement during a quiet standing task, the question remained whether this relationship would exist in larger amplitude, more voluntary tasks. Therefore, the purpose of Study 2 (Chapter 3) was to assess the postural threat effects on conscious perceptions of body position during a voluntary leaning task. Using the psychometric technique of magnitude estimation, analyses compared verbal reports of body position (relative to a maximum lean position) to actual body positions during 10 different position-based target amplitudes in LOW and HIGH height conditions. Perceived body position increased and followed a power-law relationship as actual body position increased linearly independent of height condition. This pattern of change is consistent with other psychophysical experiments that have demonstrated a power-law relationship when measuring responses as a function of stimulus strength (Bromm & Treede, 1980). Furthermore, results showed amplified perceptions of lean position when standing/leaning in the HIGH compared to LOW height condition. This height effect appeared to be greater as target amplitude increased, but failed to reach statistical significance. Therefore, during large amplitude voluntary balance tasks, the gain in perceived movement in relation to actual movement increased with height-induced postural threat, similar to Study 1.

Perceived movement during quiet stance included small amplitude sway, while perceptions of voluntary movement during leaning involved larger amplitudes of transient movement. The purpose of Study 3 (Chapter 4) was to examine how postural threat influences larger whole-body sway and conscious perception of these movements during continuous pseudo-random support surface rotations. Analyses compared conscious perceptions of trunk sway to actual trunk sway at LOW and HIGH height conditions. Actual body movement amplitude during platform oscillations was unaffected by height, consistent with previous reports examining the effect of threat (fear of falling or height) on dynamic sway to continuous perturbations (Maki et al., 1991; Young et al., 2012). However, in accordance with Studies 1 and 2, perceived movement was significantly larger when standing in the HIGH compared to LOW condition. Height-induced postural threat increased the overall gain of perceived amplitude (root mean square). Results showed threat-related increase in gain in both low frequency (below 0.2

Hz) and high frequency (between 0.2 and 0.5 Hz) bands. This study provides further support for an increase in the gain of perceived movement relative to actual movement during balance tasks, which may influence balance-related behaviour when there is a threat to standing balance.

The observations across the first three studies of this thesis extended the results of threat-related changes in perception within individual sensory systems (vision, auditory, taste), to more complex multisensory tasks such as whole-body movements during balance tasks. Furthermore, threat-related changes in perception occur across different balance tasks, including quiet and dynamic stance and voluntary movement, which utilize different control mechanisms (for example reactive compared to feed forward strategies). Given that these threat-related changes in perceived movement occur across balance tasks and control strategies, global mechanisms involved in balance control have the potential to explain the increased perceived movement, whether related to sensory processes, cortical processes or both.

6.2.3 Detection thresholds for balance-related movement during postural threat

When studying conscious perception of balance-related movements, the limits of sensory systems need to be investigated (Krewer et al., 2016). The aim of the final study was to investigate how changes in somatosensory perceptual thresholds change with increased threat, in an attempt to understand a potential mechanism that could explain observed threat-related changes in gain of perceived movement during stance. There is no one universally accepted method capable of assessing all aspects of movement sensations (Hillier et al., 2015; Krewer et al., 2016). As such, there are two aspects to consider, detection and discrimination (Krewer et al., 2016; Han et al., 2016). Assessing motion detection involves testing at-threshold stimuli, while assessing movement discrimination involves testing above-threshold stimuli (Hillier et al., 2015; Krewer et al., 2016; Han et al., 2016). Studies 1 through 3 assessed suprathreshold stimuli, where perceptions of whole-body movements were examined by discriminating between continuous (Study 1 & 3) or transient (Study 2) movements. While the perceptions of movement within these tasks involved detecting the full range of perceptible movements, it was extremely difficult to process and analyze the stimulus intensity (movement) related to perceptual thresholds. Therefore, there was still a need to address the effect of height-related threat on motion detection thresholds.

Movement detection thresholds have the potential to explain mechanisms responsible for the increased gain in perceived movements observed. Lowering the detectable threshold or amplifying the response proportional to the stimulus intensity can increase the amplitude of a perceived movement (Horak & Diener, 1994; Lim et al., 2014). Examining the detection thresholds within a balance-relevant sensory system can potentially discriminate the underlying mechanisms involved in perceptual gain changes observed with height-induced postural threat.

Experimental tasks targeted somatosensory inputs because they are thought to be heavily relied upon during whole-body sway (Thelen et al., 1998) and have the lowest threshold for movement detection (Fitzpatrick & McCloskey, 1994). These tasks specifically targeted the ankle because single segment movements isolate the somatosensory system from other visual and vestibular information. Furthermore, ankle movement is highly correlated with COM movement during anteroposterior sway (Gage et al., 2004). Therefore, the specific objective of

Study 4 (Chapter 5) was to investigate the effect of height-induced postural threat on lower leg somatosensory acuity using an ankle kinaesthetic task. Study 4 used two experiments in an attempt to understand the somatosensory receptors involved in the height-related perceptual gain changes. Experiment 1 used an adaptive staircase method to assess discriminatory perceptual thresholds for ankle dorsi- and plantar-flexions during quiet stance. Experiment 2 used the same staircase method to assess discriminatory perceptual thresholds for 3 Hz (activating slow adapting cutaneous mechanoreceptors) and 40 Hz (slow and fast adapting cutaneous mechanoreceptors) foot sole vibrations during quiet stance. Contrary to the hypothesized results, height-related postural threat increased the perceptual threshold for ankle rotations, and had no effect on perceptual thresholds for foot sole vibrations. These results suggest threat decreases the ability to detect an externally produced movement of the ankle without changing the ability to detect vibrations on the foot sole. In addition, these results indicate a reduced sensory threshold does not mediate changes in perceptual gain from height-induced threat.

Height-induced postural threat had different effects on thresholds for foot sole vibrations and ankle rotations. During a balance task, it is likely more difficult to perceive a passive ankle rotation than that of a foot sole vibration due to judgment uncertainty (Hock & Schöner, 2010), false detection rates (Chaudhuri, 2011), frequency content (Gage et al., 2004) and similarities or differences between postural sway and the psychophysical stimulus. Collectively, these effects have the potential to affect perceptions differently during threatening situations.

The successful detection of ankle rotations is reliant upon proprioceptive information from muscle spindles, cutaneous mechanoreceptors, joint receptors, and possibly GTOs

(Refshauge & Fitzpatrick, 1995). Innervation of the muscle spindle at the contractile polar ends by efferent fibers can modulate sensitivity to muscle stretch (Prochazka et al., 1985). Furthermore, movement-related gating of sensory pathways occurs during movement, while task-relevant attention alleviates this gating effect (Staines et al., 1997). During threatening situations, muscle spindle activity has been thought to be modulated in cats (Prochazka et al., 1985) and humans (Horslen et al., 2013; Davis et al., 2011), while spindle-related sensory pathways are gated (Davis et al., 2011). Detecting small amplitude foot sole vibrations depends exclusively on the information from cutaneous receptors. This receptor class has a limited, if not complete lack of, ability to change sensitivity to vibration (Hudson et al., 2015; Elam et al., 2004). However, there is potential for modulation of sensory pathways related to cutaneous stimuli. Early components of cortically evoked potentials increase in amplitude during cutaneous-relevant directed attention (Staines et al., 1997) and later cortical potentials increase during height-related threat (Horslen, 2016). The complex influence of postural threat on receptor and sensory pathways related to ankle movement compared to isolated effects on sensory pathways alone for cutaneous-related information may mediate these differences in threat-related changes.

A change in sensory noise has the potential to explain the contradictory effects of height-induced threat on perceived movement gain and ankle-based somatosensory acuity. The ability to detect whole-body movements, ankle rotations or foot sole vibrations depends on the size of the sensory signal compared to the background level of noise within the respective sensory modality and CNS (Green & Swets, 1988). Subthreshold noise facilitates the perception of weak stimuli through stochastic resonance (Collins et al., 1997; Wells et al., 2005); however, background noise levels at or above threshold can significantly deteriorate perceptual acuity in tactile (Collins et al., 1997; Wells et al., 2005) and visual systems (Sasaki et al., 2008). The changes in sensory processes (Horslen et al., 2013; Horslen, 2016), emotion (arousal effects on neural noise, see Allen et al., 2016) and behaviour (Carpenter et al., 2001) associated with standing under threatening conditions likely increase noise within sensory processing pathways, increasing the amplitude needed for detectable ankle rotations, while influencing the perceptions of suprathreshold movements. Noise-related effects on sensory perception can amplify suprathreshold stimuli while decreasing sensitivity to near threshold stimuli. For example, suprathreshold noise enhances the ability to discriminate suprathreshold auditory stimuli in individuals using cochlear implants (Behnam & Zeng, 2003). Sensory noise-related increased response gain to suprathreshold movements during postural threat conditions potentially explains the collective results of this thesis.

Seemingly conflicting findings between Studies 1-3 and Study 4 may be explained by differences in the effects of postural threat on perceiving single segment rotations or whole-body movements. In an attempt to rule out this possibility, a pilot study was designed to assess the ability to track ankle rotations. Five participants stood on a hydraulic lift with the left foot placed on a rotating platform and the right foot placed on a stable stage. The methodology from the continuous tracking paradigm (Study 3) was used in conjunction with independent ankle movement (Study 4 Experiment 1) to assess the perceived movements of the ankle during continuous pseudorandom rotations. Participants were strapped to a waist-high mount that restricted movement of the upper body, while the left ankle passively rotated for seven minutes. During these rotations, participants were required to track the ankle dorsi- and plantar-flexion movements using a hand held rotary encoder. Ankle rotations had a maximum range of ± 1° and contained six frequencies below 0.5 Hz (see Study 3 Figure 4-2 for signal). Participants performed the ankle-tracking task in a LOW (1.2 m away from edge) and HIGH (3.2 m at edge) height condition. At height, perceived amplitudes of ankle angle rotations were larger, as evidenced by an increase in QRMS (amplitude of perceived movement divided by amplitude of ankle movement) and an increase in the gain of low and high frequency movements as identified by the spectral analysis (Figure 6-1). These results provide preliminary evidence to suggest postural threat increases the gain of perceived suprathreshold movements without a concomitant decrease in the detectable threshold for the same type of movement (Study 4 Experiment 1).

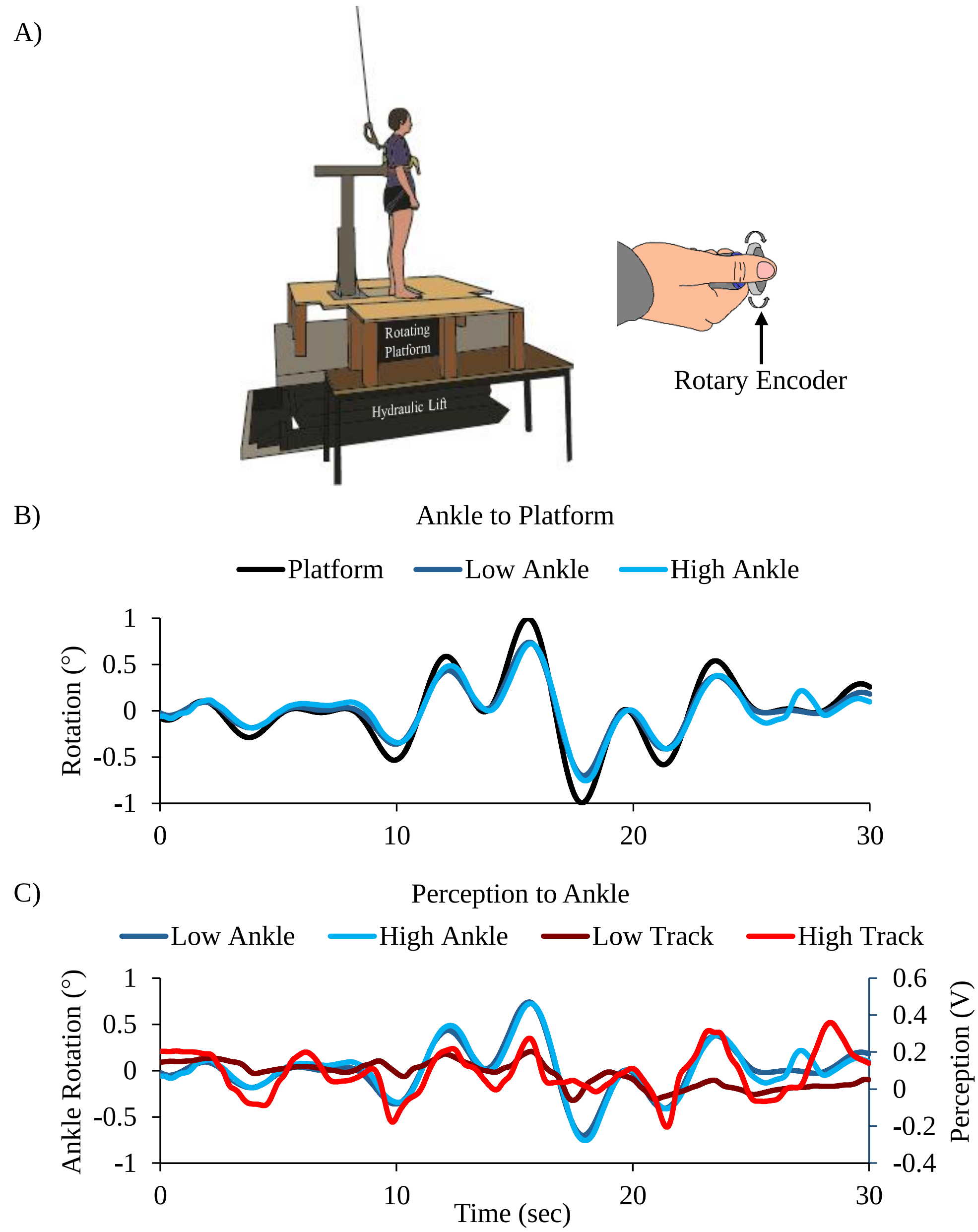

Figure 6-1 Experimental setup and representative data for pilot study

(A) Illustration of experimental setup (LOW condition only) with a participant standing on a rotating platform (left) while holding a rotary encoder (right). Representative participant traces comparing (B) platform (black) and ankle rotations during for LOW (dark blue) and HIGH (light blue) conditions, and (C) the same ankle rotations to tracked movement in the LOW (dark red) and HIGH (light red) conditions.

6.3 Can changes in attention explain results?

Behavioural changes with postural threat are associated with altered cognitive processes and attentional focus (Hauck et al., 2008; Zaback et al., 2015; 2016; Johnson et al., 2017). Throughout this thesis, the impact of these attention changes has been considered a possible mechanism to explain increased gain in perceived movements, as attention can affect the ability to detect stimuli related to vision (Posner, 1980; Verghese, 2001), audition (Jones and Yee, 1993; Haykin & Chen, 2005), touch (Craig & Evans, 1995) and movement (Yasuda et al., 2014). An internal focus of attention may cause stiffening strategies in those with a fear of falling (Young & Williams, 2015). With a threat to posture, either through an impending perturbation or elevated support surface height, there are broad changes in attention, such that individuals are more focused on their movements, threat-related stimuli, and self-regulatory strategies (Huffman et al., 2009; Zaback et al., 2015; 2016; Johnson et al., 2017). An increase in attention towards threat-related stimuli could compromise the capacity to perceive movement (Young & Williams, 2015). However, emotional state can increase cognitive workload to allow for compensatory strategies, such as focusing on movement processes, to alleviate the performance decreases from attentional bias towards a threatening stimulus (Eysenck et al., 2007; Johnson et al., 2017; Zaback et al., 2016). This increase in attention towards movement processes and other factors could facilitate the increased perceptual gain by biasing attention toward the psychophysical task (whole-body movement). While possible, it is unknown whether attentional focus shifts toward whole-body/upper trunk (Study 3) movement or other forms of (distractor) movement (weight distribution between feet or muscle contractions, Zaback et al., 2016; Johnson et al., 2017). Without a direct measurement of attentional changes for the studies in this thesis, it is difficult to disentangle the relative contributions from a change in the direction of attention or shift in attentional focus. However, attentional bias effects across height conditions are unlikely to mediate the threat-related changes in perceived movement amplitude. The instruction for an internal focus of attention on movement-related amplitude and direction given to the participants during psychophysical balance tasks did not change across height conditions. Furthermore, the null height effects observed for coherence between perceived and actual movement (Study 3) and vibratory perceptual thresholds (Study 4) provide supporting evidence against a distinct general effect of threat-related changes in attention on perceptions related to balance. Future work examining the effects of threat on perceived movement or thresholds during balance tasks should include reliable measures of attentional focus to understand possible interactions between emotion and threat, attention, and the relationship between perceived and actual movement.

6.4 Implications of threat-effects on perceived movement

Fall preventative strategies may not rely solely on automated responses, but might also be dependent on central command mechanisms and higher cortical structures to indicate postural instability (Slobounov et al., 2005). Traditionally considered a sub-consciously, automatic and/or reflex controlled task (Deliagina et al., 2006; Massion, 1998), postural control has been thought to involve cognitive “top-down” processes, including attentional requirements (Woollacott & Shumway-Cook, 2002), interpretations of sensory input (Gurfinkel et al., 1988), and conscious monitoring of body segments relative to gravity, support surfaces, and visual surroundings (Horak, 2006). For example, central processing of proprioceptive information in parietal, frontal and insular cortical regions may be relevant to balance control (Goble et al., 2011). The level of “top-down” involvement depends on the postural task and the integrity of the postural control system, as influenced by age, physiological decline, and psychological processes (Woollacott & Shumway-Cook, 2002). Interpreting and utilizing orientation-related information requires attention and cognitive effort (Yardley et al., 1999). Body scheme, an internal body representation or model, acts as a central organizational component that is involved in the control of postural activity (Gurfinkel et al., 1988).

Perceptual awareness of body motion plays an important role in balance control. This is especially true for sensorimotor-impaired individuals who rely more heavily on attentional resources to maintain balance, such as older adults with an increased fall risk (Shumway-Cook et al., 1997; Stelmach et al,. 1990) and people with Parkinson’s disease (PD), stroke, diabetes, or multiple sclerosis (Puntkattalee et al., 2016). While directing attention towards balance can alter automatic processes originally carried out with little or no conscious control and influence balance performance (McNevin & Wulf, 2002; Study 1), threat-related changes in conscious perceptions of movement can exaggerate consequences from cognitive control strategies employed by these populations.

The results of this thesis indicate postural threat can modulate those conscious perceptions of balance-related movement, changing the body scheme and potentially leading to further instability. Specifically, detecting and perceiving moments of sway during standing tasks is critical for stability for two main reasons. First, balance responses during disturbances to equilibrium rely on the interpretation of sensory signals. Second, stability relies on the perceived position of the COG’s line of action relative to the limits of the BOS. Factors that influence these perceptions can have direct impacts on balance ability. For example, amplifying the position of the COG's line of action can reduce the perceived buffer between it and the BOS limit, causing the perception of debilitating balance disturbances during minor sway deviations.

Understanding how perception contributes to balance-related movement is important to mitigate balance deficits (Puntkattalee et al., 2016) as a change in psychological, not only physiological, systems can result in decreased balance performance (Horak, 2006). The results of this thesis demonstrate incongruent changes in perceived and actual movement when standing in a threatening condition. With threat-related aversive emotional state, misjudgments may be unwarranted and amplified, further increasing the risk of a fall. Misjudgments in perceived and actual ability related to a postural task can have debilitating effects on balance performance (Delbaere et al., 2009; Butler et al., 2015; Lamarche et al., 2013; Kluft et al., 2017). These erroneous estimations can occur from a change in physiological ability without changes in perceived ability or a change in psychological factors without changes in physiological ability (Delbaere et al., 2009). For example, without a change in physiological ability, over confidence can lead to risky behaviours beyond physical abilities (Butler et al., 2015), while decreased efficacy and confidence can lead to deteriorated balance performance (Seeman et al., 1999) and activity avoidance, as in those with a fear of falling and increased risk for falls (Delbaere et al., 2004; Schepens et al., 2012). Quantifying discrepancies between actual and perceived ability can be a useful tool in understanding the psychological determinants of falls risk (Delbaere et al., 2010). Discrepancies between perceived and actual ability can be targeted using intervention programs to improve appraisals of balance performance, aiding rehabilitation of balance deficits, and assisting in maintaining a healthy balance control system (Ellmers et al., 2018).

The results of this thesis showed discrepancies between objective and subjective measures of stability. When standing in threatening conditions, perceived stability decreases when there are no changes to balance performance (Studies 2 & 3) or a decrease in postural sway (Study 1; Carpenter et al., 2001). Perceptual gain (the relationship between perceived and actual movement) changed in accordance with perceived stability across studies in this thesis. As stability is a subjectively reported characteristic of balance control, the relationship between perceived and actual stability may supplement judgements of stability across postural tasks compared to using objective behavioural measures alone.

Clinical settings can use the techniques developed throughout this thesis to better assess stability. Objective measures may not always allude to balance deficits, and current subjective measures rely on self-report measures, generally independent of the task used to quantify balance. Objective assessments of balance performance are sometimes unable to distinguish normal from pathological disease despite a perceived instability and increased fall risk (Horak et al., 1992; Schieppati et al., 1993; 1994; 1999). In addition, dissociations between subjective stability and objective balance performance occur in patient populations without any signs of pathology from otoneurological and balance tests (Huppert et al., 2013). However, subjective reports of stability (or performance) using questionnaires and scales have been advantageous in furthering our understanding of some of the psychological mechanisms involved in balance. Falls efficacy (Wulf et al., 2001; Huffman et al., 2009), balance confidence (Powell & Myers, 1995; Geh et al., 2011), and perceived stability (Schieppati et al., 1999; Hauck et al., 2008; Cleworth et al., 2012) have all been shown to modulate balance performance. However, there is still a need to support subjective perceptions of balance performance with perceptions related to movement during balance examinations to remove the possibility of memory or predictive judgment bias that may influence subjective reports (Stefanucci et al., 2009).

Clinicians and researchers generally assume balance deficits to be a consequence of a physiological (biomechanical, musculoskeletal, pathophysiological, etc.) decline. However, worsened balance ability exists during anxiety or arousal provoking situations, such as in the presence of a clinical evaluator (Geh et al., 2011). When assessing balance, fears toward a negative evaluation or social persuasion can trigger the threat-related changes in perceived movement observed in this thesis, influencing balance performance. Clinicians and researchers need to use caution when interpreting balance performance during anxiety-provoking conditions when trying to identify underlying causes of balance deficits (Maki et al., 1991).

6.5 Future research directions

Height-induced postural threat does not appear to modulate balance-relevant somatosensory thresholds in a way that can facilitate increased perceptual gain. Alternatively, height-induced threat has the potential to modulate perceptual thresholds within other sensory systems not specifically tested in this thesis (e.g. vestibular or visual). Increased vestibular gain during threatening situations (Naranjo et al., 2015; 2016; Lim et al., 2017, Horslen et al., 2014) can increase sensitivity of vestibular-related perceptual thresholds (see Peters et al., 2017 for technique used to probe vestibular perceptions) for movements during balance tasks. In addition, possible contributors to the increase in perceptual gain from sensory systems specifically tested in this thesis need further investigation. Contradictory results from two different studies have illustrated a difference in the effect of postural orientation on thresholds to cutaneous vibratory stimuli, where vibrations from a single small diameter probe showed no change (Germano et al., 2016), while vibrations from a number of probes with a larger collective diameter did show changes with postural orientation (Mildren et al., 2016). Since plantar cutaneous afferents as a population could potentially code for vertical and shear forces from the ground onto the foot sole during standing (Kennedy & Inglis, 2002), there is a need to assess height-induced threat on cutaneous perception using broader stimuli across different regions of the foot. Finally, although previous work has not examined vision-related processes under height-induced postural threat, anxiety can increase visual dependency (Redfern et al., 2007). Individuals with anxiety disorders sway more in response to a moving visual scene (Redfern et al., 2007). Future work should examine the sensitivity and perception of movement from visual stimuli during postural threat conditions to understand the visual contributions to increased perceptual gain.

The results of Study 4 were proposed to be unrelated to height-related changes in the acquisition and processing of sensory information (Horslen et al., 2013; Adkin et al., 2008; Davis et al., 2011), given that thresholds either did not change or were elevated with threat. An overlap in sensory information between the psychophysical task and postural task (Experiment 1) likely interacted with height-related behavioural changes to increase neural noise and decrease performance (Wells et al., 2005; Chaudhuri, 2011). Therefore, there is still a need to examine the influence of postural threat on perceptual thresholds during balance-relevant tasks without overlapping dual tasks, specifically for multi-segmental movements. A task that resembles feet in place standing can be used to estimate perceptual thresholds within individual sensory systems by isolating stimulations of vestibular, visual, and somatosensory sensory systems (Fitzpatrick & McCloskey, 1994). Removing the need to control balance while assessing thresholds can further assess the effect of height-induced postural threat on perceptual thresholds without succumbing to confounding dual task effects.

There is evidence for multisensory modulation with postural threat (Naranjo et al., 2015; 2016; 2017; Lim et al., 2017; Horslen et al., 2013; 2014; Davis et al., 2011). Cortical changes observed under threatening conditions (Adkin et al., 2008; Sibley et al., 2010; Horslen, 2016) may arise from this modulation in sensory acquisition. While the CNS has the ability to selectively scale sensory gain central to the receptor to enhance information required for the current task (Staines et al., 1997), little is known about the neural correlates underlying threat influences on perception of balance-relevant sensory information during postural tasks. The process involved in perceiving somatosensory stimuli include activation of cortical regions, including primary and secondary somatosensory cortices (Inui et al., 2004; Libet et al., 1967; Preissl et al., 2001; Schubert et al., 2006). In addition, cortical alpha and gamma frequency-band oscillations within somatosensory, frontal, and parietal regions play a role in the neural mechanisms underlying perception (Palva et al., 2005; Toledo et al., 2016). Examining the amplitude and synchronicity between and within sensory and other cortical regions involved in the perception of a balance-related sensory information during postural tasks can assist in our understanding of how and where perceptual modulation is occurring.

While the experimental designs in this study have started to examine the mechanisms that may explain these amplified perceptions, there remain a number of additional questions regarding the relationship between perceived and actual movement during postural threat. Future work should examine the mechanisms underlying threat-related changes in perceived and actual performance discrepancies within populations with an increase in fear-related falls risk.

6.6 Conclusions

In conclusion, the collective results of this thesis have demonstrated the effects of height-induced postural threat on perceived movements during a balance task. When young healthy adults stand at the edge of an elevated support surface, aversive psychological states emerge as evidenced by increases in anxiety, fear and physiological arousal, and decreases in balance confidence and perceived stability. In these states, amplified perceived movement, expressed using tracking tasks or discrete verbal reports, occurs during quiet standing, voluntary leaning, and dynamic externally perturbed stance, independent of whether actual movement decreased or remained constant across conditions. While height-induced postural threat amplifies balance-related movement perceptions, somatosensory-related detectable thresholds remain unchanged or increase, and are unlikely to mediate the gain changes in perceived movement. Dissociations between perceived (psychological) and actual (physiological) ability may be a significant contributor to increased falls risk. In order to fully examine and treat balance deficits, there is a need to integrate psychological determinants of performance into clinical assessments and balance interventions to further understand and subsequently mitigate balance deficits.

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Appendices

Appendix A – Psychological questionnaires

The following questionnaires were used to assess participants' self-reported balance confidence, fear of falling, perceived stability, perceived movement and state anxiety. Perceived movement was only used in Study 1, while the others were used in all studies in this thesis.

Balance Confidence:

Please use the following scale to rate how confident you are that you can maintain your balance and avoid a fall during the balance task:

0……………………………………50……………………………………100

I did not feel confident at all	I felt moderately confident	I felt extremely confident

Fear of Falling:

Using the following scale, please rate how fearful of falling you felt when performing the balance task:

0……………………………………50……………………………………100

I did not feel fearful at all	I felt moderately fearful	I felt extremely fearful

Perceived Stability:

Using the following scale, please rate how stable you felt when performing the balance task:

0……………………………………50……………………………………100

I did not feel stable at all	I felt moderately stable	I felt extremely stable

Perceived Movement:

Using the following scale, please rate the amount of sway (or movement) you perceived when performing the balance task:

0……………………………………50……………………………………100

I felt I did not sway at all	I felt I swayed (moved) some	I felt I maximally (move) swayed (moved)

State Anxiety:

Please answer the following questions about how you honestly feel just after standing at this height using the following scale:

1	2	3	4	5	6	7	8	9
I don't feel this at all				I feel this moderately				I feel this extremely

1. I felt nervous when standing at this height
2. I had lapses of concentration when standing at this height
3. I had self doubts when standing at this height
4. I felt myself tense and shaking when standing at this height
5. I was concerned about being unable to concentrate when standing at this height
6. I was concerned about doing the balance task correctly when standing at this height
7. My body was tense when standing at this height
8. I had difficulty focusing on what I had to do when standing at this height
9. I was worried about my personal safety when standing at this height
10. I felt my stomach sinking when standing at this height
11. While trying to balance at this height, I didn't pay attention to the point on the wall all of the time
12. My heart was racing when standing at this height
13. Thoughts of falling interfered with my concentration when standing at this height
14. I was concerned that others would be disappointed with my balance performance at this height
15. I found myself hyperventilating when standing at this height
16. I found myself thinking about things not related to doing the balance task when standing at this height.