The influence of emotional factors on the control of balance studied using threat and repeated threat exposure manipulations

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Abstract

Postural threat manipulations elicit changes in psychological and autonomic state and standing balance control. However, these changes are often poorly correlated and changes to balance control appear heavily dependent on the task-constraints imposed by the threat. This raises questions as to how fear and related psychological processes impact balance control and what are the neural mechanisms mediating these relationships? The studies of this thesis explored these questions using a repeated threat exposure model. Using this model, psychological and autonomic state could be manipulated within a threatening scenario, thereby decoupling these state-related changes from the threat context.

Studies 1 and 2 investigated how standing balance control changed as individuals were repeatedly exposed to a height-related postural threat. These studies demonstrated clear dissociations between specific changes in standing balance control and individuals' psychological and autonomic response to the threat. Specifically, threat-related increases in high-frequency centre of pressure power and plantar/dorsiflexor coactivation demonstrated clear habituation, while more protective components of the response to threat, such as the posterior lean and reduction in low frequency COP power, were invariant. Study 3 demonstrated that low levels of anxiety and arousal in the absence of any overt threat were sufficient to influence distinct components of standing balance control. However, these changes in behaviour did not mirror what is typically seen with a height-related postural threat. Studies 4 and 5 investigated how descending input from cortical and subcortical networks might contribute to the changes in standing balance control observed in studies 1 and 2. Corticospinal and subcortical drive to the soleus, inferred from estimates corticomuscular and intermuscular coherence, were both facilitated by height-related postural threat. However, only corticospinal drive habituated with repeated threat exposure. Cortical potentials time-locked to discrete postural events were facilitated by height-related postural threat, but did not habituate with repeated threat exposure.

This thesis demonstrates that only a subset of threat-related changes to standing balance control are tightly coupled with the psychological and autonomic state changes induced by the threat, while others appear largely context dependent. This thesis also provides insight into separate cortical mechanisms which may mediate distinct aspects of this behaviour.

Lay summary

When people stand in dangerous situations, they modify the way they maintain balance. However, it is unclear how much these changes to balance depend on the fearfulness or nervousness experienced in that situation. This thesis repeatedly exposed individuals to a dangerous scenario (standing at the edge of an elevated surface) to determine how and why their balance changed as they became less fearful in that scenario. We found that only some changes to balance varied as a function of how fearful or nervous people were, while other changes to balance were adopted regardless of how people felt. We also demonstrated that the cortex becomes more involved in the control of balance in dangerous scenarios. However, only some changes in cortical involvement depended on the extent of fearfulness experienced. This thesis highlights how threatening scenarios can elicit adaptive changes to balance control largely independent of the level of fear experienced.

Preface

In the studies included in this thesis, all data were collected by Martin Zaback (Zaback M) with assistance where outlined below, in the Neural Control of Posture and Movement Lab at the University of British Columbia (Vancouver campus). All methods were approved by the University of British Clinical Research Ethics Board (ID: H06-70316), and all participants provided written informed consent prior to their participation.

Chapter 2 is published in *Scientific Reports* [Zaback, M, Adkin, AL & Carpenter, MG (2019). Adaptations of emotional state and standing balance parameters following repeated exposure to height-induced postural threat. *Sci. Rep.* **9**, 12449]. Zaback M was responsible for the conception, experimental design, data collection and analysis, interpretation of results, and manuscript drafting and revisions. Adkin AL and Carpenter MG assisted with experimental design, interpretation of results, and manuscript revisions.

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Chapter 4 is currently under review for a peer-reviewed journal. Zaback M was responsible for the conception, experimental design, data collection and analysis, interpretation of results, and manuscript drafting and revisions. Reiter E assisted with data analysis. Reiter E, Adkin AL, and Carpenter MG assisted with experimental design, interpretation of results, and manuscript revisions.

Chapter 5 is being prepared for submission to a peer-reviewed journal. Zaback M was responsible for the conception, experimental design, data collection and analysis, interpretation of results, and manuscript drafting and revisions. Adkin AL, Chua, R, Inglis JT, and Carpenter MG assisted with experimental design, interpretation of results, and manuscript revisions.

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95%F – 95% power frequency
A-D – analog to digital
ANOVA – analysis of variance
AP – anterior-posterior
APA – anticipatory postural adjustment
Att. – attention toward
CC – co-contraction
CMC – corticomuscular coherence
COM – centre of mass
COP – centre of pressure
EDA – electrodermal activity
EDR – electrodermal response
EEG – electroencephalography
ERP – event-related potential
EVS – electrical vestibular stimulation
EMG – electromyography
HF – high-frequency
IMC – intermuscular coherence
LF – low-frequency
MEP – motor-evoked potential
MF – medium-frequency
ML – mediolateral
MP – movement processes
MPF – mean power frequency
MPOS – mean position
MSRS – Movement-specific Reinvestment Scale
MVC – maximal voluntary contraction
MVEL – mean velocity
NS-EDR.freq – non-specific electrodermal response frequency
PEP – perturbation-evoked potential
RMS – root mean square
RT – risk-taking
SD – standard deviation
SEP – somatosensory-evoked potential
SOL – soleus
SRS – self-regulatory strategies
STAI – State-Trait Anxiety Inventory
SVS – stochastic vestibular stimulation
TA – tibialis anterior
TI – task-irrelevant information
TMS – transcranial magnetic stimulation
TO – task objectives
TPL – total path length
TRS – threat-related stimuli

VAS – visual analog scale
VEMP – vestibular evoked myogenic potential
η_p^2 – partial eta squared
μS – microsiemens
μV – microvolt

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Chapter 1: Introduction

1.1 Falls and fear of falling

Falls are a leading cause of hospitalization in the elderly, with over 250,000 Canadians over the age of 65 reporting a fall-related injury between 2009 and 2010 (Public Health Agency of Canada, 2014). While multiple age-related physiological changes contribute to this increased risk of falling (Lord et al. 1994), psychological factors, such as a fear of falling, may also contribute (Li et al. 2003; Friedman et al. 2002). Fear of falling often develops after a fall, but it can develop in individuals who have never fallen (Legters, 2002). Individuals who develop a fear of falling are more likely to avoid activities they are otherwise capable of engaging in, triggering a vicious cycle that can ultimately lead to loss of independence (Yardley, 2003). Furthermore, there is growing evidence that a fear of falling may directly influence balance control (Li et al. 2002; Friedman et al. 2003). Older adults with a fear of falling have demonstrated larger amplitude postural sway when standing (Maki et al. 1991), larger balance corrective responses following postural perturbations (Okada et al. 2001), and slower anticipatory postural adjustments during gait initiation (Uemura et al. 2012) compared to non-fearful individuals matched for age and level of physical function. Since fear of falling is associated with an increased risk of falling (Li et al. 2003; Friedman et al. 2002) and is prevalent amongst older adults (Legters, 2002) and individuals with neurological deficits (Adkin et al. 2003; Schlick et al. 2015; Schmid et al. 2015), there has been considerable interest in understanding how fear and related psychological factors influence balance control.

1.2 Postural threat as a means to study how fear of falling influences balance

While cross-sectional studies have shown that balance control is different amongst individuals with and without a fear of falling (Maki et al. 1991; Okada et al. 2001; Uemura et al. 2012), this research cannot definitively show that fear of falling causes these differences. For instance, balance deficits may result from a fear of falling, or underlying balance deficits may increase the likelihood of developing a fear of falling. To address this limitation, research has examined how different postural threat manipulations affect balance control in healthy individuals. The underlying premise is that emotional and cognitive changes similar to those experienced on a daily basis by individuals living with a fear of falling can be induced by changing the perceived consequences or likelihood of falling (Adkin and Carpenter, 2018). This allows one to study how fear and related psychological factors influence balance in a controlled environment without possible confounds associated with ageing and pathology (Brown and Frank, 1997; Adkin et al. 2000). The most common postural threat manipulation has involved raising the height of the surface on which an individual stands (reviewed in Adkin and Carpenter, 2018); however, other manipulations, including social evaluative threats (Geh et al. 2011; Doumas et al. 2018), virtual height exposure (Cleworth et al. 2012; 2016; Raffegeau et al. 2020a), and the threat of an impending perturbation (Shaw et al. 2012; Horslen et al. 2013; Lim et al. 2017; Johnson et al. 2019ab) have also been used. Each of these threat manipulations induce emotional and cognitive changes that would be expected, to some degree, in individuals experiencing a fear of falling.

1.3 Emotional and cognitive changes induced by postural threat

Most studies that have employed postural threat manipulations have used a combination of self-report and physiological measures to quantify individuals' emotional and cognitive response to the threat. Self-report measures typically include assessments of balance efficacy, fear, and state anxiety. Balance efficacy (or confidence) reflects an individual's belief in their ability to maintain balance and avoid a fall while performing a given balance task (Lamarche et al. 2011). This is typically assessed immediately before individuals perform the balance task; thus, instead of providing a measure of individuals' emotional reaction to the threat, it reflects a cognitive appraisal of their ability to perform the upcoming task within the threat context. State anxiety and fear are both aversive emotional states that are accompanied by increases in arousal; however, it is generally accepted that they are distinct emotions (Sylvers et al. 2011). Fear is an aversive reaction which triggers avoidance behaviours (i.e., fight, flight, freeze) in response to a specific threat. By contrast, anxiety is associated with sustained hypervigilance in anticipation of, or in response to, a potential threat where danger is not clearly imminent (Sylvers et al. 2011; Tovote et al. 2015). Since these are distinct emotional constructs, separate self-report measures are typically used to assess retrospective fear and anxiety immediately after participants complete a given balance task. To quantify associated changes in sympathetic arousal, electrodermal activity (EDA) is typically recorded during the balance tasks. EDA is preferable compared to measures cardiovascular variability, since its variation is unequivocally related to fluctuations in sympathetic, and not parasympathetic, activation (Parati et al. 2006; Boucsein, 2012). Regardless of the threat manipulation used, individuals consistently demonstrate increases in sympathetic activation and self-report reductions in balance efficacy and increases in both fear and anxiety (Hauck et al. 2008; Davis et al. 2009; Huffman et al. 2009; Geh et al. 2011; Cleworth et al. 2012; Johnson et al. 2019a).

1.4 Influence of postural threat on standing balance control

To examine how postural threat influences standing balance control, kinetic (i.e., centre of pressure; COP), kinematic (i.e., centre of mass; COM), and electromyographic (EMG) variables are typically analyzed. The COM represents the location of the weighted average of all body segments, whereas the COP represents the weighted average of pressure exerted by the feet onto the support surface (Winter, 1995). According to the inverted pendulum model, the acceleration of COM during quiet stance is proportional to the distance between the COP and the vertical projection of COM onto the support surface (Winter, 2009). In this relationship, the COM is the controlled variable and the COP is the controller. Thus, movement of the COP is thought to represent the net neuromuscular control of postural sway. Because of this, analyzing the spatial and frequency characteristics of COP oscillations can provide insight into how postural threat influences the control of sway.

When standing and facing the edge of an elevated surface, individuals typically demonstrate a stiffer control of postural sway that is characterized by higher frequency and smaller amplitude oscillations of the COP and COM (Carpenter et al. 2001; Cleworth et al. 2012). These changes in the control of sway are most pronounced in the anterior-posterior (AP) direction (Carpenter et al. 1999; 2001; Adkin et al. 2000). It is unclear if this direction-specific effect is related to the location of the threat (i.e., in the forward direction) or differences in the mechanics of controlling the AP compared to mediolateral (ML) sway (Winter et al. 2003); although recent work that manipulated the orientation of the participant relative to the platform edge has provided some support for the former (Raffegeau et al. 2020). When standing under conditions of threat, individuals also lean backwards, away from the edge of the platform (Adkin and Carpenter, 2018). This lean contributes to changes in lower limb muscle activity, such that tibialis anterior (TA) and rectus femoris show increased activation, while the soleus (SOL) and biceps femoris show slightly reduced activation (Carpenter et al. 2001). Since the TA is normally quiescent during unperturbed standing (Day et al. 2013), this change in muscle activity results in increased coactivation of muscles at the ankle joint (Cleworth et al. 2016), which may contribute to an overall increase in ankle joint stiffness (Carpenter et al. 2001).

These same threat-related changes in standing balance are not observed with the threat of an unpredictable forward or backward perturbation (Shaw et al. 2012; Johnson et al. 2019a; 2020). With this type of threat, individuals still show an increase in the average frequency content of COP oscillations, but they tend to lean forward (Johnson et al. 2019a; 2020) and increase trunk sway (Shaw et al. 2012) and COP amplitude (Johnson et al. 2019a). This is observed despite both the threat of height and perturbation evoking comparable changes in psychological and autonomic state (Horslen et al. 2013). However, in both cases, the threat-related changes in postural strategy appear appropriate given the nature of threat. In the case of height-related threat, leaning away from the edge of the platform and limiting postural sway will minimize the likelihood of a fall toward the edge. In contrast, leaning forward and increasing postural sway may facilitate compensatory stepping and postural recovery when standing on the ground and responding to a forward or backward perturbation (Maki and Whitelaw, 1993; Rajachandrakumar et al. 2018). This suggests that some threat-related changes in standing balance may not simply be a consequence of the psychological and autonomic state changes induced by the threat, but instead reflect context-appropriate adaptations which may minimize the likelihood of a fall or injury in the face of unique postural challenges.

1.5 Influence of postural threat on dynamic balance control

The majority of research to date has focused on how postural threat influences the control of unperturbed standing. However, postural threat has also been shown to influence reactive (Brown and Frank, 1997; Carpenter et al. 2004; Adkin et al. 2008; Sibley et al. 2010) and anticipatory (Adkin et al. 2002; Yiou et al. 2011; Zaback et al. 2015; Gendre et al. 2016; Phanthanourak et al. 2016; Bax et al. 2020) balance control, as well as gait (Brown et al. 2002; MacKenzie and Brown, 2004; Tersteeg et al. 2012). When balance is disturbed by an unpredictable trunk or support surface perturbation under conditions of height-related postural threat, there is typically earlier and larger balance corrective muscle activity (i.e., muscle response between 110-220 ms post-perturbation; Carpenter et al. 2004; Sibley et al. 2010) and larger peak displacement of the COP (Sibley et al. 2010). This shorter latency and larger balance corrective response results in a smaller peak displacement of the COM toward the edge (Brown and Frank, 1997; Carpenter et al. 2004).

Anticipatory postural adjustments (APAs) are more conservative under conditions of height-related threat, as both the rate and magnitude of the APA are reduced (Adkin et al. 2002; Yiou et al. 2011; Zaback et al. 2015). However, these effects are only observed when the APA functions to accelerate the COM in the direction of the threat, while APAs which accelerate the COM away from the platform edge are unaffected by the threat (Gendre et al. 2016). Similar to what has been observed with unperturbed standing, threat-related changes to the APA depend on the type of postural threat, as the rate and magnitude of APAs are increased when individuals stand with the threat of an impending perturbation (Phanthanourak et al. 2016; Bax et al. 2020). These threat-related changes in the APA appear appropriate given the nature of each type of threat. With a height-related threat, slower and smaller APAs reduce the likelihood of pushing the COM beyond the forward limits of the base of support. With the threat of perturbation, faster and larger APAs minimize the time needed to re-establish the COM within the new base of support, thereby limiting the likelihood of experiencing the perturbation during the less stable dynamic phase of the movement (Bax et al. 2020).

Lastly, when walking along a raised, narrow surface, individuals tend to walk slower (Brown et al. 2002; MacKenzie et al. 2004; Tersteeg et al. 2012) and spend more time of the gait cycle in the double-support phase (Tersteeg et al. 2012). Collectively, this suggests that in response to height-related postural threat, individuals tend to employ more cautious movement strategies that limit movement of the body, particularly in the direction of the threat. However, the movement strategies employed appear dependent on the nature of the postural task and context of the threat.

1.6 Do threat-related changes in standing balance control scale with the emotional response to threat?

Since the purpose of the postural threat model is to manipulate emotional state, it would seem intuitive that threat-related changes in balance control should vary as a function of the emotional response to threat. However, previous work has shown inconsistent correlations between changes in standing balance control and both self-reported and physiological measures of the emotional response to a height-related threat (Carpenter et al. 2006; Hauck et al. 2008; Davis et al. 2009; Huffman et al. 2009). For example, only one study has shown a significant correlation between changes in COP amplitude during quiet standing and self-reported fear of falling (Davis et al. 2009). However, this study found a positive correlation between these variables, which is the opposite to what would be expected given that COP amplitude typically decreases with height-related threat. Other threat-related changes in standing balance, such as the increased average frequency content of COP oscillations, have shown more consistent correlations with self-reported emotional and cognitive changes (Carpenter et al. 2006; Hauck et al. 2008; Davis et al. 2009; Huffman et al. 2009). Interestingly, this specific change in standing balance control is common to both the threat of height and perturbation (Adkin and Carpenter, 2018). Other changes to standing balance control, which do not clearly covary with the psychological and autonomic state changes induced by the threat, show a different pattern of change depending on the type of threat. This could suggest that only some changes to balance control depend on the magnitude of the emotional response to threat, while others may be adopted in a context-dependent manner largely independent of this response.

1.7 Mechanisms underlying threat-related changes in balance control

While the influence of threat on standing and dynamic balance control have been well-studied, the mechanisms underlying these changes are less clear. Recent work has provided convincing evidence that postural threat influences balance-relevant reflexes (Davis et al. 2011; Horslen et al. 2013; 2014; 2017; 2018; Naranjo et al. 2015; 2016), cortical processing of balance relevant sensory information (Adkin et al. 2008; Sibley et al. 2010), and attention processes related to balance control (Huffman et al. 2009; Zaback et al. 2015; 2016; Johnson et al. 2019a). Each of these changes has the potential to influence balance control.

1.7.1 Changes in attention with threat

The earliest evidence for threat-related changes in attention comes from work by Brown and Gage and colleagues (2002; 2003) that demonstrated poorer performance on a concurrent cognitive task when standing and walking under conditions of height-related threat. They suggested this was the result of individuals reallocating attention to the control of balance in this more threatening context. This speculation was later confirmed by Huffman and colleagues (2009), who demonstrated that individuals self-report greater conscious motor processing when standing under conditions of height-related threat. This observation has since been replicated and extended, with research showing that individuals also become preoccupied with threat-related stimuli, focus more on different cognitive strategies intended to help cope with the threat, and focus less on task-irrelevant information (Zaback et al. 2016). These same changes in attention have been reported when young and older adults stand with the threat of an impending perturbation (Johnson et al. 2019ab) or walk along an elevated surface (Ellmers and Young, 2019; Ellmers et al. 2020a). Whether these threat-related changes in attention influence balance control is currently unclear.

Redirecting attention toward movement is thought to interfere with more automatic motor control processes, potentially affecting the control of both standing and dynamic balance (Young and Williams, 2015). Explicit instruction to consciously control standing balance has been shown to increase the amplitude and frequency of the COP-COM difference signal (Vuillerme and Nafati, 2007), whereas distracting participants' attention from their movement using a dual-task has the opposite effect (Nafati and Vuillerme, 2011). This suggests that increased conscious motor processing may contribute to increased ankle joint stiffness. This is consistent with observations of increased ankle joint stiffness when balancing an inverted pendulum with instruction to ‘stand still’ compared to ‘stand at ease’ (Fitzpatrick et al. 1992; Loram et al. 2001). Increased voluntary effort to control sway has also been shown to increase ankle joint coactivation (Reynolds, 2010), which can increase ankle stiffness. Interestingly, increases in ankle muscle coactivation (Reynolds, 2010) and increases in COP-COM amplitude and frequency (Vuillerme and Nafati, 2007) were not associated with changes in the amplitude of postural sway. Collectively, this suggests that threat-related changes in attention may contribute to increases in ankle joint stiffness, and consequent increases in the frequency content of COP oscillations, but may not contribute to changes in sway amplitude. Recent work has provided some support for this speculation, as distracting individuals’ attention from their movement by having them perform a cognitive dual-task under conditions of threat was shown to minimize threat-related increases in COP power between 0.5-1.8 Hz (Johnson et al. 2020). While this study did not record EMG or have any measure of ankle joint stiffness, it provides some evidence that changes in attention may contribute to specific threat-related balance changes.

1.7.2 Changes in balance relevant sensory function with threat

Recently, a series of studies probed various balance relevant reflexes under different conditions of postural threat. Short-latency stretch reflexes and vestibulospinal reflexes have been the most studied to date (Davis et al. 2011; Horslen et al. 2013; 2014; 2017; 2018; Naranjo et al. 2015; Lim et al. 2017), although recent work has probed lower limb cutaneous reflexes (Horslen, 2016) and Golgi tendon organ Ib inhibitory reflexes (Horslen et al. 2017).

1.7.2.1 Lower limb stretch reflexes

Lower limb stretch reflexes have been probed using tendon-taps (Davis et al. 2011; Horslen et al. 2013; 2018) and rapid ramp-and-hold ankle rotations (Horslen et al. 2018). Achilles tendon (T-) reflexes have been shown to be facilitated by threat of height (Davis et al.

2011; Horslen et al. 2013; 2018) and perturbation (Horslen et al. 2013). However, under these same conditions, SOL Hoffman (H-) reflexes are either decreased (Sibley et al. 2007) or unaffected (Horslen et al. 2013). Because the H- and T-reflexes can be modulated centrally (at the synapse and motor neuron pool), but only the T-reflex can be modulated at the level of the receptor, this pattern of reflex modulation has been interpreted as evidence for increased muscle spindle sensitivity (Horslen et al. 2013; 2018).

While there are technical issues with inferring changes in muscle spindle sensitivity based on H- and T-reflex comparisons (Pierrot-Deseillingny and Burke, 2012), evidence from microneurographic studies suggests that psychological and autonomic changes similar to those experienced under conditions of postural threat are capable of modulating muscle spindle sensitivity (Ribot-Ciscar et al. 2000; 2007; Hospod et al. 2009; Ackerley et al. 2017). For instance, arousal (induced through performance of a mental computation task) and emotionally provocative music have been shown to increase Ia muscle afferents discharge rate during passive ankle joint rotations (Ribot-Ciscar et al. 2000; Ackerley et al. 2017). Likewise, directing attention to movement at the ankle has been shown to alter muscle spindle static and dynamic sensitivity (Ribot-Ciscar et al. 2007; Hospod et al. 2009). Recent work has also shown that short-latency stretch reflexes, evoked by ramp-and-hold plantar flexion perturbations, have increased velocity scaling when threatened (Horslen et al. 2018). Collectively, this work provides evidence that muscle spindle dynamic (and possibly static) sensitivity is increased when standing under conditions of postural threat.

It is unclear if changes in muscle spindle dynamic sensitivity contribute to threat-related changes in standing balance control. Individuals with Charcot-Marie-Tooth type 1A polyneuropathy, a disorder characterized by selective demyelination of large diameter sensory fibres, show normal control of standing balance (Nardone et al. 2000). This may suggest that velocity sensitive input from type 1a muscle afferents is not critical to the control of stance. However, it may be that redundant sensory input is capable of compensating for this specific sensory loss. Primary muscle afferent discharge has also been shown to predict future joint angular velocity with an advance of ~160 ms (Dimitriou and Edin, 2010). Thus, increases in dynamic muscle spindle sensitivity may allow for better prediction of postural sway, and consequently faster and more fine-tuned postural adjustments during stance.

1.7.2.2 Vestibular-evoked responses

The vestibular nuclei are extensively interconnected with autonomic and emotional centres of the nervous system. For example, they receive direct and/or indirect input from the amygdala, parabrachial nuclei, locus coeruleus, and dorsal raphe nucleus (Balaban and Thayer, 2001; Balaban, 2002; Staab et al. 2013). Thus, it should not be surprising that vestibular-evoked responses are modifiable under conditions of threat. These responses have been probed using both mechanical (Naranjo et al. 2015; 2016) and electrical stimuli (Horslen et al. 2014; Lim et al. 2017). Vestibular evoked myogenic potentials (VEMPs) are short-latency reflexes that can be evoked in tonically contracted muscles using short, auditory tone bursts that are thought to directly activate vestibular hair cells in the otoliths (Welgampola and Colebatch, 2005). These reflexes can be evoked in muscles of the neck, eye, and limbs, and therefore can probe reflexes mediated by different vestibular nuclei. When standing under conditions of height-related threat, VEMPs in muscles of the neck, eye, and lower limbs are facilitated (Naranjo et al. 2015; 2016). Significant correlations between changes in VEMP amplitude and self-reported fear and anxiety suggest that the extent of this reflex facilitation scales with the emotional response to the threat (Naranjo et al. 2015; 2016).

Unlike VEMPs, electrical vestibular stimulation (EVS) is thought to bypass the vestibular end-organ and stimulate the primary vestibular afferent directly. This evokes a highly organized pattern of muscle activity, that when summed vectorially, generates forces to counteract the vestibular error signal generated by the EVS (Fitzpatrick and Day, 2004). Using stochastic vestibular stimulation (SVS), a form of continuous electrical vestibular stimulation that varies in terms of amplitude and frequency, the influence of postural threat on early vestibular-evoked responses has been examined. With both the threat of height (Horslen et al. 2014) and perturbation (Lim et al. 2017), there is greater coupling and gain between the SVS and motor response (measured from horizontal ground reaction forces or muscle activity). Other work using square-wave EVS has failed to show that postural threat facilitates early vestibular-evoked responses (Osler et al. 2013). However, this study only examined trunk kinematic outcomes in response to the EVS. It is likely that the high frequency threat-related changes in ground reaction forces and muscle activity would be less detectable in the trunk kinematics due to mechanical filtering (Dakin et al. 2010; Horslen et al. 2015).

Collectively, these observations suggest that postural threat alters central processing of vestibular information, such that for a given vestibular input, there is a larger motor response. This facilitation could reflect a generalized increase in excitability at the level of the vestibular nuclei, as responses are facilitated in some muscles not involved in the control stance (e.g., neck and ocular muscle; Naranjo et al. 2015; 2016) and increases in vestibular-motor coupling are not specific to the direction of threat (Horslen et al. 2014; Naranjo et al. 2015). Given that the lateral vestibular nucleus is a site of integration of balance relevant input from both vestibular and somatosensory sources (Pompeiano, 1972; McCall et al. 2017) and interacts extensively with other descending motor pathways (i.e., reticulospinal tract), increased excitability at the level of the vestibular nuclei may increase feedback gain from both vestibular and somatosensory inputs. This may contribute to higher frequency postural adjustments during the control of stance.

1.7.3 Cortical changes associated with postural threat

Postural threat has also been shown to alter cortical processing of balance relevant information. The N1 component of the perturbation-evoked potential (PEP) has been shown to be facilitated when standing under conditions of height-related postural threat (Adkin et al. 2008; Sibley et al. 2010). This component of the PEP peaks approximately 85-165 ms after the onset of a postural perturbation and is widely distributed over fronto-central cortical regions (Bolton, 2015; Varghese et al. 2017). The neural processes that this cortical potential reflect are not entirely clear. The earliest interpretations suggested it may reflect sensory processing related to the balance disturbance (Dietz et al. 1985; Quant et al. 2004a). However, since the amplitude of the PEP-N1 is substantially reduced when a perturbation is predictable (Dietz et al. 1985; Adkin et al. 2006; 2008; Mochizuki et al. 2009), some have suggested it may reflect an error signal with a more general role in detecting instability (Adkin et al. 2006; 2008; Mochizuki et al. 2009). Other work using dipole source localization techniques have shown that the largest component contributing to the N1 originates in the supplementary motor area, suggesting it may have a role in planning later components of the compensatory postural response (Marlin et al. 2014). Regardless of its underlying function, the observation that this cortical potential is facilitated under conditions of threat provides evidence that there is increased cortical involvement in reactive postural control.

It is less clear if there is greater cortical involvement during the control of unperturbed standing. Previous work examining somatosensory-evoked potentials (SEPs) following tibial nerve stimulation (Davis et al. 2011), tendon taps (Davis et al. 2011), and sural nerve stimulation

(Horslen, 2016) have observed that the earliest cortical potentials, which likely reflect the earliest processing of sensory input at the primary somatosensory cortex, are unaffected by postural threat. However, later components, such as the P110-N140, which are thought to reflect later processing of sensory input at the secondary somatosensory and posterior parietal cortices (Schubert et al. 2006), show evidence of facilitation (Horlsen, 2016). This facilitation of later cortical potentials may contribute to altered perceptions of balance relevant movements under conditions of height-related threat (Cleworth and Carpenter 2016; Cleworth et al. 2018). Other work using transcranial magnetic stimulation (TMS) has shown that while motor-evoked potentials (MEPs) of trunk muscles are facilitated under conditions of threat, MEPs for muscle acting at the ankle joint are either suppressed (Tokuno et al. 2018) or unaffected (Johannsson et al. 2017; Tokuno et al. 2018). These results could suggest there is little change in corticospinal excitability to muscles primarily engaged in the control of standing balance. However, since TMS preferentially excites the fastest-conducting monosynaptic corticospinal tract projections, and not slower conducting monosynaptic or polysynaptic fibres (Lemon, 2002; Porter and Lemon, 1995), this only suggests that the excitability of a specific population of corticomotoneurons are not facilitated by threat. Furthermore, TMS only provides a snapshot into the state of corticospinal excitability, which is constantly varying (Bestmann and Krakauer, 2015). Previous work has provided evidence of altered cortical engagement in the control of balance during discrete moments of instability (Slobounov et al. 2005; Varghese et al. 2015). It is possible that the cortex is only intermittently involved in the control of sway and motor-evoked potentials triggered randomly during quiet stance fail to capture these moments of cortical engagement. Thus, different approaches are required to fully understand how postural threat influences cortical involvement in the control of standing balance.

1.8 Goals of this thesis

While a considerable body of work has used postural threat manipulations to investigate how fear and related psychological factors influence the control of balance, shortcomings of the threat manipulations have limited our understanding of this relationship. In particular, there is mounting evidence that some threat-related changes to balance control are not simply a consequence of the psychological and autonomic state changes induced by the threat, but instead may reflect balance adaptations in response to highly specific postural challenges (Adkin and Carpenter, 2018). Therefore, the overarching goal of this thesis was to isolate the influence of the psychological and autonomic state changes induced by postural threat in order to understand how these factors shape balance control and balance-relevant processes independent of threat context. To address this goal, each of the studies outlined in this thesis use a novel, repeated threat exposure manipulation.

1.8.1 Repeated exposure as a model to manipulate the emotional response to threat

Repeated exposure to fear-provoking stimuli, or exposure therapy, is one of the most effective cognitive-behaviour treatments for a variety of anxiety disorders (Craske et al. 2014). When repeatedly presented with a fear-provoking stimulus, individuals' emotional response to that stimulus progressively wanes. This has been attributed partially to habituation, a form of non-associative learning whereby an individuals' responsiveness to a particular stimulus is reduced after repeated or prolonged exposure (Groves and Thompson, 1970). If no real or perceived harm is experienced over the course of repeated exposure, associative learning processes also contribute to the attenuation of the emotional response as an individual's expectations about the likelihood and/or severity of feared consequences are repeatedly disconfirmed (Foa et al. 2006). Previous work has examined the efficacy of exposure therapy for individuals with acrophobia (Emmelkamp et al. 2001; Baker et al. 2010; Coelho et al. 2009). Both in vivo (Emmelkamp and Felten, 1985; Baker et al. 2010) and virtual (Emmelkamp et al. 2001; Coelho et al. 2009) height exposure are effective for reducing state anxiety when standing in a height-related scenario. Thus, it should be possible to manipulate psychological and autonomic state within a threatening context using a repeated threat exposure manipulation.

One concern when using a repeated exposure manipulation is the amount of time required to sufficiently reduce an individual's emotional response to threat, since this has the potential to introduce undesirable order effects due to physical and/or mental fatigue. Therefore, given the aims of this thesis, it is important to structure the exposure protocol in such a way that it maximizes the rate of fear reduction within an experimental session. The most effective way to achieve this is by using a massed and constant exposure protocol, whereby the same fear-provoking stimulus is presented across uniformly-spaced trials within a single block (Rowe and Craske, 1998; Lang and Craske, 2000). This is in contrast to protocols which vary the conditions of exposure in terms of timing, intensity, and/or context. While more variable protocols are more effective for maximizing long-term fear reduction, they tend to sustain within-session anxiety and arousal (Craske et al. 2008; 2012), making them undesirable for the studies outlined in this thesis. Therefore, each of the studies outlined in this thesis used massed and constant repeated threat exposure protocols.

For each of the studies outlined in this thesis, an unperturbed standing balance task was the focus of investigation. Studies 1 and 2 of this thesis examined how threat-related changes in standing balance control changed as a function of repeated exposure to a height-related threat. Study 1 used a relatively short exposure period in combination with regression-based statistics to determine how threat-related changes in standing balance control covary with individuals' emotional response to threat. Study 2 used an extended threat exposure protocol to determine if threat-related changes in standing balance control persist after near complete attenuation of the emotional response to threat. Study 3 of this thesis did not involve exposure to a height-related threat, but instead focused on how state anxiety and balance change over the course of repeated testing in individuals naïve to balance assessment. While this study did not involve the use of an overt threat, having balance assessed in an unfamiliar environment is a form of social evaluative threat. Since there was no overt threat, this experiment was able to explore how low levels of anxiety influences balance control independent of task-constraints imposed by a physical threat. Studies 4 and 5 of this thesis investigated potential mechanisms contributing to threat-related changes in standing balance control. Specifically, study 4 used analyses of corticomuscular and intermuscular coherence to examine how cortical and subcortical drive to muscles engaged in balance control were affected by threat and repeated threat exposure. Assuming that only some threat-related changes in standing balance control covary with changes in psychological and autonomic state, examining how these estimates of descending drive change as a function of repeated threat exposure can provide insight into how they contribute to specific threat-related balance changes. Study 5 used a similar approach, but analyzed cortical potentials time-locked to discrete postural adjustments to infer how cortical processing of balance relevant information might contribute to threat-related balance changes. Overall, these studies improve our understanding of how fear and related psychological processes impact balance control and provide insight into potential mechanisms underlying these relationships.

Chapter 2: Study 1 - Adaptation of emotional state and standing balance parameters following repeated exposure to height-induced postural threat

2.1 Introduction

Fear of falling is prevalent in older adults (Legters, 2002) and individuals with movement disorders (Adkin et al. 2003; Schmid et al. 2015). Cross-sectional studies have shown that older adults with a fear of falling demonstrate differences in standing (Maki et al. 1991), reactive (Okada et al. 2001), and anticipatory (Uemura et al. 2012) postural control compared to non-fearful individuals matched for age and level of physical function. These observations, combined with neuroanatomical evidence of direct connections between networks responsible for emotional processing and sensorimotor control of balance (Balaban, 2002), suggest that fear of falling may directly influence on balance control, potentially contributing to the increased risk of falling documented amongst these individuals (Friedman et al. 2002; Hadjistavropoulos et al. 2011; Li et al. 2003).

To examine how fear of falling influences balance control independent of ageing and pathology, research has exposed healthy individuals to different postural threats (Brown and Frank, 1997; Geh et al. 2011; Johnson et al. 2019a). The most common approach has involved elevating the height of the surface on which individuals stand (Brown and Frank, 1997; Adkin et al. 2000; 2002; Carpenter et al. 2001). When standing at the edge of an elevated platform, individuals demonstrate a robust emotional response; there are increases in state anxiety and sympathetic arousal (typically estimated from tonic electrodermal activity; EDA) and reductions in balance specific self-efficacy (Carpenter et al. 2006; Cleworth et al. 2012; Davis et al. 2009; Hauck et al. 2008; Huffman et al. 2009; Zaback et al. 2015). In addition, individuals demonstrate broad changes in attention, directing more attention toward the internal mechanics of their movement, threat-related stimuli, and strategies to regulate their emotional state (Zaback et al. 2016). These changes in emotional and cognitive state are accompanied by stereotyped changes in standing balance control (Adkin and Carpenter, 2018). Individuals typically lean backwards and demonstrate stiffer control of balance characterized by smaller amplitude and higher frequency postural adjustments and increased co-contraction of lower leg muscles (Adkin et al. 2000; Carpenter et al. 2001; 2006; Cleworth et al. 2012; Davis et al. 2009; Hauck et al. 2008; Huffman et al. 2009; Zaback et al. 2015).

Given the potential links between fear of falling and balance deficits and falls (Friedman et al. 2002; Hadjistavropoulos et al. 2011; Li et al. 2003), it is important to understand if individuals' emotional response to a perceived threat can be attenuated and if there are meaningful changes in postural control as a result. One way to explore this is through repeated threat exposure. When repeatedly exposed to a fear-provoking stimulus, individuals typically demonstrate progressive reductions in their emotional response (Foa et al. 2006). This has been attributed partially to habituation, a non-associative learning process whereby individuals' responsiveness to a particular stimulus is reduced following repeated or prolonged exposure (Groves and Thompson, 1970). Assuming no real or perceived harm is experienced over the course of repeated threat exposure, associative learning processes also contribute to fear reduction, as individuals' expectations about the likelihood and severity of feared consequences are gradually disconfirmed (Foa et al. 2006). Previous work has shown that repeated exposure to height can substantially reduce the psychological and social consequences associated with a fear of heights (Baker et al. 2010; Coelho et al. 2009; Emmelkamp et al. 2001; Lang and Craske, 2000). However, little attention has focused on how individuals' postural behaviour is affected following this form of intervention.

Thus, the primary aim of this study was to determine if repeated exposure to a height-induced postural threat influences threat-induced changes in standing balance control. It was hypothesized that after repeated threat exposure, balance confidence would increase and fear of falling, state anxiety, sympathetic arousal, and attention toward one's movements, threat-related stimuli, and self-regulatory strategies would decrease. These changes in emotional and cognitive state were expected to be accompanied by changes in standing balance control. In particular, after repeated threat exposure, individuals were expected to lean less far away from the platform edge and demonstrate larger amplitude and lower frequency postural adjustments and less ankle muscle co-contraction.

A secondary aim of this study was to explore associations between threat-induced changes in emotional and cognitive state and standing balance control. Previous studies have shown inconsistent correlations between individuals' emotional response to threat and changes in balance control, with specific balance outcomes (i.e., average frequency of postural adjustments) showing more consistent correlations than others (i.e., amplitude of postural adjustments) (Carpenter et al. 2006; Davis et al. 2009; Hauck et al. 2008; Huffman et al. 2009). This suggests that some threat-induced changes in balance control are more closely linked with individuals' emotional response to threat than others. Alternatively, since the emotional response to threat is multifaceted, with changes in anxiety, arousal, and attention not necessarily varying in lockstep (Staab et al. 2013), bivariate correlations may not adequately identify associations between the emotional response to threat and changes in balance control. Thus, this study aimed to determine if a linear combination of emotional and cognitive state changes could account for variance in different balance outcomes when initially threatened, and after having been repeatedly exposed to threat.

2.2 Methods

2.2.1 Participants

Sixty-eight healthy young adults (mean age ±SD: 22.95 ±4.06 years; 36 females) participated in this study. Participants were free of musculoskeletal and neurological disorders that could influence balance control. No participants self-reported having an extreme fear of heights. The University of British Columbia Clinical Research Ethics Board approved the experimental procedures, which accorded with the Declaration of Helsinki. All participants provided written informed consent.

2.2.2 Procedures

Participants stood barefoot on a force plate (40cm × 60cm; AMTI, USA) positioned at the edge of a 2.13m × 1.52m hydraulic lift (Penta-lift, Canada) and completed five two-minute trials of quiet standing under two conditions of height-induced postural threat (Figure 2-1). Throughout all trials, participants stood with their toes aligned to the anterior edge of the force plate with a stance width equal to their foot length. The borders of the participants' feet were traced onto the force plate to ensure foot position was consistent across all trials. For the LOW threat condition, the hydraulic lift was positioned at its lowest height (0.8m above the ground). To minimize anxiety at this condition, an additional support (0.6m × 1.52m) surface was positioned in front of, and flush with, the anterior edge of the force plate, creating 60cm of continuous support surface in front of the participant (Carpenter et al. 2001). For the HIGH threat condition, the hydraulic lift was elevated 3.2m above the ground and participants stood directly at the platform edge.

Participants were instructed to stand quietly with their arms at their sides and fixate on a visual target 3.87m in front of them. To maximize adaptation to threat, the five quiet standing trials were completed in a blocked order at each threat condition (Lang and Craske, 2000; Rowe and Craske, 1998). Two-minutes of seated rest were given between trials, during which time participants completed questionnaires to assess emotional and cognitive state (see *Data collection*). To minimize possible order effects, approximately half of the participants completed the LOW condition first (n=37), while the others completed the HIGH condition first. Throughout all trials, participants wore a harness secured to the ceiling. The harness did not provide support that could assist in the postural task.

2.2.3 Data collection

Ground reaction forces and moments were recorded from the force plate and sampled at 100Hz. Surface electromyography (EMG) was recorded from pairs of Ag/AgCl electrodes placed in bipolar configurations (2cm inter-electrode distance) over the muscle bellies of the soleus (SOL) and tibialis anterior (TA) of the right leg. A common ground electrode was placed over the lateral malleolus. EMG data were amplified (500×), sampled at 3000Hz (Telemyo 2400R-G2, Noraxon, USA), bandpass filtered online (10-1000Hz), and then A-D sampled at 2000Hz. Electrodermal activity (EDA) was recorded (2502SA, CED, UK) from two Ag/AgCl electrodes placed on the thenar and hypothenar eminences of the non-dominant hand and sampled at 100Hz. Due to technical issues, EDA was not available for two participants.

Before each trial, participants self-reported their confidence in their ability to maintain balance and avoid a fall during the upcoming balance task. After each trial, participants completed single item self-report questions to assess fear of falling and cognitive and somatic anxiety experienced during the trial. Responses to these questions were provided on visual analog scales ranging from 0 to 100 with graduations marked every 10 units. Higher scores reflected greater balance confidence, fear of falling, and cognitive and somatic anxiety. Scores from the cognitive and somatic anxiety questions were averaged to create a state anxiety score (Johnson et al. 2019a).

Focus of attention was also assessed after each trial using a 5-item questionnaire that asked participants to rate how much they thought about or paid attention to different information throughout each trial (Johnson et al. 2019a). In particular, single questions were used to estimate attention toward 1) movement processes (i.e., conscious control or monitoring of movement; Att. MP); 2) threat-related stimuli (i.e., feelings of anxiety or worry; Att. TRS); 3) self-regulatory strategies (i.e., coping strategies to help remain calm, confident, and/or focused; Att. SRS); 4) task objectives (i.e., focus on specific task instructions; Att. TO); and 5) task-irrelevant information (i.e., thoughts unrelated to the task; Att. TI). Each item was rated on a 9-point Likert scale with higher scores reflecting more attention to each particular loci of attention. The terminology and items used in this questionnaire were developed from open-ended questionnaire and interview data describing the changes in attention associated with height-induced postural threat (Zaback et al. 2016).

2.2.4 Data analysis

2.2.4.1 Centre of pressure

Ground reaction forces and moments from the force plate were low-pass filtered offline using a second-order dual-pass Butterworth filter with a cut-off frequency of 10Hz. From these data, centre of pressure (COP), which reflects the weighted average of pressure applied by the feet onto the support surface (Winter, 1995), was calculated in the anterior-posterior direction, as postural threat effects are most pronounced in this plane when facing the platform edge (Adkin et al. 2000). From the COP signal, mean position (MPOS; referenced to the front edge of the force plate) was first calculated to provide an estimate of how far individuals leaned backwards. The MPOS was then subtracted from the COP signal to remove the bias, and a linear detrend was applied to minimize the influence of linear drifts in COP position within each trial that can skew measures of COP amplitude. From the debiased signal, root mean square (RMS) and mean power frequency (MPF) were calculated. RMS reflects the amplitude of COP movement, while MPF reflects the average frequency content contained within the COP power spectrum.

While MPF of COP oscillations typically increases when threatened, it is unclear if this results from a reduction in the power of low frequency COP oscillations, an increase in the power of high frequency COP oscillations, or some combination of the two. Thus, to quantify how COP power changes across different frequencies bands with initial and repeated threat exposure, comparisons of spectra across a bandwidth of relevant COP frequencies (0-5Hz) were performed (Halliday et al. 1995; Reynolds, 2010). For these analyses, COP data were concatenated across participants for the following trials: LOW-1, HIGH-1, and HIGH-5. Power spectral densities of the concatenated data were calculated using a method developed by Halliday and colleagues (1995). Data were first split into equal length, non-overlapping segments (length: 60s; number of segments: 136). Fast Fourier transformations were applied to each segment, which were then summed and converted to power spectra (frequency resolution: 0.0167Hz). Log ratios of these power spectra were computed for the following pairs of trials: HIGH-1 : LOW-1 (initial threat effect) and HIGH-5 : HIGH-1 (adaptation to threat effect). For each comparison, 95% confidence limits were set using an F-distribution based on the number of segments used to generate each power spectra (Halliday et al. 1995). Frequency bands where COP power significantly differed between conditions were identified. To determine the onset of each band, the frequency bins where data first exceeded a respective confidence limit for at least 3 of 5 consecutive bins were identified. The end of each band was identified as the bin where data returned within the confidence limits for at least 3 of 5 consecutive bins. Mean COP power within specific frequency bands identified were then calculated for each participant (specific frequency bands identified are described in the *Comparison of spectra* section of the *Results*).

2.2.4.2 SOL-TA co-contraction

EMG data for SOL and TA were debiased, full-wave rectified, and normalized to mean rectified EMG of maximal voluntary contractions from respective muscles. These data were linear enveloped using a second-order dual-pass Butterworth filter with a low-pass cut-off of 3Hz. SOL-TA co-contraction was calculated as the integrated area of overlap between SOL and TA linear envelopes (Crenna et al. 1992; Frost et al. 1997).

2.2.4.3 Sympathetic arousal

To provide an estimate of tonic electrodermal activity, the frequency of non-specific electrodermal responses (NS-EDR.freq) were calculated (Boucsein et al. 2012). Electrodermal data were low-passed filtered offline using a fifth-order dual-pass Butterworth filter with a cut-off frequency of 1Hz. A customized algorithm then identified and counted all EDRs with amplitudes greater than 0.05 uS (Boucsein et al. 2012). As movement artefacts can be mistakenly identified as EDRs, data were visually inspected and any false positives were removed manually (Boucsein 2012).

2.2.5 Statistical analyses

A series of 2 (threat: LOW vs HIGH) × 2 (trial: 1 vs 5) repeated measures (RM-) ANOVAs were conducted for self-report (balance efficacy, fear, anxiety, and attention focus), autonomic (NS-EDR.freq), and behavioural measures (MPOS, RMS, MPF, and SOL-TA co-contraction). Significant threat × trial interactions were followed-up with paired-samples t-tests that examined the effect of threat at trials 1 and 5 and the effect of trial for LOW and HIGH threat conditions. Since SOL-TA co-contraction was positively skewed, these data were log-transformed.

To determine if a linear combination of emotional and cognitive state changes could account for changes in behavioural measures when first exposed to the threat, multiple linear regressions were conducted. For these analyses, change scores between the first LOW and HIGH trial (HIGH-1 – LOW-1) were calculated for all emotional, cognitive, and behavioural measures. Change scores for emotional and cognitive state measures were included as independent variables, while change scores for behavioural measures were the dependent variables. A separate set of multiple regressions were conducted to determine if emotional and cognitive state changes could account for changes in behavioural measures over the course of repeated exposure to threat. For these analyses, change scores between trials 1 and 5 of the HIGH threat condition (HIGH-5 – HIGH-1) were calculated for all emotional and cognitive state measures (independent variables), and behavioural measures (dependent variables). Bivariate correlations between emotional and cognitive state measures and behavioural measures were calculated to supplement the multiple regressions. For all statistical tests, alpha was set at 0.05.

2.3 Results

2.3.1 Emotional and cognitive adaptations

Significant threat × trial interactions were observed for measures of balance confidence, anxiety, fear of falling, NS-EDR.freq, and Att. MP, TRS, and TI (all p-values $\leq$0.006; Table 2-1). Paired t-tests revealed the effect of threat was significant for each of these measures at trial 1, such that individuals were less confident and more anxious, fearful, and physiologically aroused, and directed less attention toward task-irrelevant information and more attention toward movement processes and threat-related stimuli when standing at the HIGH compared to LOW threat. By trial 5, the effect of threat was reduced, but remained significant for all measures except for Att. TI, which returned to LOW threat values. In all cases, the effect of threat was attenuated due to greater changes observed from trial 1 to 5 at the HIGH compared to LOW threat (Figure 2-2).

Of the remaining emotional and cognitive state measures, significant main effects of threat and trial were observed for Att. SRS and TO. In both cases, individuals directed more attention toward this information at the HIGH compared LOW threat condition (p-values <0.001) and directed less attention toward this information from trial 1 to 5 independent of threat condition (p-values <0.001).

2.3.2 Standing balance adaptations

A significant threat × trial interaction was only observed for SOL-TA co-contraction (p<0.001; Table 2-1). Paired t-tests revealed the effect of threat was significant for SOL-TA co-contraction at trial 1, such that individuals co-contracted more at the HIGH compared to LOW threat. The effect of threat remained significant by trial 5, but was reduced. Paired t-tests revealed this was due to significant decreases in co-contraction from trial 1 to 5 across only the HIGH threat condition (Figure 2-3).

For all other behavioural measures, significant main effects of threat were observed. When standing at the HIGH compared to LOW threat condition, MPOS shifted away from the platform edge, RMS decreased, and MPF increased (p-values $\leq$0.008). For each of these measures, no interactions or main effects of trial were observed, demonstrating that these measures were affected by threat, but did not change over the course of repeated threat exposure.

2.3.2.1 Comparison of spectra

With initial threat exposure (HIGH-1 : LOW-1), COP power was reduced at frequencies lower than 0.05Hz and was increased at frequencies between 0.48-0.52Hz and above 0.59Hz (Figure 2-4a). With repeated threat exposure (HIGH-5 : HIGH-1), COP power was reduced at frequencies 0.92-0.98Hz, 1.72-1.77Hz, and above 1.833Hz (Figure 2-4b).

Based on these results, mean COP power was calculated within the following frequency bands: 0-0.05Hz (low frequency), 0.59-1.82Hz (medium frequency), and 1.83-5Hz (high frequency). The low frequency band was selected as this was the only region where COP power was reduced with threat and this region, while small, contains the most power in the COP power spectrum. The medium frequency band was selected as this was a region where COP power increased with threat, but showed negligible adaptation with repeated threat exposure. The high frequency band was selected as this was a region where COP power increased with initial threat exposure and showed significant adaptation with repeated exposure. Change scores (HIGH-1 – LOW-1 and HIGH-5 – HIGH-1) were calculated for these measures of mean COP power and included as dependent variables in the multiple linear regressions.

2.3.3 Associations between changes in emotional and cognitive state and standing balance parameters

2.3.3.1 Initial threat exposure

Anxiety and fear of falling had variance inflation factors (VIFs) greater than 2.5, indicating substantial multicollinearity with the other independent variables entered into these multiple regressions. Therefore, these variables were not included as independent variables in these multiple regressions. Thus, each multiple regression included 7 independent variables (balance confidence, NS-EDR.freq, and Att. MP, TRS, SRS, TO, and TI). As shown in Table 2-2, significant multiple regressions were observed for MPF (R^2=0.465, p<0.001), high frequency COP power (R^2=0.337, p=0.001), and SOL-TA co-contraction (R^2=0.354, p<0.001), showing that a linear combination of emotional and cognitive state changes could account for variance in these behavioural measures when initially threatened. The only significant individual predictor for changes in MPF and high frequency COP power was Att. TRS (MPF: β=.542, p<0.001; high frequency COP power: β=.420, p=0.007). No significant individual predictors were observed for SOL-TA co-contraction.

Results from the bivariate correlations were generally consistent with the multiple linear regression analyses, with changes in MPF, high frequency COP power, and SOL-TA co-contraction showing the strongest and most consistent correlations with a number of emotional and cognitive state changes (Table 2-3).

2.3.3.2 Repeated exposure to threat

Fear of falling had a VIF greater than 2.5; therefore, this variable was not entered as an independent variable in these multiple regressions. Thus, each multiple regression included 8 independent variables (balance confidence, anxiety, NS-EDR.freq, and Att. MP, TRS, SRS, TO, and TI). Significant multiple regressions were observed for MPOS (R^2=0.261, p=0.020), high frequency COP power (R^2=0.268, p=0.017), and SOL-TA co-contraction (R^2=0.323, p=0.003), showing that a linear combination of emotional and cognitive state changes could account for variance in these behavioural measures after repeated exposure to threat. Significant individual predictors of changes in MPOS were balance confidence (β=-.315, p=0.016), anxiety (β=-.437, p=0.018), and Att. TI (β=.270, p=0.043). The only significant individual predictor for high frequency COP power was Att. MP (β=.376, p=0.013). No significant individual predictors were observed for SOL-TA co-contraction (Table 2-2).

With the exception of the model for MPOS, results from the bivariate correlations were generally consistent with the multiple linear regression analyses, with changes in high frequency COP power and SOL-TA co-contraction showing the strongest and most consistent correlations with changes in emotional and cognitive state following repeated threat exposure (Table 2-3).

2.4 Discussion

The primary aim of this study was to understand how standing balance control adapts following repeated exposure to height-induced postural threat. Consistent with previous research, this study showed that height-induced postural threat induces a robust emotional response that is accompanied by changes in standing balance control; in particular, individuals leaned away from the edge of the platform and showed smaller amplitude and higher frequency COP adjustments (Adkin and Carpenter, 2018). This study was also the first to demonstrate that changes in COP MPF with threat are due to decreases in lower frequency COP components (≤0.05 Hz) and increases in higher frequency COP components (>0.5 Hz). As hypothesized, threat-induced changes in emotional and cognitive state were significantly attenuated following repeated threat exposure. In particular, individuals demonstrated increases in balance confidence and attention toward task-irrelevant information, and reductions in anxiety, fear of falling, sympathetic arousal, and attention toward movement processes and threat-related stimuli. However, with the exception of attention toward task-irrelevant information, these emotional and cognitive outcomes remained elevated above LOW threat values, showing that complete adaptation was not achieved. Contrary to what was hypothesized, few changes in standing behaviour were observed after repeated threat exposure, with changes in high frequency COP power (>1.83Hz) and SOL-TA co-contraction representing the only behavioural outcomes to show any adaptation across multiple exposures to the HIGH threat condition. Thus, despite significant adaptation of the emotional response to threat, individuals' behavioural response to threat was largely preserved.

A secondary aim of this study was to further explore associations between threat-induced changes in standing balance and emotional and cognitive state. Changes in several standing balance outcomes were related to a combination of emotional and cognitive state changes when initially threatened as well as after having been repeatedly exposed to threat; this included high frequency COP power (1.83-5Hz) and SOL-TA co-contraction. Some standing balance outcomes were unrelated to a combination of emotional and cognitive state changes (i.e., RMS and low frequency COP power) or only showed significant relationships with either initial (i.e., MPF) or repeated (i.e., MPOS) threat exposure. These findings are somewhat consistent with previous work. Of the COP outcomes typically assessed in postural threat studies, changes in MPF have been most consistently correlated with emotional and cognitive state changes (Carpenter et al. 2006; Davis et al. 2009; Hauck et al. 2008; Huffman et al. 2009). The present study replicated this observation and provides evidence to suggest this is due to a strong link between changes in higher frequency COP components and individuals' emotional response to threat. By contrast, threat-induced changes in COP amplitude, typically assessed by calculating RMS of COP, are seldom associated with emotional and cognitive state changes (Carpenter et al. 2006; Hauck et al. 2008; Huffman et al. 2009). Even after accounting for the combined influence of multiple emotional and cognitive state changes, threat-induced changes in RMS and lower frequency COP components could not be accounted for. Collectively, these results suggest that some threat-induced changes in standing balance are more closely linked with individuals' emotional response to threat than others.

2.4.1 Why were behavioural adaptations limited?

There are several possible explanations for why individuals' behavioural response to threat was largely preserved following repeated threat exposure. First, it is possible that a non-linear relationship exists between some threat-induced changes in behaviour and individuals' emotional response to threat, such that considerable or near complete adaptation is needed before some behavioural outcomes show any sign of adaptation. The results from the regression-based analyses can support this speculation, as several behavioural outcomes that did not show adaptation at a group level were significantly related to either a combination of emotional and cognitive outcomes (i.e., MPOS and MPF) or showed several moderate correlations with emotional and cognitive outcomes (i.e., medium frequency COP power). These significant relationships may have been the result of behavioural adaptations starting to manifest in only those individuals who showed the greatest emotional and cognitive adaptation. If this is the case, broader behavioural adaptations may have been observed with a longer exposure period and greater emotional and cognitive adaptation at a group level.

It is also possible that some threat-induced changes in behaviour are primarily context-dependent, such that they are adopted irrespective of individuals' emotional response to threat. Previous work has shown that the behavioural response to postural threat differs depending on the type of threat (Shaw et al. 2012; Johnson et al. 2019a). In particular, when standing with the threat of an unpredictable forward or backward perturbation, healthy young adults show higher frequency postural adjustments, consistent with what is seen with a height-induced threat, but tend to lean forward and show larger amplitude postural adjustments (Shaw et al. 2012; Johnson et al. 2019a). This difference in postural strategy is observed despite individuals reporting similar emotional and cognitive state changes in both threat scenarios. If some components of the behavioural response to threat are primarily related to the context of the threat, they may be less amendable following repeated threat exposure.

Lastly, some threat-induced changes in behaviour may be associated with state-related changes not measured in the present study. For example, it has been shown that there are broad, multi-sensory changes when individuals are exposed to height-induced threat, whereby balance relevant proprioceptive (Davis et al. 2011; Horslen et al. 2013; 2017; 2018) and vestibular (Horslen et al 2014; Naranjo et al. 2015; 2016) reflexes are facilitated. It is unclear if these changes in sensory processing scale linearly with individuals' emotional response to threat. In addition, cognitive factors known to influence vestibular reflex gain, such as vigilance or tonic alertness (Collins and Poe, 1962; Collins, 1988), were not accounted for in the present study and may not vary linearly with changes in emotional state as measured in this study. Since threat-induced changes in sensory processing may increase reflex feedback gain and allow for more accurate monitoring of postural state, maintenance of these changes following repeated exposure could explain why some threat-induced changes in behaviour do not show adaptation.

2.4.2 *Functional implications*

The threat-induced changes in standing balance that appear most susceptible to adaptation following repeated threat exposure are the highest frequency components of COP movement and ankle muscle co-contraction. These behavioural outcomes are highly correlated to each other (Table 2-4), with co-contraction likely driving higher frequency COP oscillations (Warnica et al. 2014; Wuehr et al. 2017). These particular components of the behavioural response to threat may be maladaptive for several reasons. First, while slower fluctuations in the COP position have been argued to serve an exploratory role, providing the nervous system with an increased inflow of balance relevant sensory information (Carpenter et al. 2010), very high frequency COP oscillations may interfere with or mask relevant somatosensory input (Collins et al. 1997; Mildren et al. 2016). It has been argued that this is why individuals with orthostatic tremor, a disorder characterized by a 13-18Hz tremor of the lower limbs and trunk during stance, have difficulty processing proprioceptive and cutaneous inputs (Bacsi te al. 2005). High frequency COP oscillations (>2Hz) also contribute negligibly to the control of the centre of mass during stance due to the large moment of inertia of the centre of mass (Gage et al. 2004). Lastly, increased ankle muscle co-contraction may impair muscle spindle coding of ankle joint rotations (Peters et al. 2017) and interfere with dynamic balance control (Nagai et al. 2013). By contrast, other threat-induced changes in standing balance that may serve a more protective role, such as the reduced amplitude of COP movement and lean away from the platform edge, appear less prone to adaptation. The tendency for maladaptive behaviours to be minimized and more protective behaviours to be preserved may be beneficial for interventions designed to reduce fear of falling. For instance, reducing an individual’s fear of falling in a particular scenario may not make them more prone to employing risky postural strategies, but it may reduce their tendency to employ strategies that interfere with sensorimotor processes underlying the control of balance.

2.4.3 Limitations and future directions

The exposure period used in this study was relatively brief and only resulted in a fairly modest reduction of the emotional response to threat at a group level (approximately 50% reduction of the initial effect of threat for most emotional and cognitive outcomes). Future work should use a longer exposure period, either within a single testing session or across multiple sessions, to determine if some components of the behavioural response to threat are still preserved following near complete adaptation of the emotional response.

While this study provides evidence that attenuating the emotional response to a perceived threat is accompanied by specific changes in standing balance control, these results are only generalizable to healthy young adults exposed to a height-induced threat. It is unclear if older adults or patient populations with a fear of falling would show a similar pattern of adaptation following repeated exposure to different scenarios they perceive as threatening to balance. This is an important avenue of future research in order to establish the clinical efficacy of repeated threat exposure as an intervention for individuals who regularly experience a fear of falling.

Lastly, while the regression coefficients (beta weights) for individual predictors entered into the multiple regression models are reported, interpretation of these results has been restrained. While independent variables were screened for extreme collinearity, there was still considerable shared variance amongst them. Mild collinearity can lead to substantial inaccuracies in estimated regression coefficients in modest predictive models ($R^2 > .5$) with small samples ($n < 100$; Mason and Perreault, 1991).To accurately parse the unique influence of individual emotional and cognitive factors to specific changes in balance control using a multiple regression approach, a much larger sample is needed (Mason and Perreault, 1991; Maxwell, 2000). Alternatively, future studies may seek to independently manipulate specific emotional and cognitive factors associated with threat to understand which are most important in shaping behaviour.

2.5 Conclusions

Individuals demonstrated modest reductions of their emotional response to threat following a relatively short period of blocked repeated threat exposure. However, threat-induced changes in standing balance control were largely preserved, with higher frequency COP oscillations and ankle muscle co-contraction representing the only behavioural outcomes to show any adaptation. Regression-based analyses demonstrated that these components of the behavioural response to threat are most closely linked with individuals' emotional response to threat. This suggests that not all threat-induced changes in standing balance control are related, or at least linearly related, to changes in emotional state, emphasizing the need to further explore the mechanisms underlying the relationship between postural threat and standing balance control. Results from this study are promising for the design of interventions for individuals who live with fear of falling (e.g., frail elderly and/or individuals with balance deficits) or work in environments that may induce fear of falling (e.g., construction workers), since attenuating individuals' emotional response to threat appears to have the greatest effect on the most maladaptive balance control changes, while preserving those that may be more protective in nature.

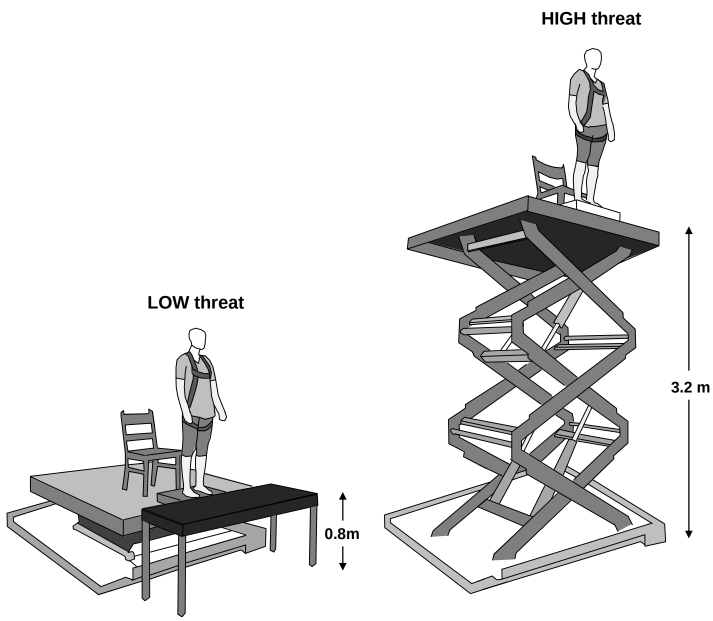

Figure 2-1: Schematic illustrating the LOW and HIGH postural threat conditions. At the LOW threat condition, participants stood at an elevation of 0.8 m. To minimize anxiety at this condition, an additional support (0.6 m × 1.52 m) surface was positioned in front of, and flush with, the platform edge, creating 60 cm of continuous support surface in front of the participant[16]. At the HIGH threat condition, participants stood at an elevation of 3.2 m and were positioned directly at the edge of the platform. At both threat conditions, participants wore a harness that was secured to the ceiling.

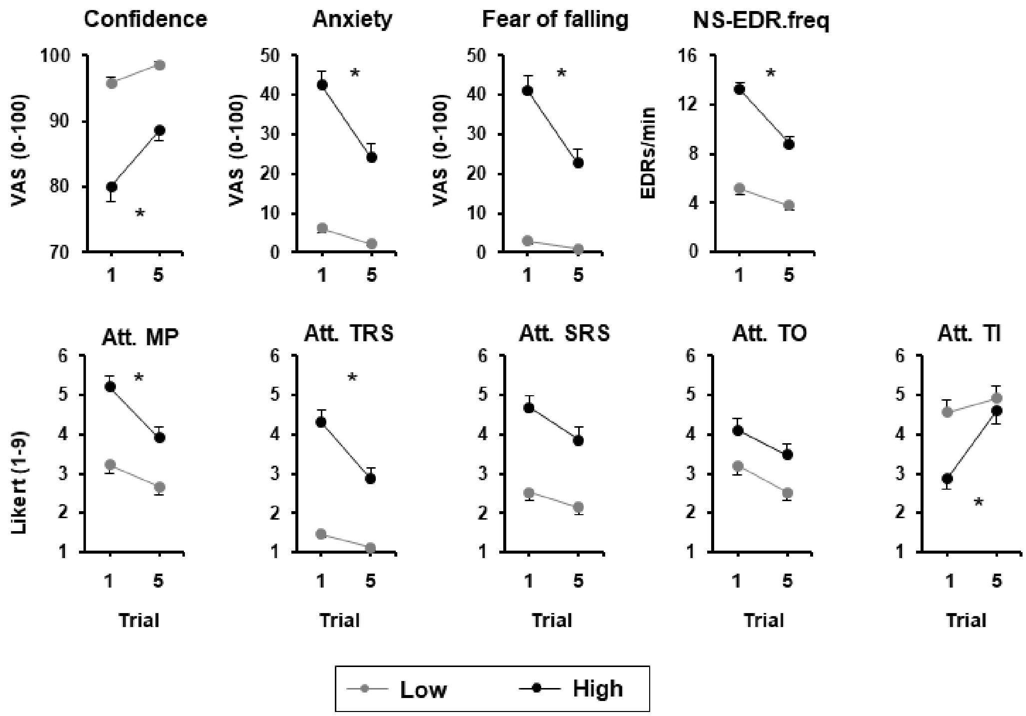

Figure 2-2: Effect of trial and threat across emotional and cognitive state measures. Group means and standard errors for the first and fifth trials across LOW and HIGH threat conditions are shown. NS-EDR.freq = non-specific electrodermal response frequency; Att. = attention toward; MP = movement processes; TRS = threat-related stimuli; SRS = self-regulatory strategies; TO = task objectives; TI = task irrelevant information. Asterisks indicate significant threat × trial interactions.

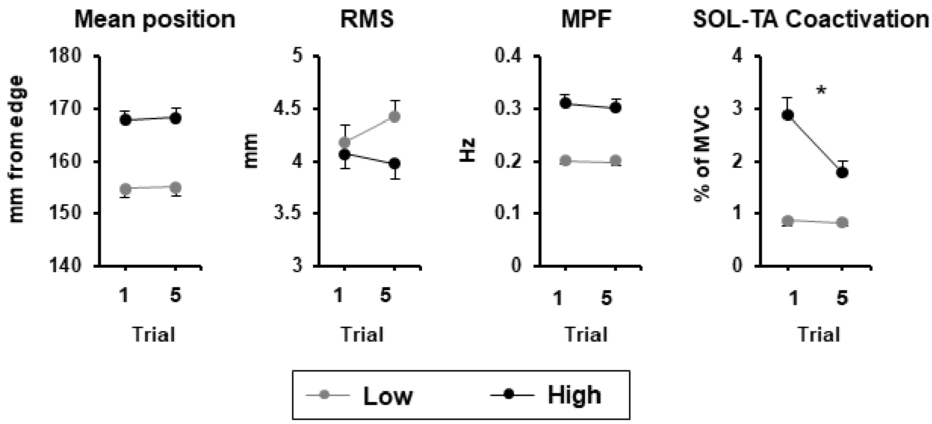

Figure 2-3: Effect of trial and threat across standing balance measures. Group means and standard errors standing balance measures for the first and fifth trials across LOW and HIGH threat conditions are shown. RMS = root mean square of centre of pressure; MPF = mean power frequency of centre of pressure; SOL = soleus; TA= tibialis anterior. Asterisks indicate significant threat × trial interactions.

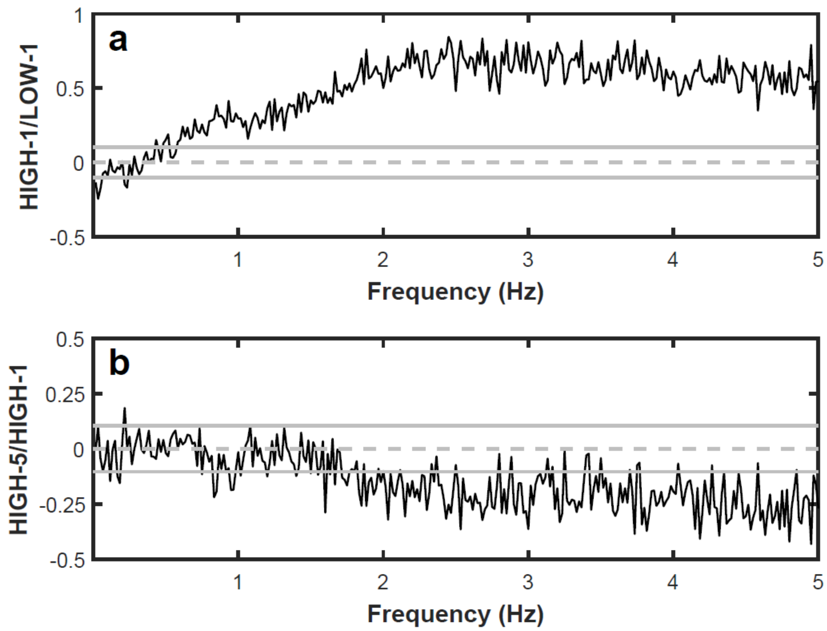

Figure 2-4: Centre of pressure comparison of spectra analyses illustrating the effects of initial and repeated threat exposure. Data shown reflect the log ratio of COP power spectral density between the first HIGH and LOW trial (a) and fifth and first HIGH trial (B) across frequencies (resolution 0.0167Hz). Horizontal grey lines reflect 95% confidence limits.

Table 2-1: Summary of statistical test results for 2×2 repeated-measures ANOVAs for emotional and cognitive state and behavioural measures

	Emotional and cognitive outcomes								
	Threat × Trial interaction			Threat			Trial		
	F	*p*	η^2	*F*	*p*	η^2	*F*	*p*	η^2
Balance confidence	**12.003**	**0.001**	**0.152**	**69.667**	**<0.001**	**0.510**	**24.290**	**<0.001**	**0.266**
Anxiety	**37.158**	**<0.001**	**0.357**	**96.322**	**<0.001**	**0.590**	**83.855**	**<0.001**	**0.556**
Fear of falling	**37.707**	**<0.001**	**0.360**	**88.014**	**<0.001**	**0.568**	**58.716**	**<0.001**	**0.467**
NS-EDR.freq	**34.637**	**<0.001**	**0.348**	**200.571**	**<0.001**	**0.755**	**144.814**	**<0.001**	**0.690**
Att. MP	**8.017**	**0.006**	**0.107**	**49.253**	**<0.001**	**0.424**	**35.348**	**<0.001**	**0.345**
Att. TRS	**26.517**	**<0.001**	**0.284**	**86.628**	**<0.001**	**0.564**	**57.938**	**<0.001**	**0.464**
Att. SRS	2.379	0.128	0.034	**62.825**	**<0.001**	**0.484**	**13.944**	**<0.001**	**0.172**
Att. TO	0.034	0.885	0.001	**23.985**	**<0.001**	**0.264**	**15.996**	**<0.001**	**0.193**
Att. TI	**21.858**	**<0.001**	**0.246**	**26.136**	**<0.001**	**0.281**	**37.242**	**<0.001**	**0.357**
	Behavioural outcomes								
MPOS	0.028	0.867	<0.001	**112.477**	**<0.001**	**0.627**	0.262	0.610	0.004
RMS	1.689	0.198	0.025	**7.433**	**0.008**	**0.100**	0.567	0.454	0.008
MPF	0.221	0.640	0.003	**64.226**	**<0.001**	**0.489**	0.321	0.573	0.005
SOL-TA CC	**23.328**	**<0.001**	**0.258**	**77.110**	**<0.001**	**0.535**	**17.716**	**<0.001**	**0.209**

Note. NS-EDR.freq = non-specific electrodermal response frequency; Att. = attention toward; MP = movement processes; TRS = threat-related stimuli; SRS = self-regulatory strategies; TO = task objectives; TI = task-irrelevant information; MPOS = mean position of centre of pressure; RMS = root mean square of centre of pressure; MPF = mean power frequency of centre of pressure; SOL-TA CC = soleus-tibialis anterior co-contraction. Significant effects are bolded.

Table 2-2: Multiple correlations (R^2) and standardized beta weights for regressions between changes in emotional and cognitive state measures and behavioural measures

	MPOS	RMS	MPF	LF power	MF power	HF power	SOL-TA CC
Initial threat							
Balance confidence	.070	.154	-.170	.146	-.015	-.102	-.228
NS-EDR.freq	.070	.045	.031	.038	.195	.100	.210
Att. MP	.074	.253	-.174	.253	.019	.097	.153
Att. TRS	.306	-.206	**.542*** **	-.223	.199	**.420** **	.138
Att. SRS	.035	.030	.134	.042	.108	.013	.119
Att. TO	.147	-.197	.105	-.171	.015	.031	-.071
Att. TI	.238	-.167	.039	-.084	-.042	-.011	-.191
Model R^2	*.196*	*.127*	***.456****	*.106*	*.184*	***.337***	***.354****
Model p-value	*0.067*	*0.313*	***<0.001***	*0.455*	*0.091*	***0.001***	***<0.001***
Repeated threat exposure							
Balance confidence	**-.315***	.047	-.198	.083	-.011	-.081	-.209
Anxiety	**-.437***	.045	.008	-.001	-.073	.038	-.011
NS-EDR.freq	.171	.038	-.049	.079	.149	-.014	.229
Att. MP	.241	**.406***	-.043	**.330***	**.356***	**.376***	.089
Att. TRS	.290	-.245	.345	-.162	-.085	.311	.120
Att. SRS	.051	-.150	.142	-.162	.139	-.099	.169
Att. TO	.137	-0.065	-.043	-.024	-.047	-.034	-.079
Att. TI	**.270***	-.130	.237	-.107	.204	.115	-.198
Model R^2	***.261****	*.157*	*.191*	*.113*	*.196*	***.268****	***.323*****
Model p-value	***0.020***	*0.248*	*0.123*	*0.515*	*0.109*	***0.017***	***0.003***

Note. Independent and dependent variables reflect change scores (Initial threat = HIGH1-LOW1; Repeated threat exposure = HIGH1-HIGH5). NS-EDR.freq = non-specific electrodermal response frequency; Att. = attention toward; MP = movement processes; TRS = threat-related stimuli; SRS = self-regulatory strategies; TO = task objectives; TI = task-irrelevant information; MPOS = mean position of centre of pressure; RMS = root mean square of centre of pressure; MPF = mean power frequency of centre of pressure; LF power = low frequency centre of pressure power; MF power = medium frequency centre of pressure power; HF power = high frequency centre of pressure power; SOL-TA CC = soleus-tibialis anterior co-contraction. *$p<0.05$; **$p<0.01$; ***$p<0.001$; significant β's and R^2's are bolded.

Table 2-3: Bivariate correlations between emotional and cognitive and behavioural outcomes when initially threatened and after repeated threat exposure

	MPOS	RMS	MPF	LF power	MF power	HF power	SOL-TA CC
Initial threat							
Confidence	-.085	.204	**-.374*** **	.200	-.111	**-.278***	**-.339****
Anxiety	**.291***	-.144	**.518*****	-.140	**.327****	**.418****	**.623*****
Fear	**.256***	-.094	**.571*****	-.094	**.388****	**.496****	**.555*****
EDR.freq	.236	-.101	**.386****	-.101	**.339****	**.322****	**.378****
Att. MP	.213	.140	.170	.129	.174	**.313****	**.317****
Att. TRS	**.382****	-.100	**.638*****	-.120	**.386****	**.572*****	**.488*****
Att. SRS	**.311****	.022	**.444****	.009	**.379****	**.397****	**.433*****
Att. TO	.078	-.103	.090	-.097	.037	.033	.024
Att. TI	.097	-.172	-.026	-.098	-.116	-.085	-.198
Repeated threat exposure							
Confidence	**-.239***	.038	-.153	.067	.031	-.037	-.162
Anxiety	.007	-.009	.161	-.013	.148	**.260***	**.299***
Fear	.040	-.020	**.269***	-.010	.225	**.323****	**.361****
EDR.freq	.189	-.009	.119	.020	.236	.132	**.374****
Att. MP	.220	**.254***	.007	.222	.220	**.322****	.209
Att. TRS	.131	-.083	**.242***	-.048	.065	**.301***	**.305***
Att. SRS	.114	-.014	.229	-.025	**.346****	**.273***	**.379****
Att. TO	.144	-.046	.027	.050	.108	.152	.063
Att. TI	.139	-.159	.101	-.138	.062	-.120	**-.282***

Note. Variables reflect change scores (Initial threat = HIGH1-LOW1; Repeated threat exposure = HIGH1-HIGH5). EDR.freq = non-specific electrodermal response frequency; Att. = attention toward; MP = movement processes; TRS = threat-related stimuli; SRS = self-regulatory strategies; TO = task objectives; TI = task-irrelevant information; MPOS = mean position of centre of pressure; RMS = root mean square of centre of pressure; MPF = mean power frequency of centre of pressure; LF power = low frequency centre of pressure power; MF power = medium frequency centre of pressure power; HF power = high frequency centre of pressure power; SOL-TA CC = soleus-tibialis anterior co-contraction. **p<0.05; **p<0.01;*** p<0.001*

Table 2-4: Bivariate correlations between ankle muscle co-contraction and COP outcomes

	Initial threat					
	MPOS	RMS	MPF	LF power	MF power	HF power
Initial threat	**.337****	.064	**.453*****	.026	**.511*****	**.531*****
Repeated threat exposure	**.344****	.014	**.346****	-.007	**.381****	**.459*****

Note. Variables reflect change scores (Initial threat = HIGH1-LOW1; Repeated threat exposure = HIGH1-HIGH5). COP = centre of pressure; MPOS = mean position of centre of pressure; RMS = root mean square of centre of pressure; MPF = mean power frequency of centre of pressure; LF power = low frequency centre of pressure power; MF power = medium frequency centre of pressure power; HF power = high frequency centre of pressure power. $^*p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$

Chapter 3: Study 2 - Selective preservation of changes to standing balance control despite psychological and autonomic habituation to a postural threat

3.1 Introduction

Fear of falling is prevalent amongst older adults (Legters, 2002) and individuals with movement disorders (Adkin et al. 2003; Schmid et al. 2015). Older adults with a self-reported fear of falling demonstrate differences in static (Maki et al. 1991) and dynamic (Okada et al. 2001; Uemura et al. 2012) balance control compared to individuals matched for age and level of physical function. These observations suggest that emotional factors have the potential to directly influence the control of balance, potentially contributing to the increased risk of falling documented amongst individuals living with a fear of falling (Friedman et al. 2002; Li et al. 2003). As a result, there is a clear need to understand the nature of fear-related balance changes and the potential for training to effectively impact these behaviours.

To examine how fear of falling influences balance control, different postural threat manipulations have been used. The underlying premise is that emotional and cognitive changes similar to those experienced on a daily basis by individuals living with a fear of falling can be induced by changing the perceived consequences or likelihood of falling (Brown and Frank, 1997; Adkin et al. 2000; Horslen et al. 2013). Commonly used threat manipulations have involved either raising the height of the surface on which individuals stand (height-induced threat) or having individuals stand at ground level with or without the expectation of a sudden, unpredictable balance perturbation (threat of perturbation) (Adkin and Carpenter, 2018). With both threat manipulations, individuals demonstrate hallmarks of increased sympathetic activation (i.e., increased tonic electrodermal activity) and self-report greater anxiety and changes in cognitive appraisals that would be expected in individuals experiencing a fear of falling (i.e., reductions in balance-specific efficacy and perceived ability to cope with the threat) [Horslen et al. 2013; Carpenter et al. 2006; Hauck et al. 2008). These changes in psychological and autonomic state are accompanied by changes in standing balance control that appear to be moderated by the context of the threat. With height-induced threat, individuals typically lean away from the platform edge and demonstrate higher frequency and smaller amplitude postural adjustments (Adkin and Carpenter, 2018). By contrast, with the threat of an unpredictable forward or backward perturbation, individuals lean forward and demonstrate higher frequency and larger amplitude postural adjustments (Shaw et al. 2012; Johnson et al. 2019a).

Recent work has shown that after being repeatedly exposed to height-induced threat (Zaback et al. 2019) or the threat of perturbation (Johnson et al. 2019b), individuals' emotional response to the threat was significantly attenuated, yet most changes in standing balance control were preserved. With repeated exposure to height, the only threat-induced changes in standing balance to show any attenuation included very high frequency centre of pressure (COP) oscillations (>1.8 Hz) and coactivation of plantar and dorsiflexor muscles (Zaback et al. 2019). By contrast, the posterior lean and reductions in the low-frequency COP oscillations (<0.05 Hz) and average amplitude of COP oscillations did not habituate. Similar changes in COP dynamics were observed following repeated exposure to the threat of perturbation, with habituation limited to relatively high frequency COP oscillations (0.5-1.8 Hz) and mean power frequency (MPF) of COP (Johnson et al. 2019b). It is unclear why this pattern of adaptation, or lack thereof, was observed. One possible explanation is that only some changes in standing balance control are related to the psychological and autonomic state changes induced by the threat. Unlike threat-induced changes in the average frequency content of COP oscillations, changes in leaning and

COP amplitude have shown inconsistent correlations with self-report and physiological indicators of individuals' emotional response to threat (Carpenter et al. 2006; Hauck et al. 2008; Davis et al. 2009; Huffman et al. 2009; Zaback et al. 2019) and exhibit different directions of change depending upon the type of threat experienced (height or perturbation threat) (Adkin and Carpenter, 2018). This could suggest that these changes in standing balance are employed in a context-dependent manner largely independent of individuals' psychological and autonomic response to the threat.

Alternatively, there may be a non-linear relationship between some threat-induced changes in standing balance control and the magnitude of individuals' emotional response to threat, such that complete, or near complete, attenuation of psychological and autonomic state changes induced by the threat are needed before specific standing balance adaptations begin to manifest. The aforementioned studies used relatively brief exposure periods, and self-reported and physiological measures of individuals' emotional response to threat in these samples seldom approached values comparable to non-threatening conditions (Zaback et al. 2019; Johnson et al. 2019b). Thus, it remains possible that some threat-induced changes in standing balance control may begin to show adaptation only following a longer period of exposure that more thoroughly attenuates the cognitive-emotional responses to the threat.

Therefore, the current study used an extended exposure protocol to determine if threat-induced changes in standing balance persist following complete or near-complete adaptation of individuals' psychological and autonomic response to a height-induced threat. To address this question, two separate sets of analyses were completed. The first set of analyses examined how threat-induced changes in standing balance adapt over the course of a long bout of repeated threat exposure across the sample as a whole. The second set of analyses focused exclusively on a subgroup of participants who demonstrated complete attenuation of their psychological and autonomic response to threat. It was expected that the majority of participants would show near complete adaptation of their psychological and autonomic response to threat and these changes would be accompanied by reductions in high-frequency COP oscillations and plantar/dorsiflexor coactivation (Zaback et al. 2019; Wuehr et al. 2019). On the basis that threat-induced changes in leaning and COP amplitude are context-dependent and adopted largely independent of individuals' psychological and autonomic response to threat, these were expected to show minimal change over the course of repeated threat exposure, even amongst individuals who showed complete adaptation of their psychological and autonomic response to threat.

A secondary aim of this study was to examine the extent to which standing balance adaptations acquired following repeated threat exposure are retained. Repeated exposure to activities perceived as threatening is an important component of cognitive-behavioural interventions designed to reduce fear of falling (Zijlstra et al. 2009; Dorresteijn et al. 2016). However, no studies to date have examined if any standing balance adaptations acquired during repeated threat exposure are retained when re-exposed to a similar threat. To address this question, participants from this study were re-exposed to the same height-induced postural threat 2-4 weeks after they completed the extended threat exposure protocol. Based on previous studies that have repeatedly exposed individuals to height-related situations, it was hypothesized that individuals' psychological and autonomic response to threat would be attenuated (relative to their initial exposure to threat) following a short retention period (Lang and Craske, 2000; Baker et al. 2010). This reduced emotional response to threat was expected to be accompanied by smaller threat-induced increases in high-frequency COP oscillations and plantar/dorsiflexor coactivation. Other threat-induced changes in standing balance which were not expected to show adaptation with repeated threat exposure (i.e., leaning and COP amplitude) were not expected to be any different between visits.

3.2 Methods

3.2.1 Participants

Thirty-seven healthy young adults (mean age ±SD = 23.4 ±4.4 years; 22 females) naïve to the postural threat manipulation participated in this study. Participants were free of musculoskeletal and neurological disorders that could impair their balance. No participants self-reported having an extreme fear of heights. All procedures were performed in accordance with relevant guidelines and regulations, and were reviewed and cleared by the University of British Columbia's Clinical Research Ethics Board. Participants provided written informed consent.

Prior to completing the experimental procedures, participants provided basic demographic information and completed a battery of personality questionnaires. This included the trait version of the State-Trait Anxiety Inventory (Spielberger et al. 1983) to assess trait anxiety, the Movement-Specific Reinvestment Scale (Masters et al. 2005) to assess individuals' propensity to reinvest attention in their movement, and the recreational subscale of the Domain Specific Risk-Taking Scale (Blais and Weber, 2006) to assess physical risk-taking. Participant demographic and personality trait information are provided in Table 1.

3.2.2 Procedures

Participants completed a series of 90-s quiet standing trials at two different postural threat conditions on two visits to the lab separated by approximately 2-4 weeks (mean retention period ±SD = 20.3 ±4.0 days). Throughout each trial, participants stood barefoot on a force plate (BP400600, AMTI, USA) positioned at the edge of a hydraulic lift (1.52 m × 2.13 m; Pentalift, Canada) with a stance width equal to the length of their foot and their toes were aligned to the anterior edge of the force plate. The borders of participants' feet were traced onto the force plate to ensure consistent foot placement across all trials within each session. At the LOW condition, the platform was positioned at its lowest height (0.8 m above ground) and a table (0.6 m × 1.6 m) was positioned in front of the platform, creating 60 cm of continuous support surface in front of the participant (Carpenter et al. 2001). For the HIGH condition, the table was removed, and the platform was elevated 3.2 m above the ground.

During their first visit (initial session), participants completed 2 quiet standing trials at the LOW condition before (LOW_{pre}) and after (LOW_{post}) a block of 20 trials at the HIGH condition. This blocked presentation order was selected to maximize within-session habituation of the psychological and autonomic response to threat (Rowe and Craske, 1998; Lang and Craske, 2000). Throughout all trials, participants were instructed to stand quietly with their arms at their sides and fixate on an eye-level visual target positioned 3.8 m in front of them. To minimize potential fatigue effects associated with the extensive number of standing trials, at least 2-minutes of seated rest were completed between all trials. Prior to the experimental trials, participants completed a 90-s practice trial at the LOW condition to minimize potential first trial effects (Adkin et al. 2000).

During their second visit (retention session), participants completed an abbreviated version of the initial session. In particular, they completed two standing trials at the LOW condition (LOW_{pre}) followed by 5 trials at the HIGH condition. Similar to the initial session, the standing trials were 90-s in length and at least 2-minutes of seated rest were completed between consecutive trials. Participants also completed a 90-s practice trial prior to the LOW_{pre} trials. No participants reported engaging in any height-related activities during the time between the two visits. Figure 1 provides a schematic illustration of experimental procedures across both visits.

Throughout all trials during both visits, participants wore a safety harness that was securely fastened by climbing rope to an overhead support beam. The tension of the rope was adjusted such that the harness did not provide support that would assist in the balance task, but would support the participant's body weight above the platform surface in the event of a fall. A trained spotter was also seated behind the participants to prevent a fall if the participant appeared unsteady. No falls occurred during this experiment and the spotter did not have to intervene to provide support at any point.

3.2.3 Data collection

Ground reaction forces and moments were sampled from the force plate at 100 Hz. Electromyography (EMG) was recorded bilaterally from the soleus (SOL) and tibialis anterior (TA) using Ag/AgCl surface electrodes positioned in a bipolar arrangement (interelectrode distance of ~1.25 cm). EMG data were sampled at 3000 Hz (Telemyo 2400R G2, Noraxon, USA), bandpass filtered online (10-1000 Hz), and then A-D sampled at 2000 Hz (Power1401, CED, UK). Skin conductance was recorded from Ag/AgCl surface electrodes placed on the thenar and hypothenar eminences of the non-dominant hand and sampled at 100 Hz (Model 2502SA, CED, UK).

Self-reports of emotional and cognitive state were probed at pre-defined trials throughout the experiment. During the initial session, this included all trials at the LOW condition and trials 1-5, 8, 11, 14, 17, and 20 at the HIGH condition. This order was selected since the greatest reduction in the emotional response to threat is likely to occur within the first five trials at the HIGH threat condition (Zaback et al. 2019). Self-reports were probed at all trials during the retention session (Figure 3-1). Before each of these trials, participants reported how confident they were that they could maintain their balance and avoid a fall during the upcoming balance task. After these trials, they completed single-item questions that assessed cognitive and somatic anxiety and fear of falling. Responses to each of these questions were completed on visual analog scales (VAS) ranging from 0 to 100. Higher scores reflected greater balance confidence, cognitive and somatic anxiety, and fear of falling. Scores on the measures of cognitive and somatic anxiety were averaged to create a state anxiety score (Zaback et al. 2019; Johnson et al. 2019b). Focus of attention was also assessed after these trials using a 5-item questionnaire that asked participants to rate how much they thought about or paid attention to different information. Single questions were used to probe attention toward 1) movement processes (i.e., conscious control or monitoring of movement); 2) threat-related stimuli (i.e., feelings of anxiety or worry); 3) self-regulatory strategies (i.e., coping strategies to help remain calm, confident, and/or focused); 4) task objectives (i.e., constraints of the task); and 5) task-irrelevant information (i.e., thoughts unrelated to the balance task). Responses were rated on 9-point Likert scales, with higher scores indicating greater attention to each loci of attention (Zaback et al. 2019; Johnson et al. 2019b). The items and terminology incorporated into this questionnaire were derived from qualitative research investigating changes in attention associated with height-induced threat (Zaback et al. 2016).

3.2.4 Data analysis

3.2.4.1 Centre of pressure (COP) outcomes

Ground reaction forces and moments were low-pass filtered offline (10 Hz cutoff, 2^{nd} order dual-pass Butterworth filter). From these data, only anterior-posterior COP was calculated since the effect of height-induced threat is greatest in this plane when facing the platform edge

(Adkin and Carpenter, 2018). From the COP data, the mean COP position (MPOS-COP) was calculated to provide a measure of how far individuals leaned away from the platform edge. The mean was then subtracted from the COP signal to remove the bias and a linear detrend was applied. From these data, root mean square (RMS-COP) and mean power frequency (MPF-COP) were calculated to provide estimates of the amplitude and average frequency content of COP oscillations, respectively. When individuals stand under conditions of height-induced threat, MPF-COP typically increases, and recent work has shown this is due to reductions in the amplitude of lower frequency COP oscillations (<0.05 Hz) and increases in the amplitude of higher frequency COP oscillations (>0.5 Hz) (Zaback et al. 2019). Furthermore, following a relatively short period of repeated threat exposure, only oscillations greater than 1.8 Hz show significant attenuation (Zaback et al. 2019). Thus, mean COP power was calculated within three frequency bands: 0-0.05 Hz (low), 0.5-1.8 Hz (medium), and 1.8-5.0 Hz (high) (Zaback et al. 2019; Johnson et al. 2019b).

3.2.4.2 Tonic muscle activity and coactivation

EMG data from bilateral SOL and TA were debiased, full-wave rectified, and normalized to mean rectified EMG during maximal voluntary contractions. From these data, tonic activation levels were calculated as mean rectified EMG (averaged between both legs). EMG data were then low-pass filtered (3 Hz cutoff, 5th order dual-pass Butterworth filter) creating linear envelopes. SOL-TA coactivation for each leg was then determined by calculating the absolute overlap of SOL and TA linear envelopes (Crenna et al. 1992; Frost et al. 1997). Coactivation estimates for both legs were then averaged for each participant.

3.2.4.3 Sympathetic arousal

To provide an estimate of sympathetic arousal, non-specific electrodermal response frequency (EDR.freq) was calculated from skin conductance data. Skin conductance data were first low-pass filtered (1 Hz cutoff, 5^{th} order dual-pass Butterworth filter) and then a customized algorithm identified and counted all electrodermal responses with peak amplitudes greater than 0.05 μS (Boucsein et al. 2012). All identified EDRs were visually inspected and any false positive due to movement artifacts were rejected (Boucsein, 2012).

3.2.4.4 Identification of "Adaptors"

Participants' whose emotional response to threat returned to LOW threat values during the first visit were identified as "Adaptors". To be considered an Adaptor, the following criteria needed to be met. First, participants needed to have a self-reported increase of at least 5 points on the fear of falling VAS during the first HIGH trial relative to the mean of the first two LOW trials. Participants then needed measures of self-reported fear of falling and EDR.freq to return to LOW threat values. A threshold for what would be considered LOW threat values for each participant was calculated as the mean +1SD for each of these measures based on the first two LOW trials. The HIGH trial at which point both fear of falling and EDR measures returned to a value equal to or less than the LOW threshold was noted and all psychological, autonomic, and standing balance outcomes for this trial and the subsequent HIGH trial were calculated and averaged ($HIGH_{adapted}$). The only exception to this was if these criteria were met only by the time of the final HIGH trial, in which case there would be no subsequent HIGH trial, so only data from $HIGH_{20}$ were used (n=1). These trials (i.e., $HIGH_{adapted}$) were included in the statistical procedures as opposed to the last two HIGH trials (i.e., $HIGH_{19 \text{ and } 20}$) in order to minimize possible fatigue or boredom effects which may manifest with continued exposure after the point of complete adaptation.

3.2.5 Statistics

3.2.5.1 Within-session adaptation

To examine how measures of psychological and autonomic state and standing balance adapt over the course of repeated threat exposure, a series of two-way (Threat: LOW vs HIGH; Trial: Pre vs Post) repeated measures ANOVAs were conducted. For the factor Trial, data were averaged across the first two (LOW_{pre}) and last two (LOW_{post}) LOW trials for the Pre and Post levels of the LOW condition, while the first ($HIGH_1$) and last ($HIGH_{20}$) HIGH trials were used for the Pre and Post levels of the HIGH condition, respectively. Significant threat × trial interactions were followed-up with Bonferroni corrected paired-samples t-tests that examined the effect of threat across both levels of trial and the effect of trial across both levels of threat (alpha = 0.0125).

A separate set of statistics were conducted for individuals identified as Adaptors in order to determine if threat-induced changes in standing balance control are preserved in individuals whose emotional response to threat returned fully to LOW threat values. Dependent measures for the following trials were included in one-way repeated measures ANOVAs: LOW_{pre} (average of the first two LOW trials), $HIGH_{pre}$ (average of first two HIGH trials), and $HIGH_{adapted}$. The reason blocks of two trials were averaged was to reduce variability of the standing balance measures, since fewer participants were expected to be included in these analyses. Significant main effects were followed up with Bonferroni corrected paired-samples t-tests comparing $HIGH_{pre}$ and $HIGH_{adapted}$ with LOW_{pre} (alpha = 0.025).

3.2.5.2 Retention of adaptations

To determine if any adaptations were retained between visits, two-way (Visit: 1 vs 2; Trial: $HIGH_1$ vs $HIGH_5$) repeated measures ANOVAs were conducted for measures of psychological and autonomic state and standing balance control for all participants. For the factor Trial, dependent measures at $HIGH_1$ and $HIGH_5$ were expressed as change scores relative to LOW_{pre} data from respective visits (Δ $HIGH_1 = HIGH_1 – LOW_{pre}$; Δ $HIGH_5 = HIGH_5 – LOW_{pre}$). Significant interactions were followed up with Bonferroni corrected paired-samples t-tests examining the effect of trial across both levels of visit and the effect of visit across both levels of trial (alpha = 0.0125).

3.3 Results

Two participants (1 female) reported increases in fear of falling from the first to last HIGH trial during the initial session. Because the primary aim of this study was to determine if threat-induced changes in standing balance persist after *attenuation* of the emotional response to threat, these participants were excluded from statistical analyses. Due to technical issues, EMG data were missing for one participant and skin conductance data were missing for another. Several dependent measures were positively skewed; this included low-, medium-, and high-frequency COP power, tonic TA activation, and SOL-TA coactivation. To correct for this non-normality, log transformations were applied to these data.

3.3.1 Visit 1 within-session adaptation: psychological and autonomic outcomes

Significant threat × trial interactions were observed for all psychological and autonomic state measures except for attention toward task objectives (p-values $\leq$0.017; Table 3-2). Follow-up comparisons (summarized in Table 3-3) revealed that when individuals were initially exposed to the threat, they were less confident and more anxious, fearful, and physiologically aroused. Participants also directed more attention toward their movement, threat-related stimuli, and self-regulatory strategies, and less attention toward task-irrelevant information when initially exposed to the threat. For each of the aforementioned outcomes, the effect of threat was significantly reduced after repeated threat exposure. In all cases, the reduced effect of threat resulted from each psychological and autonomic state measure showing a rapid, non-linear attenuation across the block of HIGH trials (Figure 3-2). While the effect of threat was substantially reduced, all outcomes, except attention toward task-irrelevant information, remained significantly different from LOW_{post} values (Table 3-3). For attention toward task objectives (which did not show a significant threat × trial interaction), there were significant main effects of threat and trial, such that individuals directed more attention toward task objectives in the HIGH condition independent of trial, but less attention toward this information across both threat conditions over time (Figure 3-2; Table 3-2). Collectively, this pattern of results indicates that repeated exposure to the HIGH condition resulted in substantial within-session habituation of individuals' psychological and autonomic response to threat.

3.3.2 Visit 1 within-session adaptation: standing balance outcomes

Significant threat × trial interactions were observed for MPF-COP, medium- (0.5-1.8 Hz) and high- (1.8-5 Hz) frequency COP power, tonic TA activation, and SOL-TA coactivation (p-value range: 0.025 – 0.001; Table 3-2). Follow-up comparisons (summarized in Table 3-3) revealed that when individuals were initially exposed to the threat, they demonstrated greater MPF-COP, medium- and high-frequency COP power, tonic TA activation, and SOL-TA coactivation. By the last HIGH trial, the effect of threat was attenuated for each of these outcomes but remained significantly different from LOW_{post} values. The reduced effect of threat resulted from significant reductions in each standing balance outcome occurring across only the HIGH condition (Table 3-3). Similar to the psychological and autonomic state measures, these standing balance outcomes demonstrated rapid, non-linear attenuation over the course of repeated threat exposure (Figure 3-3).

Significant threat × trial interactions were also observed for RMS-COP and tonic SOL activation (p-values ≤0.020; Table 3-2). Unlike the aforementioned standing balance outcomes, follow-up comparisons revealed that these interactions resulted from the effect of threat only becoming significant after the initial exposure to height (Table 3-3; Figure 3-3; Figure 3-4). When individuals were first exposed to the threat, RMS-COP and tonic SOL activation did not differ from LOW_{pre} values (p-values: 0.191 and 0.441, respectively). However, by the last HIGH trial both outcomes were significantly lower compared to LOW_{post} (p-values <0.001). For tonic SOL activation, this was the result of significant decreases in SOL activation occurring from the first to last HIGH trial, while for RMS-COP, this was the result of non-significant increases from the first to last LOW trials and non-significant decreases from the first to last HIGH trial (Table 3-3). This pattern of results indicates that the effect of threat for each of these outcomes does not diminish over the course of repeated threat exposure, but instead becomes more pronounced.

For MPOS-COP and low-frequency COP power (0-0.05 Hz), there were no significant threat × trial interactions. However, there were significant main effects of threat for each of these outcomes (p-values <0.001), such that individuals reduced the power of low-frequency COP oscillations and leaned away from the platform edge at the HIGH compared to LOW condition independent of trial. There was also a significant main effect of trial for MPOS-COP (p=0.008), such that individuals leaned forward as a function of time independent of threat condition (Table 3-2; Figure 3-3). Collectively, this indicates that the effect of threat for these outcomes does not diminish over the course of repeated threat exposure despite substantial reductions in the psychological and autonomic response to threat.

3.3.3 Visit 1 within-session adaptation for the "Adaptor" subgroup: psychological and autonomic outcomes

Fifteen participants (demographics summarized in Table 3-1) met the criteria to be identified as "Adaptors" (median trial at which point criteria to be fully adapted were met = $HIGH_8$; range: $HIGH_3$ – $HIGH_{20}$).

One-way repeated measures ANOVAs were significant for all psychological and autonomic outcomes (p-value range: 0.041 - <0.001; Table 3-4). Follow-up planned comparisons demonstrated a significant effect of threat when individuals were first exposed to the HIGH condition ($HIGH_{initial}$ vs LOW_{pre}) for all outcomes except for attention toward task objectives and task-irrelevant information. In particular, when initially exposed to threat, the "Adaptors" were less confident and more anxious, fearful, and physiologically aroused. In addition, these participants directed more attention toward movement processes, threat-related stimuli, and self-regulatory strategies. However, by the trial at which point they met the criteria for complete adaptation, the effect of threat for each of these outcomes was no longer significant ($HIGH_{adapted}$ vs LOW_{pre}) (p-value range: 1.00 - 0.094; Figure 3-5).

3.3.4 Visit 1 within-session adaptation for the "Adaptor" subgroup – standing balance outcomes

Significant one-way repeated measures ANOVAs were observed for MPOS-COP, MPF-COP, medium- and high-frequency COP power, tonic TA activation, and SOL-TA coactivation (p-value range: 0.008 - <0.001; Table 3-5). For each of these outcomes, follow-up planned comparisons demonstrated a significant effect of threat when individuals were first exposed to the HIGH condition. For medium- and high-frequency COP power, tonic TA activation, and SOL-TA coactivation, the effect of threat was no longer significant once participants demonstrated complete adaptation of their psychological and autonomic response to threat (p-value range: 0.751 - 0.279; Figure 3-5). However, the effect of threat remained significant for MPOS-COP (p<0.001) and MPF-COP (p=0.017). One-way repeated measures ANOVAs did not reach significance for RMS-COP (p=0.084), low-frequency COP power (p=0.183), and tonic SOL activation (p=0.07).

3.3.5 Visit 1 and 2 between-session comparisons: psychological and autonomic outcomes

Two participants did not return for visit 2, reducing the sample of participants to 33 for these analyses.

No significant visit × trial interactions were observed for any psychological and autonomic state outcomes. However, significant main effects of trial were observed for all psychological and autonomic outcomes (all p-values <0.001; Table 3-5) such that individuals' emotional response to threat was attenuated from $HIGH_1$ to $HIGH_5$ independent of the visit (Figure 3-6; Table 3-5). Significant main effects of visit were observed for most self-report outcomes. In particular, the changes observed between HIGH and LOW threat were smaller on the retention compared to initial session for confidence, anxiety, fear of falling, and attention toward movement and threat-related stimuli. No main effect of visit was observed for EDR.freq (p=0.072) and attention toward self-regulatory strategies (p=0.404), task objectives (p=0.386), and task-irrelevant information (p=0.146) (Table 3-5).

3.3.6 Visit 1 and 2 between-session comparisons: standing balance outcomes

Significant visit × trial interactions were observed for MPOS-COP and tonic SOL activation. For MPOS-COP, this interaction resulted from individuals leaning non-significantly further backward from the $HIGH_1$ to $HIGH_5$ during the initial session (p=0.210) and non-significantly further forward during the retention session (p=0.021; Figure 3-6). For tonic SOL activation, the interaction resulted from SOL activity showing further decreases from $HIGH_1$ to $HIGH_5$ during the initial session (p=0.001), but not changing across these same trials during the retention session (p=0.513; Figure 3-6). Of the remaining variables, significant main effects of trial were observed for MPF-COP, medium- and high-frequency COP power, tonic TA activation, and SOL-TA co-activation. In all cases, threat-induced changes in these standing balance outcomes were attenuated from $HIGH_1$ to $HIGH_5$ independent of visit (p-value range: 0.011 - <0.001; Table 3-5). A significant main effect of visit was only observed for high-frequency COP power, with individuals demonstrating smaller threat-induced increases in high-frequency COP power during the retention session (p=0.008; Table 3-5). No significant interactions or main effects were observed for RMS-COP or low-frequency COP power (Table 3-5).

3.4 Discussion

The primary aim of this study was to determine if threat-induced changes in standing balance persist following near complete attenuation of individuals' psychological and autonomic response to a height-induced threat. Consistent with previous work, when individuals were initially exposed to the threat, they leaned significantly away from the platform edge, significantly increased MPF-COP and plantar/dorsiflexor coactivation, and tended to decrease RMS-COP (Adkin and Carpenter, 2018). Changes in MPF-COP were the result of significant reductions in low-frequency COP power (<0.05 Hz) and increases in higher-frequency COP power (>0.5 Hz). With repeated threat exposure, individuals demonstrated a rapid and substantial attenuation of their psychological and autonomic response to the threat. However, only some threat-induced changes in standing balance tended to follow a similar pattern of adaptation. In particular, MPF-COP, higher-frequency COP power (>0.5 Hz), and plantar/dorsiflexor coactivation were significantly reduced over the course of repeated threat exposure. Other threat-induced changes in standing balance, including the posterior lean and decreased amplitude of COP displacements and low-frequency COP power, did not change over the course of repeated threat exposure. This same pattern of adaptation was still observed in a subgroup of participants whose psychological and autonomic response to threat returned to LOW threat values. These observations suggest that while some threat-induced changes in standing balance vary closely with individuals' psychological and autonomic response to threat, other balance changes may be employed in a given threat context independent of psychological and autonomic state.

A secondary aim of this study was to determine if standing balance adaptations are retained across repeated visits. Consistent with our hypotheses, individuals self-reported a reduced psychological response to threat upon re-exposure following a 2-4-week retention period. However, individuals' autonomic response to threat, as measured by the frequency of non-specific electrodermal responses, did not differ significantly across visits. Furthermore, few standing balance outcomes showed retention, with only high-frequency COP oscillations (>1.8 Hz) demonstrating a reduced effect of threat at the time of the retention session. These results suggest that some standing balance adaptations acquired during a single block of repeated threat exposure can be retained, but retention of additional balance adaptations may require that the psychological, along with the autonomic response to threat, are minimized upon re-exposure.

3.4.1 Standing balance outcomes prone to adaptation following repeated threat exposure

Previous studies have shown that threat-induced changes in MPF-COP, high-frequency COP oscillations, and plantar/dorsiflexor coactivation are highly correlated with individuals' psychological and autonomic response to threat (Zaback et al. 2019; Wuehr et al. 2019). Thus, it is not surprising that these changes in standing balance control appeared to change in parallel with measures of psychological and autonomic state over the course of repeated threat exposure and even returned to LOW threat values in the Adaptor subgroup. Collectively, this further supports the notion that these particular changes in standing balance are heavily dependent on individuals' psychological and autonomic response to threat.

It is unclear if these particular threat-induced changes in standing balance serve a functional role when individuals are confronted with a threat to balance. Plantar/dorsiflexor coactivation increases ankle joint stiffness during standing, but there is little evidence this provides additional stability (Latash, 2018; Yamagata et al. 2019). Rather, plantar/dorsiflexor coactivation is an energetically costly compensatory strategy (Peterson and Martin, 2010) that may interfere with voluntary and reactive postural control (Nagai et al. 2013; 2017). Some have suggested that increased ankle stiffness may improve postural recovery following perturbations, but only if accompanied by reductions in sensorimotor gain (Le Mouel and Brette, 2019). Moreover, some perturbations, such as support surface rotations, are more destabilizing as ankle stiffness and stretch sensitivity increase (Carpenter et al. 1999b; Allum et al. 2002). Since postural threat has been shown to facilitate muscle afferent (Davis et al. 2011; Horslen et al. 2013; 2018) and vestibular reflexes (Horslen et al. 2014; Naranjo et al. 2015), such changes in coactivation may be maladaptive in this context. High-frequency COP oscillations may also serve a limited functional role, since COP movement greater than 2 Hz has a negligible influence on the control of sway during standing due to the body's large moment of inertia (Gage et al. 2004). If anything, these unnecessary movements may interfere with or mask balance-relevant somatosensory inputs (Collins et al. 1997; Mildren and Bent, 2016). Thus, it would appear favourable that these particular components of the behavioural response to threat are most prone to rapid habituation with repeated threat exposure.

3.4.2 Context-dependent standing balance changes

Previous studies have shown that when individuals are repeatedly exposed to height or the threat of an impending perturbation, some threat-induced changes in standing balance control are largely invariant (Zaback et al. 2019; Johnson et al. 2019b). This has been taken to suggest that some components of the behavioural response to threat may be adopted irrespective of psychological and autonomic state changes. The present study supports this supposition and casts doubt on the possibility that the lack of standing balance adaptations seen in previous studies were the result of insufficient habituation (Zaback et al. 2019; Johnson et al. 2019b). This is because threat-induced changes in COP mean position and low-frequency power still showed little sign of attenuation, even in the Adaptor subgroup. Furthermore, threat-induced reductions in RMS-COP and tonic SOL activation tended to become greater over the course of repeated threat-exposure.

While these standing balance outcomes do not appear to be strongly influenced by individuals' psychological and autonomic response to threat, previous studies suggest they are heavily dependent on the nature of the postural threat. Both the threat of height and impending perturbation elicit similar changes in psychological and autonomic state (Horslen et al. 2013). However, when standing with the expectation of an unpredictable forward or backward perturbation, individuals shift their weight forward and increase the amplitude postural sway

(Maki and Whitelaw, 1993; Shaw et al. 2012; Johnson et al. 2019a). This is opposite to what is observed with a height-induced threat, where individuals tend to lean away from the edge of the platform and restrict postural sway (Adkin and Carpenter, 2018). In both instances, these standing balance changes appear appropriate given the nature of the threat. Leaning backward and limiting postural sway reduces the likelihood of a fall over the platform edge when standing at height, while leaning forward and increasing postural sway may facilitate compensatory stepping and postural recovery when standing on the ground and responding to a perturbation (Maki and Whitelaw, 1993; Rajachandrakumar et al. 2018). Thus, these components of the behavioural response to threat appear to reflect context-appropriate adaptations to minimize the likelihood of a fall or injury in the face of unique postural challenges.

3.4.3 Retention of psychological, autonomic, and standing balance outcomes

When participants were re-exposed to the height-induced threat 2-4 weeks after their initial block of exposure, they demonstrated within-session adaptations similar to what was seen during their initial session. In particular, their self-reported and autonomic response to threat decreased over time, and this was accompanied by similar reductions in MPF-COP, higher-frequency COP power (>0.5 Hz), and plantar/dorsiflexor coactivation. One exception was mean position of COP, as individuals showed a tendency to lean slightly forward over the course of the abbreviated exposure period during the retention session only.

One of the most striking findings was that few of the standing balance adaptations acquired during the initial visit were retained, with only high-frequency COP oscillations (>1.8 Hz) showing a smaller effect of threat at follow-up. This was likely a consequence of only modestly retained reductions in the psychological and autonomic response to threat. While individuals did report greater confidence and less fear, anxiety, and attention toward their movement when they were re-exposed to the threat after 2-4 weeks, their autonomic response, as measured by the frequency of non-specific electrodermal responses, was not significantly reduced. Spontaneous recovery of a previously habituated emotional response is commonly observed following exposure therapy (Rachman, 1989), and the exposure protocol used in the present study was not well-suited to minimize this (Craske et al. 2008; 2014).

The present study used a massed and constant exposure protocol. This form of exposure was selected in order to maximize within-session habituation of the psychological and autonomic response to threat (Rowe and Craske, 1998; Lang and Craske, 2000). This was crucial to address the primary goal of this study, which was to determine if threat-induced changes in standing balance persist after near complete attenuation of the psychological and autonomic response to threat. Although effective in this regard, this form of exposure does not promote the encoding, consolidation, and retrieval processes thought to be critical for long-term fear reduction (Lang et al. 1999; Craske et al. 2008; 2014). Furthermore, the exposure protocol was entirely unguided. That is, participants were not instructed to avoid using coping strategies, such as distraction or cognitive avoidance, which can facilitate within-session habituation, but limit long-term fear reduction (Foa et al. 2006; Craske et al. 2014). Exposure protocols which explicitly limit the use of such strategies and vary the conditions of the exposure in terms of timing, intensity, and/or the context of threat presentations are more effective in minimizing individuals' emotional response to a similar threat on subsequent exposures (Rowe and Craske, 1998; Tsao and Craske, 2000; Foa et al. 2006; Craske et al. 2008; 2014). However, these types of exposure protocols were considered undesirable for the present study since they tend to result in sustained within-session anxiety and arousal (Craske et al. 2008; 2014). Nevertheless, given that the standing balance adaptations acquired over the course of repeated threat exposure generally appear beneficial to the control of balance, future work should determine if improved retention can be obtained using different exposure protocols.

3.4.4 Limitations, implications, and future directions

A strength of this study was that the extended threat exposure protocol was sufficient to completely diminish the psychological and autonomic response to threat to LOW values in a subgroup of participants during the initial session. However, since only 15 participants met the criteria to be included in this subgroup, results related to these analyses are underpowered and should be interpreted with caution. Multiple factors may have contributed to between-subjects variability in habituation to the height-induced threat. Personality traits that have been shown to predict individuals' response to height-induced postural threat (Zaback et al. 2015) were recorded and did not differ between Adaptors and Non-adaptors (Table 1). However, it is unclear how other personality traits or previous experiences with height-related activities may have influenced habituation in this context. The results of this study are also only generalizable to healthy young adults. Previous work has shown that young and older adults show a similar pattern of psychological, autonomic, and standing balance adaptations when repeatedly exposed to the threat of perturbation (Johnson et al. 2019b). However, it is not clear if this is the case for different types of postural threat or with different clinical populations (e.g., Parkinson's disease, stroke survivors, etc.). We believe it is important to first investigate the underlying mechanisms of emotional influences on balance in healthy individuals unbiased from any underlying fear or anxiety issues known to accompany balance disorders due to age or disease (Legters, 2002; Adkin et al. 2003; Schmid et al. 2015). However, given the therapeutic potential of repeated threat exposure for minimizing fear of falling and fall risk in different clinical populations, future work is needed to determine if similar psychological, autonomic, and standing balance adaptations are observed in different clinical populations in response to unique threat scenarios.

This study also demonstrated that the emotional response to threat decreased rapidly with repeated exposure, such that the effect of threat for most psychological and autonomic outcomes was reduced by more than 50% within as few as five 90-s standing trials. Studies using postural threat manipulations need to take this rapid habituation into account, particularly if multiple conditions or trials need to be completed under a HIGH threat scenario. Since changes in the autonomic and behavioural response to threat are poorly retained across visits, studies requiring participants to be highly fearful or aroused across multiple threat conditions could be advised to complete their experiment over separate days to minimize confounds related to habituation.

3.5 Conclusions

This study demonstrates that while some threat-induced changes in standing balance are heavily dependent on individuals' psychological and autonomic response to threat, and are therefore amendable to intervention, others are more resistant to change and appear to be employed in a primarily context-dependent manner. While the changes to standing balance observed following a single block of repeated threat exposure appear functional to the control of balance, they are not readily retained after 2-4 weeks without exposure. This is likely a consequence of inadequate emotional learning inherent to the massed and constant exposure protocol used in the present study. However, given the potential for exposure interventions to minimize potentially maladaptive changes in balance, it is incumbent upon future work to determine how to most effectively structure exposure exercises to maximize long-term fear reductions and associated balance changes. Such interventions may have the potential to reduce fall-risk amongst individuals living and/or working with a fear of falling.

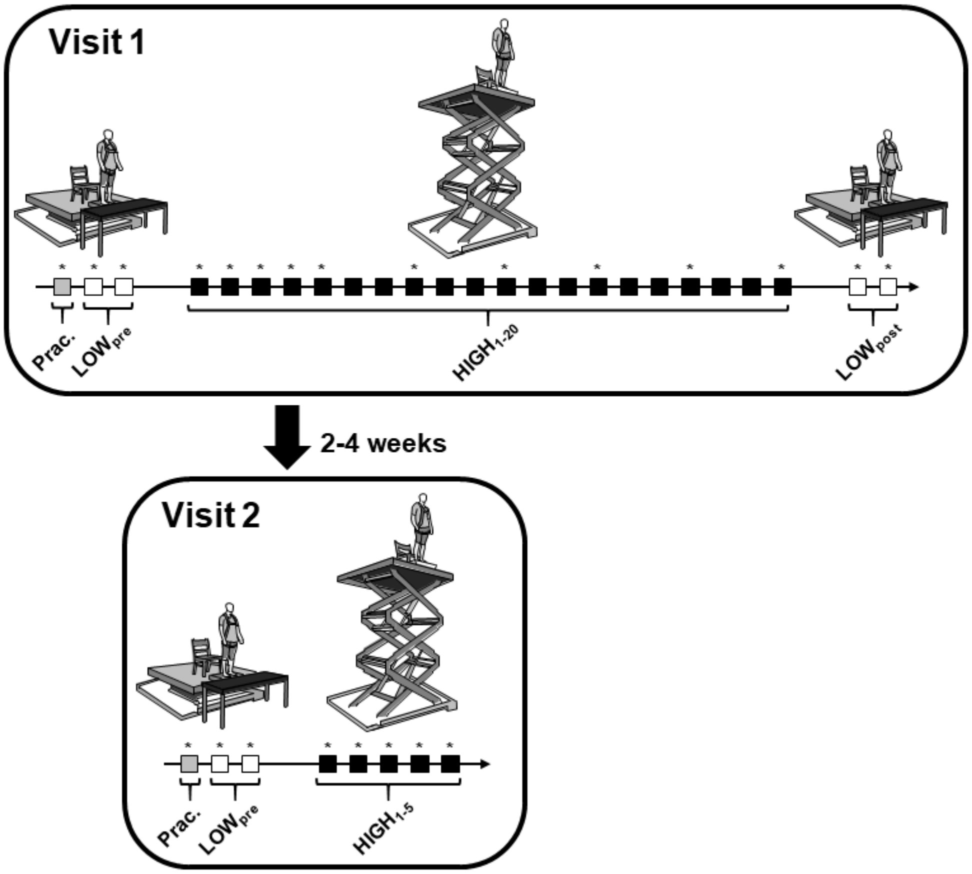

Figure 3-1: Flow chart outlining the experimental protocol. Participants completed a series of 90-s trials of quiet standing at LOW (0.8m above ground, away from edge) and HIGH (3.2m above ground, at edge) threat conditions on two visits to the lab separated by 2-4 weeks. Each square represents a single 90-s trial; open squares (□) represent trials completed at the LOW condition, while filled black squares (■) represent trials completed at the HIGH condition. During both visits, participants first completed a single 90-s practice trial (■) at the LOW condition. Trials in which questionnaires were administered to assess cognitive and emotional state are indicated with an asterisk.

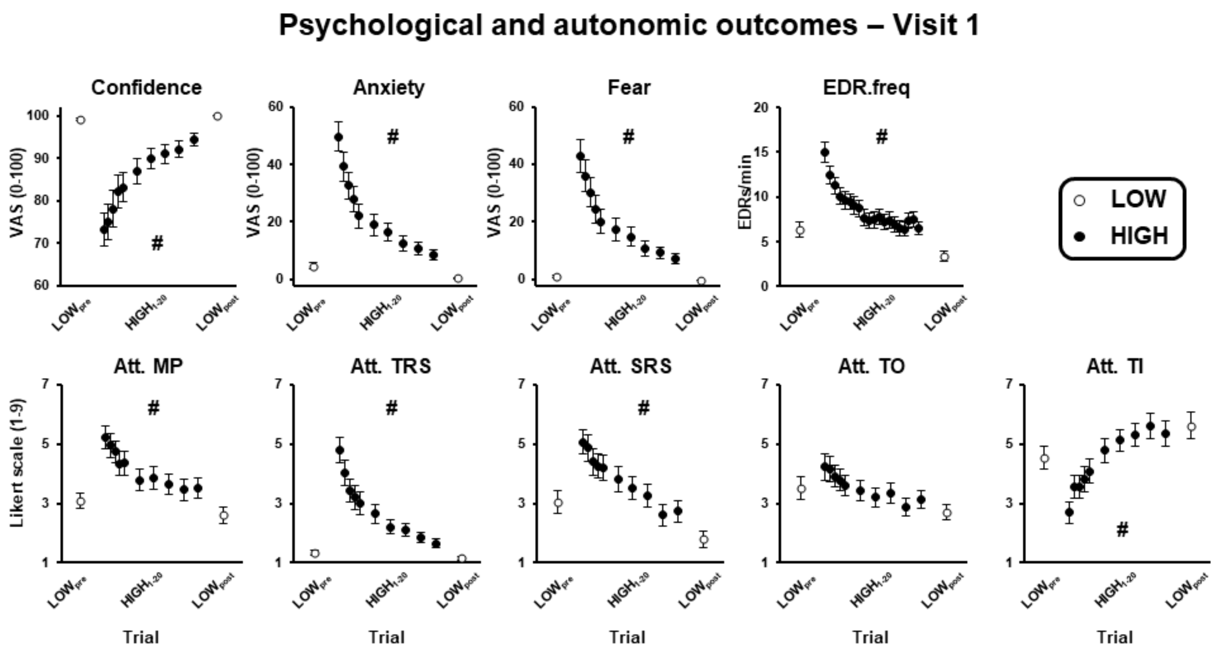

Figure 3-2: Effect of threat and trial on psychological and autonomic outcomes. Data presented reflect group means and standard errors. The first two and last two LOW trials have been averaged (LOW_{pre} and LOW_{post}, respectively) and are represented as open circles, while data across HIGH trials 1-20 are represented as filled black circles. Att. = attention toward; EDR.freq = non-specific electrodermal response frequency; MP = movement process; SRS = self-regulatory strategies; TI = task-irrelevant information; TO = task objectives; TRS = Threat-related stimuli; VAS = visual analog scale. Hashtags indicate significant threat × trial interactions resulting from a reduced effect of threat as a function of repeated exposure.

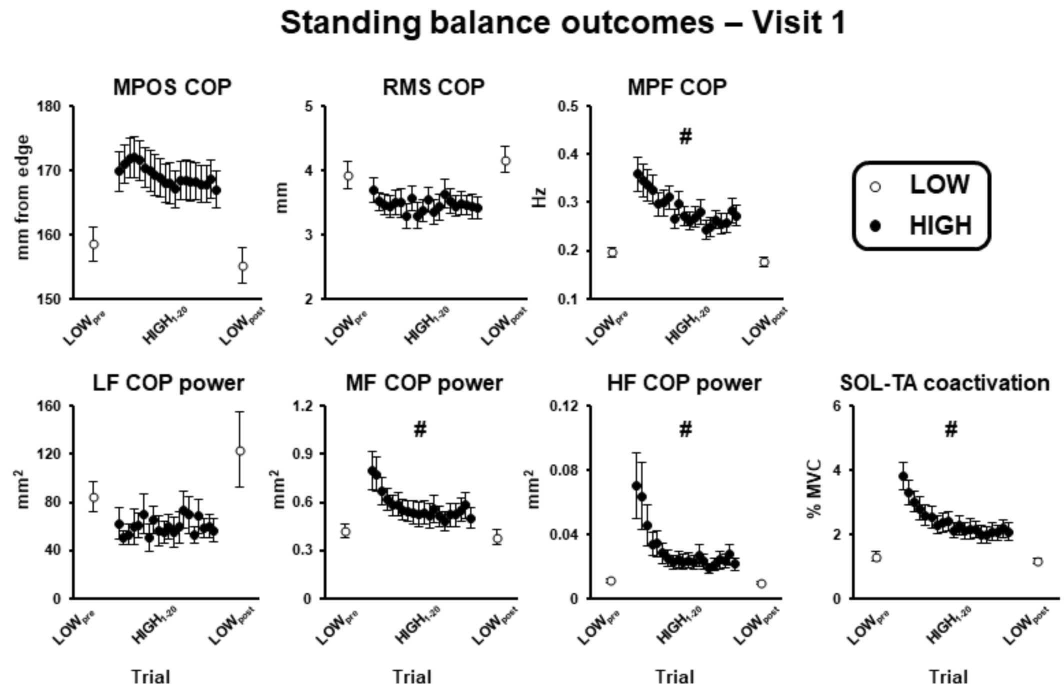

Figure 3-3: Effect of threat and trial on standing balance outcomes. Data presented reflect group means and standard errors. The first two and last two LOW trials have been averaged (LOW_{pre} and LOW_{post}, respectively) and are represented as open circles, while data across HIGH trials 1-20 are represented as filled black circles. COP = centre of pressure; HF = high frequency (1.8-5 Hz); LF = low frequency (0-0.05 Hz); MF = medium frequency (0.5-1.8 Hz); MPF = mean power frequency; MPOS = mean position; RMS = root mean square; SOL-TA = soleus-tibialis anterior. Hashtags indicate significant threat × trial interactions resulting from a reduced effect of threat as a function of repeated exposure.

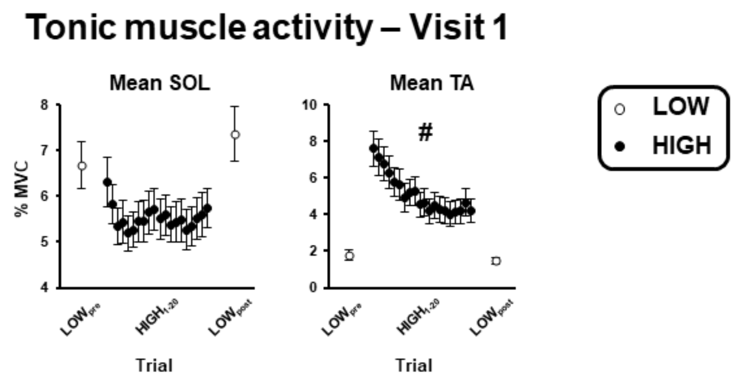

Figure 3-4: Effect of threat and trial on tonic activation of soleus (SOL) and tibialis anterior (TA) muscles. Data presented reflect group means and standard errors. The first two and last two LOW trials have been averaged (LOW_{pre} and LOW_{post}, respectively) and are represented as open circles, while data across HIGH trials 1-20 are represented as filled black circles. Hashtags indicate significant threat × trial interactions resulting from a reduced effect of threat as a function of repeated exposure.

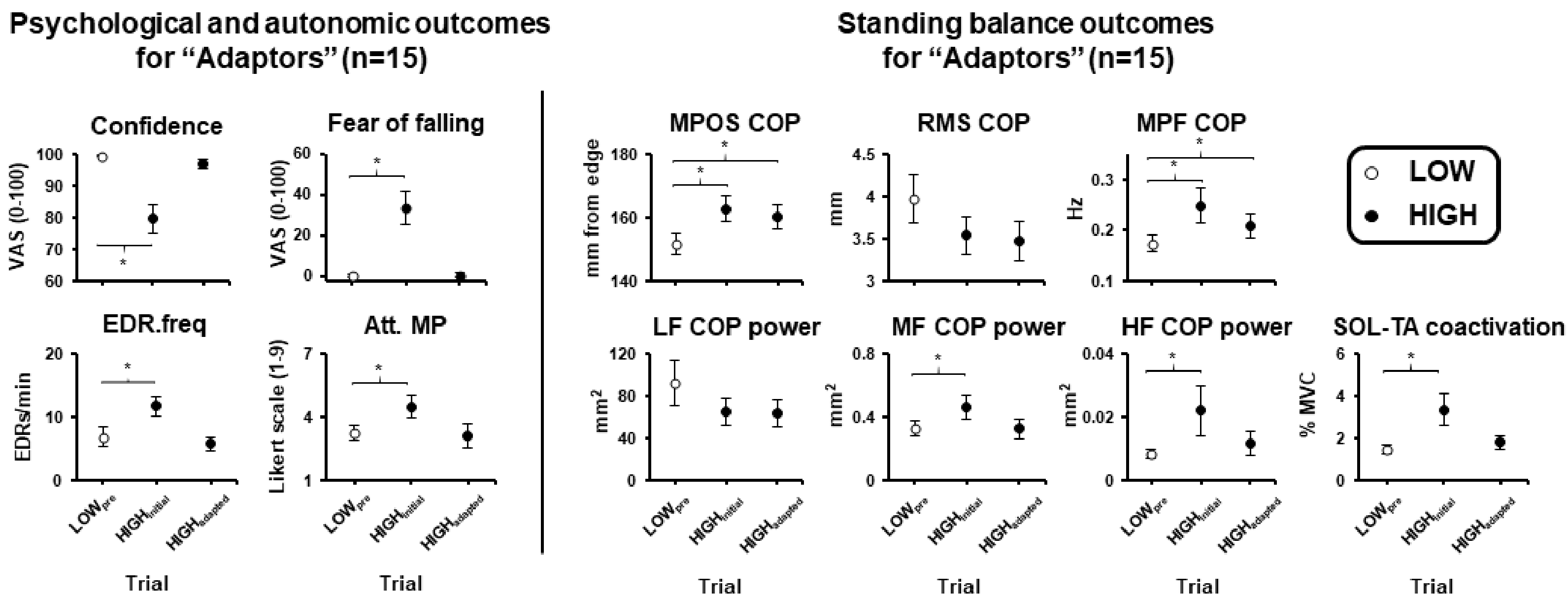

Figure 3-5: Effect of threat and trial on psychological, autonomic, and standing balance outcomes in the "Adaptor" subgroup (n=15). Data presented reflect group means and standard errors. The first two LOW trials for each subject were averaged (LOW_{pre}) and are presented as open circles. The first two HIGH trials for each subject were averaged ($HIGH_{initial}$). The trial by which the participant was identified as an "Adaptor" and the subsequent HIGH trial were averaged ($HIGH_{adapted}$). Both $HIGH_{initial}$ and $HIGH_{adapted}$ are presented as filled black circles. Att. MP= attention toward movement processes; COP = centre of pressure; EDR.freq = non-specific electrodermal response frequency; HF = high frequency (1.8-5 Hz); LF = low frequency (0-0.05 Hz); MF = medium frequency (0.5-1.8 Hz); MPF = mean power frequency; MPOS = mean position; RMS = root mean square; SOL-TA = soleus-tibialis anterior; VAS = visual analog scale. Brackets with asterisks indicate significant planned follow-up comparisons (p<0.025).

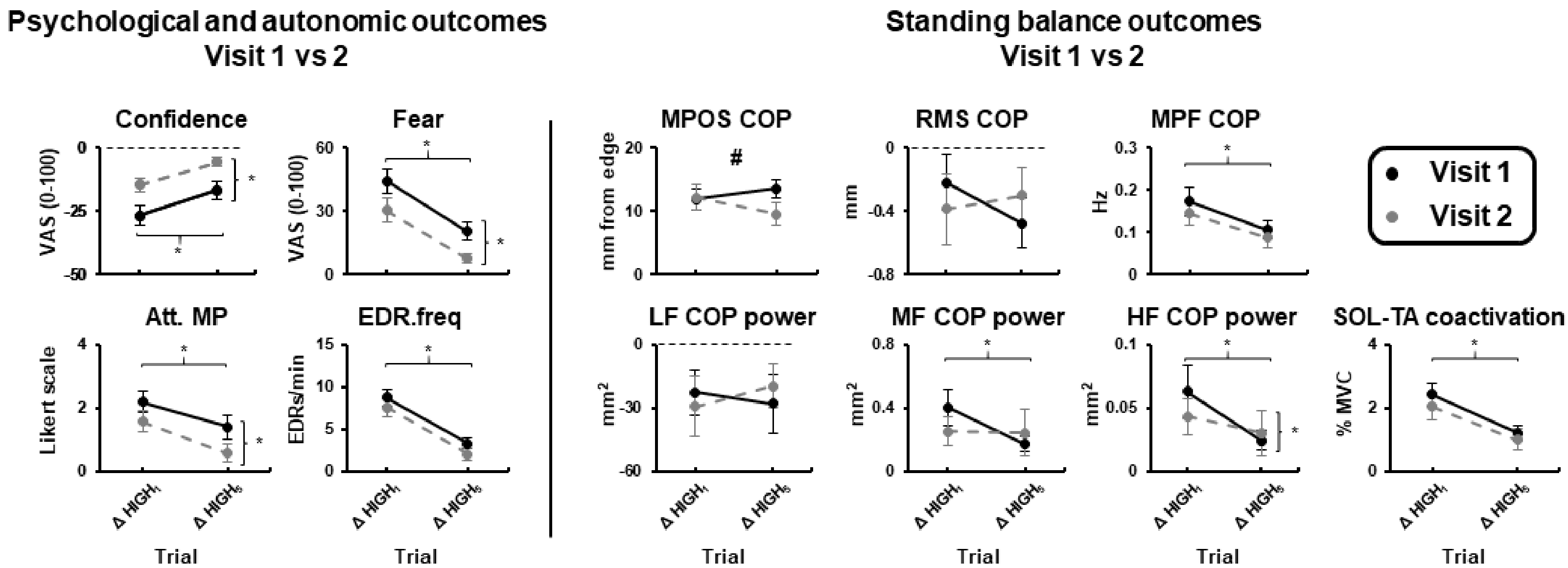

Figure 3-6: Effect of visit and trial on psychological, autonomic, and standing balance outcomes. Data presented reflect group means and standard errors of change scores (Δ $HIGH_1 = HIGH_1 - LOW_{pre}$; Δ $HIGH_5 = HIGH_5 - LOW_{pre}$). Change scores for visit 1 and 2 are presented as filled black and grey circles, respectively. Att. MP = attention toward movement processes; COP = centre of pressure; EDR.freq = non-specific electrodermal response frequency; HF = high frequency; LF = low frequency; MF = medium frequency; MPF = mean power frequency; MPOS = mean position; RMS = root mean square; SOL = soleus; TA = tibialis anterior; VAS = visual analog scale. Vertical and horizontal brackets with asterisks indicate significant main effect of visit and trial, respectively *(p*<0.05). Hashtags represent significant visit × trial interaction (*p*<0.05).

Table 3-1: Demographic and personality information for all participants and Adaptor subgroups

	Age	Sex	Height (cm)	Weight (kg)	STAI	MSRS	RT
Full sample	23.6 (4.6)	15M, 22F	171.9 (10.3)	66.2 (13.6)	39.7 (7.5)	36.7 (7.2)	24.8 (8.5)
Adaptors (n=15)	21.8 (2.8)	4M, 11F	168.5 (10.7)	62.5 (13.1)	39.4 (6.8)	36.1 (8.0)	27.6 (7.3)
Non-adaptors (n=22)	24.8 (5.3)	11M, 11F	174.3 (9.5)	68.7 (13.7)	39.9 (8.1)	37.1 (6.8)	23.1 (8.9)

Values provided reflect means and standard deviations (with the exception of sex, in which case sums are provided). Scores range from 20-80 on the State-Trait Anxiety Inventory (STAI; higher scores reflect greater trait anxiety), 10-60 on the Movement-Specific Reinvestment Scale (MSRS; higher scores reflect greater propensity for movement reinvestment), and 6-42 on the Domain Specific Risk-Taking Scale (RT; higher scores reflect greater propensity for recreational risk-taking). Note, personality data were not collected for two participants, both of whom were in the Adaptor subgroup.

Table 3-2: Two-way repeated-measures ANOVAs (Threat: LOW vs HIGH; Trial: Pre vs Post) examining within-session habituation of self-report, autonomic, and standing balance outcomes at visit 1

	Threat × trial interaction			Threat main effect			Trial main effect		
	F	*p*	η_p^2	F	*p*	η_p^2	F	*p*	η_p^2
Psychological and autonomic outcomes									
Confidence	36.306	<**0.001**	0.516	45.032	**<0.001**	0.570	40.141	**<0.001**	0.541
Anxiety	69.469	<**0.001**	0.671	85.034	**<0.001**	0.714	89.698	**<0.001**	0.725
Fear of falling	51.102	<**0.001**	0.600	55.222	**<0.001**	0.619	51.577	**<0.001**	0.603
EDR.freq	32.727	<**0.001**	0.498	101.787	**<0.001**	0.755	94.735	**<0.001**	0.742
Att. MP	18.284	<**0.001**	0.350	41.194	**<0.001**	0.548	27.369	**<0.001**	0.446
Att. TRS	58.237	<**0.001**	0.631	65.455	**<0.001**	0.658	71.278	**<0.001**	0.677
Att. SRS	6.262	**0.017**	0.156	46.394	**<0.001**	0.577	46.693	**<0.001**	0.579
Att. TO	0.558	0.460	0.016	10.274	**0.003**	0.232	9.985	**0.003**	0.227
Att. TI	12.970	**0.001**	0.276	18.436	**<0.001**	0.352	21.354	**<0.001**	0.386
Standing balance outcomes									
MPOS-COP	0.085	0.772	0.003	60.840	**<0.001**	0.642	7.938	**0.008**	0.189
RMS-COP	6.004	**0.020**	0.150	12.505	**0.001**	0.269	0.017	0.898	<0.001
MPF-COP	5.530	**0.025**	0.140	32.120	**<0.001**	0.486	8.529	**0.006**	0.201
LF-COP power	3.026	0.091	0.082	13.388	**0.001**	0.283	0.158	0.694	0.005
MF-COP power	5.904	**0.021**	0.148	18.883	**<0.001**	0.357	12.759	**0.001**	0.273
HF-COP power	11.347	**0.002**	0.250	38.360	**<0.001**	0.530	14.319	**<0.001**	0.296
Tonic SOL activation	8.219	**0.007**	0.199	8.593	**0.006**	0.207	0.049	0.826	0.001
Tonic TA activation	16.234	**<0.001**	0.330	65.618	**<0.001**	0.665	22.730	**<0.001**	0.408
SOL-TA Co-Ac	25.387	**<0.001**	0.435	66.157	**<0.001**	0.667	29.053	**<0.001**	0.468

Note. EDR.freq = non-specific electrodermal response frequency; Att. = attention toward; MP = movement processes; TRS = threat-related stimuli; SRS = self-regulatory strategies; TO = task objectives; TI = task-irrelevant information; MPOS = mean position; RMS = root mean square; MPF = mean power frequency; LF = low-frequency (0-0.05 Hz); MF = medium-frequency (0.5-1.8 Hz); HF = high-frequency (1.8-5 Hz); SOL = soleus; TA = tibialis anterior; Co-Ac = coactivation.

Table 3-3: Follow-up pairwise comparisons for significant Threat × Trial interactions for two-way RM-ANOVAs examining within-session habituation at visit 1

	$HIGH_1$ vs LOW_{pre}		$HIGH_1$ vs $HIGH_{20}$		$HIGH_{20}$ vs LOW_{post}		LOW_{pre} vs LOW_{post}	
	Δ (±SD)	*p-value*	*Δ (±SD)*	*p-value*	*Δ (±SD)*	*p-value*	*Δ (±SD)*	*p-value*
				Psychological and autonomic outcomes				
Confidence	**-26.10 (±22.78)**	**<0.001**	**-21.11 (±20.14)**	**<0.001**	**-5.74 (±8.65)**	**<0.001**	**-0.76 (±1.58)**	**0.008**
Anxiety	**44.92 (±28.53)**	**<0.001**	**41.19 (±26.64)**	**<0.001**	**8.03 (±10.30)**	**<0.001**	**4.29 (±6.06)**	**<0.001**
Fear	**41.90 (±32.49)**	**<0.001**	**35.80 (±29.41)**	**<0.001**	**7.49 (±11.09)**	**<0.001**	1.39 (±3.16)	0.014
EDR.freq	**8.63 (±5.43)**	**<0.001**	**8.48 (±4.78)**	**<0.001**	**3.14 (±3.06)**	**<0.001**	**2.97 (±4.03)**	**<0.001**
Att. MP	**2.14 (±1.90)**	**<0.001**	**1.71 (±1.79)**	**<0.001**	**0.91 (±1.33)**	**<0.001**	0.49 (±1.15)	0.016
Att. TRS	**3.46 (±2.50)**	**<0.001**	**3.14 (±2.26)**	**<0.001**	**0.50 (0.74)**	**<0.001**	0.19 (0.47)	0.026
Att. SRS	**2.01 (±2.24)**	**<0.001**	**2.31 (±2.45)**	**<0.001**	**0.96 (±1.20)**	**<0.001**	**1.26 (±1.38)**	**<0.001**
Att. TI	**-1.84 (±2.37)**	**<0.001**	**-2.66 (±2.94)**	**<0.001**	-0.271 (±1.40)	0.260	-1.09 (±2.48)	0.014
				Standing balance outcomes				
RMS-COP (mm)	-0.226 (±1.00)	0.191	0.279 (±1.087)	0.138	**-0.748 (±1.058)**	**<0.001**	-0.243 (±0.997)	0.159
MPF-COP (Hz)	**0.162 (±0.197)**	**<0.001**	**0.086 (±0.180)**	**0.008**	**0.096 (±0.105)**	**<0.001**	0.020 (±0.068)	0.089
MF-COP power (mm^2)	**0.379 (±0.633)**	**<0.001**	**0.295 (±0.623)**	**0.002**	**0.119 (±0.250)**	**0.005**	0.036 (0.138)	0.099
HF-COP power (mm^2)	**0.059 (0.117)**	**<0.001**	**0.049 (±0.115)**	**<0.001**	**0.012 (±0.020)**	**<0.001**	0.001 (0.005)	0.255
Tonic SOL activation (% MVC)	-0.369 (±2.762)	0.441	0.566 (±2.588)	0.211	**-1.628 (±1.881)**	**<0.001**	**-0.692 (±1.455)**	**0.009**
Tonic TA activation (% MVC)	**5.792 (±4.838)**	**<0.001**	**3.388 (±4.183)**	**<0.001**	**2.723 (±3.280)**	**<0.001**	0.319 (±0.982)	0.073
SOL-TA Co-Ac (% MVC)	**2.487 (±2.041)**	**<0.001**	**1.724 (±2.000)**	**<0.001**	**0.924 (±1.328)**	**<0.001**	0.161 (±0.531)	0.057

Note. Mean differences (Δ) and p-values for each comparison are presented. Significant effects after Bonferroni correction (alpha 0.0125) are boldfaced. EDR.freq = non-specific electrodermal response frequency; Att. = attention toward; MP = movement processes; TRS = threat-related stimuli; SRS = self-regulatory strategies; TO = task objectives; TI = task-irrelevant information; COP = centre of pressure; RMS = root mean square; MPF = mean power frequency; LF = low-frequency (0-0.05 Hz); MF = medium-frequency (0.5-1.8 Hz); HF = high-frequency (1.8-5 Hz); MVC = maximal voluntary contraction; SOL = soleus; TA = tibialis anterior; Co-Ac = coactivation.

Table 3-4: One-way repeated measures ANOVAs for “Adaptor” subgroup

	F	*p*	η^2
Psychological and autonomic outcomes			
Confidence	19.829	**<0.001**	0.586
Anxiety	25.918	**<0.001**	0.649
Fear of falling	18.729	**0.001**	0.572
EDR.freq	26.348	**<0.001**	0.653
Att. MP	3.807	**0.034**	0.214
Att. TRS	18.124	**<0.001**	0.564
Att. SRS	5.533	**0.009**	0.283
Att. TO	7.599	**0.007**	0.352
Att. TI	9.969	**0.001**	0.416
Standing balance outcomes			
MPOS-COP	12.499	**<0.001**	0.606
RMS-COP	2.716	0.084	0.162
MPF-COP	6.138	**0.014**	0.305
LF-COP power	1.808	0.183	0.114
MF-COP power	8.014	**0.002**	0.364
HF-COP power	7.363	**0.008**	0.345
Tonic SOL activation	2.948	0.070	0.185
Tonic TA activation	14.082	**<0.001**	0.520
SOL-TA Co-Ac	15.853	**<0.001**	0.549

Note. EDR.freq = non-specific electrodermal response frequency; Att. = attention toward; MP = movement processes; TRS = threat-related stimuli; SRS = self-regulatory strategies; TO = task objectives; TI = task-irrelevant information; MPOS = mean position; RMS = root mean square; MPF = mean power frequency; LF = low-frequency (0-0.05 Hz); MF = medium-frequency (0.5-1.8 Hz); HF = high-frequency (1.8-5 Hz); SOL = soleus; TA = tibialis anterior; Co-Ac = coactivation.

Table 3-5: Two-way repeated-measures ANOVAs (Visit: 1 vs 2; Trial: Δ $HIGH_1$ vs Δ $HIGH_5$) examining retention and within-session adaptation of self-report, autonomic, and standing balance outcomes across visits

	Visit × trial interaction			Visit main effect			Trial main effect		
	F	*p*	η^2	F	*p*	η^2	F	*p*	η^2
Psychological and autonomic outcomes									
Confidence	0.063	0.803	0.002	25.204	**<0.001**	0.441	23.69	**<0.001**	0.425
Anxiety	1.756	0.194	0.052	29.968	**<0.001**	0.484	67.160	**<0.001**	0.677
Fear of falling	0.064	0.802	0.002	23.918	**<0.001**	0.428	43.606	**<0.001**	0.577
EDR.freq	0.026	0.872	0.001	3.479	0.072	0.101	75.863	**<0.001**	0.710
Att. MP	0.212	0.648	0.007	4.176	**0.050**	0.119	16.041	**<0.001**	0.341
Att. TRS	0.070	0.793	0.002	17.685	**<0.001**	0.356	48.802	**<0.001**	0.604
Att. SRS	0.254	0.618	0.008	0.714	0.404	0.022	15.258	**<0.001**	0.323
Att. TO	0.021	0.885	0.001	0.772	0.386	0.024	15.201	**<0.001**	0.322
Att. TI	0.721	0.402	0.022	2.218	0.146	0.065	35.645	**<0.001**	0.527
Standing balance outcomes									
MPOS-COP	6.371	**0.017**	0.166	1.442	0.239	0.043	0.383	0.540	0.012
RMS-COP	2.226	0.145	0.065	<0.001	0.992	<0.001	0.492	0.488	0.015
MPF-COP	0.099	0.755	0.003	2.140	0.153	0.063	11.771	**0.002**	0.269
LF-COP power	0.578	0.453	0.018	0.009	0.925	<0.001	0.350	0.559	0.011
MF-COP power	0.202	0.656	0.006	4.016	0.054	0.112	7.376	**0.011**	0.187
HF-COP power	0.460	0.503	0.014	8.129	**0.008**	0.203	21.418	**<0.001**	0.401
Tonic SOL activation	7.747	**0.009**	0.195	0.631	0.433	0.019	8.230	**0.007**	0.205
Tonic TA activation	1.541	0.224	0.046	3.257	0.081	0.092	37.602	**<0.001**	0.540
SOL-TA Co-Ac	0.085	0.773	0.003	2.488	0.125	0.072	59.271	**<0.001**	0.649

Note. EDR.freq = non-specific electrodermal response frequency; Att. = attention toward; MP = movement processes; TRS = threat-related stimuli; SRS = self-regulatory strategies; TO = task objectives; TI = task-irrelevant information; MPOS = mean position; RMS = root mean square; MPF = mean power frequency; LF = low-frequency (0-0.05 Hz); MF = medium-frequency (0.5-1.8 Hz); HF = high-frequency (1.8-5 Hz); SOL = soleus; TA = tibialis anterior; Co-Ac = coactivation.

Chapter 4: Study 3 - Initial experience of balance assessment introduces ‘first trial’ effects on emotional state and postural control

4.1 Introduction

Studies have used a variety of emotional induction techniques to demonstrate that fear and anxiety influence the control of balance. The most common manipulations have involved exposing individuals to different forms of postural threat, such as standing at the edge of an elevated surface or at ground level with the expectation of an impending balance perturbation. These threat manipulations induce considerable changes in psychological and autonomic state and have been shown to elicit changes in static and dynamic balance control (Adkin and Carpenter, 2018). However, even mild manipulations of emotional state have been shown to affect balance control. For example, passively viewing emotionally provocative pictures (Horslen and Carpenter, 2011) or completing a mental arithmetic task (Maki and McIlroy, 1996) have been shown to increase self-reported and physiological indicators of anxiety and induce changes in balance. Even day-to-day variations in state anxiety have been associated with clinical balance performance (Bolmont et al. 2004).

Established links between changes in emotional state and balance control underscore the potential confounding effects of anxiety and arousal on balance assessments. This possibility has been highlighted by the observation of a ‘white-coat’ effect on balance control, with both young and older women self-reporting greater anxiety while performing clinical balance tests in the presence of an expert evaluator (Geh et al. 2011). While these changes in anxiety had minimal influence on balance performance in young participants, older participants demonstrated larger amplitude and higher frequency centre of pressure (COP) oscillations during quiet stance and shorter one-legged stance duration (Geh et al. 2011). Likewise, Doumas and colleagues (2018) observed significant decreases in COP amplitude in young adults standing in the presence of an evaluator coupled with negative feedback about their prior performance.

The ‘first trial’ effect, where performance on the initial trial of a given balance task differs from subsequent trials, has also been attributed, in part, to potential changes in emotional state. This was first demonstrated when examining balance responses to external perturbations, as individuals demonstrated larger balance corrective responses to the first compared to subsequent perturbations (Maki and Whitelaw, 1993). While multiple factors, including motor learning, may contribute to this rapid adaptation, estimates of sympathetic arousal decreased with repeated testing and were significantly correlated with reductions in the magnitude of the balance response (Maki and Whitelaw, 1993). First trial effects have also been observed in static balance tasks, with individuals demonstrating smaller amplitude and higher frequency COP oscillations during the first of two consecutive quiet standing trials in a low-threat condition (Adkin et al. 2000). This tighter control of standing balance is similar to that seen when individuals stand under conditions of height-induced postural threat, suggesting that individuals may have been more anxious or less confident during their first experience of having their balance evaluated in an unfamiliar lab environment. However, this interpretation is speculative since no direct assessments of state anxiety or autonomic activity were recorded to confirm if the first trial did, in fact, elicit an emotional response. Furthermore, since the testing period was not extended beyond two trials, it is unclear if the changes in balance and emotional state continue to change with repeated testing or reach a point of saturation with additional experience.

Given that studies often rely on a single baseline assessment when examining the effects of an intervention or experimental manipulation, it is crucial that we develop a better understanding of the extent to which first trial effects may influence postural measures to avoid the risk of falsely claiming a treatment effect. Furthermore, it is important to understand how postural adaptations over repeated balance assessment vary with changes in emotional and cognitive factors to gain insight into the possible mechanisms mediating these effects and allow for these factors to be properly controlled or accounted for in future studies. Thus, the present study examined how emotional state and standing balance parameters changed over the course of repeated testing in a sample of participants who were naïve to balance assessment. Quiet standing was assessed because it is widely used in research and clinical settings and avoids confounds associated with learning which may be inherent to reactive balance control and/or more challenging balance tasks. We hypothesized that individuals would be less confident, more anxious and physiologically aroused, and direct more attention toward their movement during the first trial. Individuals were also expected to demonstrate smaller amplitude and higher frequency COP oscillations (Adkin et al. 2000) and a slight forward lean (Maki and McIlroy, 1996) during the first trial. These changes in psychological and autonomic state and standing balance control were expected to normalize after completion of the first trial of quiet standing.

4.2 Methods

4.2.1 Participants

Seventy-five healthy young adults (mean age=22.6±4.1 years; 41 females) naïve to balance assessment participated in this study. Participants had no neurological or musculoskeletal disorders that would affect their balance. Written informed consent was provided prior to participation. All procedures were reviewed and cleared by UBC's Clinical Research Ethics Board.

4.2.2 Procedure

Participants completed a series of five 120-s quiet standing trials on a force plate (AMTI, USA) positioned on the ground. Participants stood barefoot with a stance width equal to their foot length. The borders of participants' feet were traced onto the force plate to ensure foot position was consistent across trials. Participants were instructed to stand quietly with their arms at their sides and gaze fixated on an eye-level visual target 3.8 m away. Immediately following completion of the five trials, most participants (n=65) completed a second, unrelated, study involving exposure to a height-related threat. The two studies were always performed in the same order and participants were aware that the upcoming protocol involved standing on an elevated platform. Therefore, in order to preserve the ability to test our hypotheses about first trial effects while minimizing the potentially confounding influence of anticipatory anxiety related to imminent height exposure, the final (fifth) trial of the current study was excluded from analysis to ensure there was a clear buffer between experiments.

4.2.3 Data collection and analysis

Ground reaction forces and moments were sampled at 100 Hz and low-pass filtered offline at 10 Hz (second order, dual-pass Butterworth filter). Centre of pressure (COP) was calculated in the anteroposterior (AP) and mediolateral (ML) directions. AP- and ML-COP mean positions (MPOS) were calculated and subtracted from the corresponding COP time series. From the debiased COP data, the following summary measures were calculated: ellipse area, total path length (TPL), and AP and ML root mean square (RMS), range, mean velocity (MVEL), mean power frequency (MPF), and 95% power frequency. These were selected since they provide a breadth of commonly used measures which describe the amplitude, speed, and frequency content of COP oscillations (Prieto et al. 1996). $MPOS_{AP}$ was also included to provide an estimate of forward/backward leaning.

To estimate changes in sympathetic activation, skin conductance was recorded from two Ag/AgCl electrodes placed on the thenar and hypothenar eminences of the non-dominant hand. Skin conductance was amplified and sampled at 100 Hz (model 2502SA, CED, UK). Data were low-pass filtered offline at 1 Hz (fifth-order dual-pass Butterworth filter). The frequency of non-specific electrodermal responses (EDR.freq) were calculated offline using a semi-automated algorithm that identified all EDRs with peak amplitudes greater than 0.05 ųS (Boucsein et al. 2012).

Prior to each trial, participants reported their confidence in their ability to maintain balance and avoid a fall during the upcoming task on a visual analog scale ranging from 0 (not confident at all) to 100 (completely confident). Following each trial, participants completed questionnaires assessing worry and somatic anxiety, and attentional focus. Participants rated how worried and physically anxious they felt on visual analog scales ranging from 0 (I was not worried; I did not feel anxious at all) to 100 (I was very worried; I felt very anxious). Participants then used a Likert scale from 1 (not at all) to 9 (very much so) to rate how much they directed attention toward movement-related processes (Att.MP), task objectives (Att.TO), threat-related stimuli (Att.TRS), self-regulatory strategies (Att.SRS), and task-irrelevant information (Att.TI) (Zaback et al. 2016; Johnson et al. 2019a).

4.2.4 Statistical analysis

All variables were screened for normality and statistical outliers. Logarithmic transformations were performed on non-normal data (worry, somatic anxiety, Att.TRS, and confidence) and any statistical outliers were converted to the closest non-outlying value. To limit the analysis of COP summary measures to only those that provided unique information about COP behaviour, Pearson correlations were calculated between all COP summary measures for Trial 1 (T_1) (Table 4-1). A correlation coefficient threshold of $r \geq 0.9$ was used to identify highly correlated variables that could be excluded from further analysis.

Trial effects were examined for all dependent variables using within-subject repeated measures (RM-) ANOVAs (4 levels: T_1, T_2, T_3, and T_4). Significant ANOVAs were followed-up with Bonferroni corrected ($p=0.0167$) contrasts that compared each of the first three trials to the final trial (T_4). Since the final trial was assumed to represent a stable baseline, these comparisons were selected to determine how many trials were needed before each dependent variable no longer significantly changed with repeated testing.

4.3 Results

4.3.1 Psychological and autonomic outcomes

Significant main effects of trial were observed for EDR.freq, balance confidence, worry, and somatic anxiety (Table 4-2). During the first trial, participants were more physiologically aroused and reported significantly less confidence and more worry and somatic anxiety compared to the final trial (Figure 4-1). With repeated testing, participants showed reductions in EDR.freq, worry, and somatic anxiety, and increases in confidence which were most pronounced after completing the first trial (Table 4-2). Contrasts revealed that worry was no longer significantly different from the final trial by T_2, while confidence and somatic anxiety were no longer different from the final trial by T_3. While EDR.freq showed progressive reductions with repeated testing, it still differed from the final trial at T_3.

Significant main effects of trial were also observed for Att.MP, SRS, and TO (Table 4-2). During the first trial, participants directed more attention toward their movement, self-regulatory strategies, and the task (Figure 4-1). With repeated testing, participants directed less attention to each of these, with the greatest reductions occurring after the first trial (Table 4-2). Contrasts revealed that Att.MP and SRS no longer differed from the final trial by T_2, whereas Att.TO showed progressive reductions with repeated testing and still differed from the final trial at T_3. No significant main effects of trial were observed for Att.TRS and TI (Table 4-2).

4.3.2 COP outcomes

Measures of range, TPL, and 95% frequency were removed from further analysis, as they had high covariance ($r \geq .90$) with RMS, MVEL, and MPF in the AP and ML directions, respectively (Table 1). The latter measures were retained, as they are more commonly used and provide more reliable and meaningful interpretation of the COP behaviour. COP Ellipse and $MPOS_{AP}$ were also retained because they were not correlated with any variables above the predetermined threshold of $r \geq .90$.

Significant main effects of trial were observed for $MPOS_{AP}$, $MVEL_{ML}$, and MPF_{ML} (Table 4-2). For $MPOS_{AP}$ and $MVEL_{ML}$, contrasts revealed that participants leaned further forward and had higher velocity COP_{ML} movement during the first compared to final trial (Figure 4-2). With repeated testing, participants shifted their weight backward and showed slower velocity COP movement, with $MPOS_{AP}$ no longer different from the final trial by T_2, and $MVEL_{ML}$ no longer different from the final trial by $T_{3.}$ For MPF_{ML}, contrasts revealed that there was only significantly higher frequency COP_{ML} during T_2 compared to the final trial, although this effect did trend toward significance when comparing the first to final trial (p=0.045). No significant main effects of trial were observed for RMS_{AP}, MPF_{AP}, $MVEL_{AP}$, RMS_{ML}, and ellipse area (Table 4-2).

4.4 Discussion

To determine if emotional factors have the potential to confound standard balance assessment in the absence of any overt threat, this study examined how emotional state and standing balance control changed over the course of repeated testing in participants naïve to balance assessment. It was demonstrated that there were significant changes in emotional state across the four trials of quiet standing, with self-report and autonomic measures indicating that participants were more anxious during the first trial. This emotional response showed rapid attenuation after participants had completed the first trial. However, only a subset of self-report measures no longer significantly differed from the final (baseline) trial after this point; this included self-reported worry, and attention toward movement and self-regulatory strategies. The common element across each of these self-report measures is that they reflect specific cognitive strategies that individuals use to cope with threat or anxiety (Sibrava and Borkovec, 2006; Zaback et al. 2016), suggesting that individuals use different cognitive strategies immediately after having gained some initial familiarity with the balance task. By contrast, other measures of psychological and autonomic state continued to change after participants had completed the first trial, although the continued attenuation for each of these outcomes was subtle compared with the changes observed after the first trial (Figure 4-1). This included self-reported estimates of balance confidence and somatic anxiety, which appeared to plateau by the third trial, and tonic EDA and attention toward the task, which showed continued attenuation across all four trials. These results may suggest that individuals still experience some residual level of anxiety after the first trial. Alternatively, the continuous decline in physiological arousal could be linked to changes in alertness (Oken et al. 1995; 2006) associated with repeated performance of a relatively low-cognitively demanding task such as quiet stance (Woollacott and Shumway-Cook, 2002). This explanation coincides with the continuous decline in self-reported attention toward the task (Figure 4-1).

Despite significant changes in psychological and autonomic state over the course of repeated testing, only some COP outcomes showed significant changes. In particular, individuals leaned further forward during the first compared to final trial. This shift in $MPOS_{AP}$, is consistent with that observed when arousal is increased by having an individual perform a mental arithmetic task (Maki and McIlroy, 1996). Individuals have also been shown to lean forward when standing with the threat of an unpredictable forward or backward perturbation (Maki and Whitelaw, 1993; Johnson et al. 2019a), and this lean has been found to habituate in parallel with measures of tonic EDA following repeated exposure to the perturbation (Maki and Whitelaw, 1993). This suggests that when anxiety or arousal are induced in specific contexts, individuals adopt a slight forward lean. Therefore, the emotional response participants experienced during the first trial of the present study may have been sufficient to cause a similar change in behaviour.

Significant trial effects were also observed for MPF_{ML} and $MVEL_{ML}$ of COP. Recent work that has repeatedly exposed individuals to different postural threats has shown that estimates of MPF and high frequency (>0.5 Hz) COP power (which has a strong influence of estimates of MVEL) are closely related to individuals' psychological and autonomic response to threat (Johnson et al. 2019b; Zaback et al. 2019; 2021a). Thus, it is possible that the order effects observed in the present study for these variables may be related to changes in emotional state that occurred over the course of repeated testing. However, this is unclear since both MPF_{ML} and $MVEL_{ML}$ showed limited change from the first to second trial despite the greatest changes in psychological and autonomic state occurring at that time. Thus, it is possible that the order effects observed for these variables were caused by factors unrelated to the changes in emotional state with repeated testing.

In contrast to previous work (Adkin et al. 2000), no significant first trial nor order effects were observed for measures of COP amplitude (i.e., ellipse area or $RMS_{AP/ML}$) or MPF_{AP}. Differences in the testing conditions between studies may have contributed to these discrepant findings. Quiet standing trials in the present study were completed at ground level and well in advance of trials at a high-threat condition (see methods). By contrast, participants in the study by Adkin and colleagues (2000) completed their two quiet standing trials on a slightly elevated (40 cm) hydraulic lift immediately before completing trials at higher surface heights. Standing on a platform under such conditions is not usually sufficient to elicit changes in postural control (Carpenter et al. 2001), but the slightly more threatening condition and anticipation of the forthcoming threat trials may have accentuated first trial anxiety and contributed to greater changes in postural control. The lack of first trial and/or order effects for estimates of COP amplitude may also be related to the poor association between these COP variables and emotional state. Measures of COP amplitude have shown inconsistent correlations with changes in psychological and autonomic state when individuals are exposed to postural threats (Hauck et al. 2008; Huffman et al. 2009; Zaback et al. 2019) and are invariant over the course of repeated threat exposure despite habituation of individuals' emotional response to the threat (Johnson et al. 2019b; Zaback et al. 2019; 2021a).

4.4.1 Recommendations

This study demonstrated that when individuals complete a simple balance task for the first time in a laboratory setting, there are significantly elevated levels of anxiety which habituate rapidly with repeated testing. This emotional response is not negligible, with changes in self-reported anxiety and tonic EDA from the first to second trial equal to approximately 13-16% and 23-24% of the change typically seen for the same outcomes, respectively, when standing at a 3.2 m height-related threat (Zaback et al. 2019; 2021a). Thus, it is critical that these order effects are controlled for when designing experiments or interventions involving balance assessment. For the assessment of quiet, unperturbed stance, it is recommended that at least one familiarization trial be provided, since this will be sufficient to reduce the majority of first trial effects on emotional state and standing balance control. However, a second familiarization trial may be ideal to minimize residual levels of anxiety, especially if effect sizes are expected to be small or the outcomes under examination are known to be sensitive to changes in emotional state.

4.4.2 Limitations and future directions

This study only examined how emotional state changed over the course of repeated testing for one type of balance task during a single experimental session. It is therefore unclear if a similar emotional response will re-emerge during the performance of a different balance task during the same experimental session, or performance of the same balance task during a subsequent experimental session. In addition, it is unclear if greater first trial effects are observed for more complex and/or unfamiliar balance tasks. These represent important avenues for future research since they will provide insight into how to efficiently structure the timing of familiarization trials within and across experimental sessions to control for anxiety-related confounds.

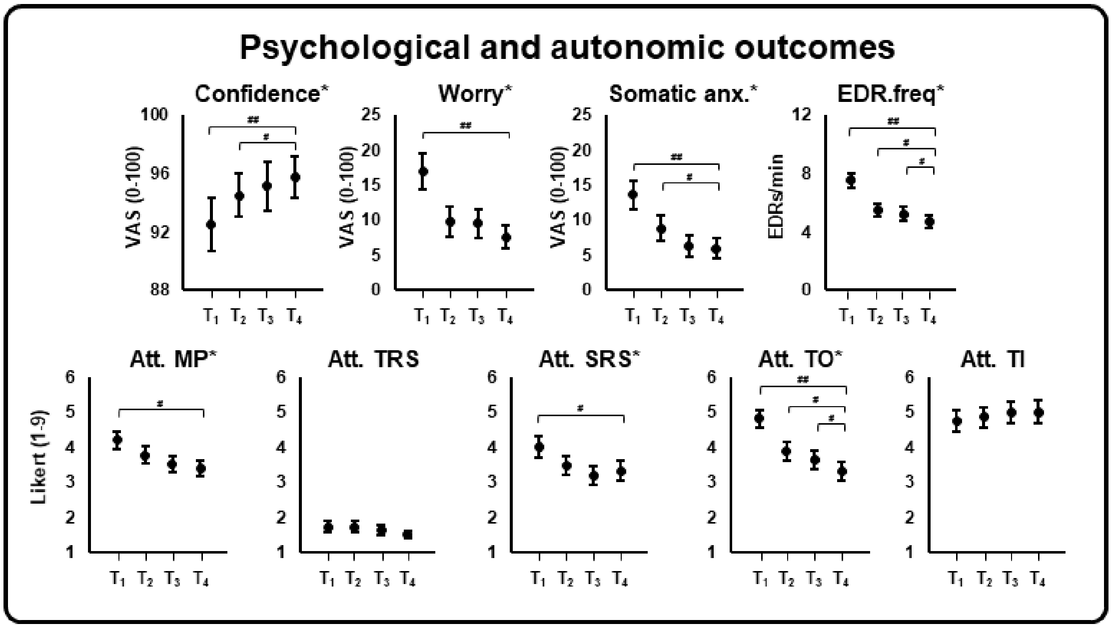

Figure 4-1: Effect of repeated testing on psychological and autonomic state measures. Data presented reflect group means and standard errors across the four quiet standing trials ($T_1 - T_4$). Anx. = anxiety; Att. = attention toward; EDR.freq = frequency of non-specific electrodermal responses; MP = movement-related processes; SRS = self-regulatory strategies; TI = task-irrelevant information; TO = task objectives; TRS = threat-related stimuli; VAS = visual analog scale. * indicates variables which had significant main effects of trial ($p < 0.05$); # and ## indicate significant simple contrasts at $p < 0.0167$ and $p < 0.001$, respectively.

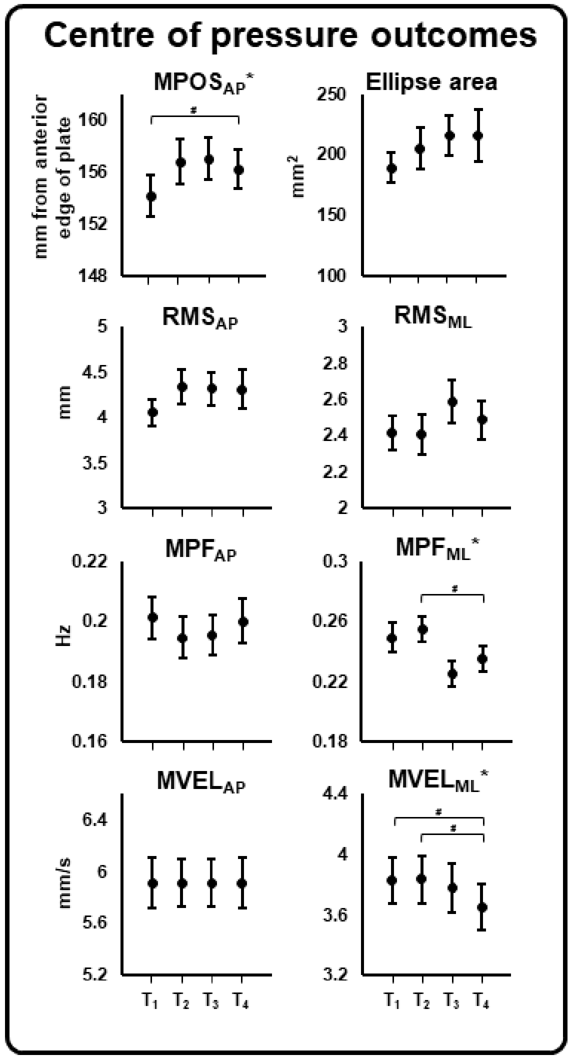

Figure 4-2: Effect of repeated testing on COP summary measures. Data presented reflect group means and standard errors across the four quiet standing trials ($T_1 – T_4$). AP = anteroposterior; ML = mediolateral; MPF = mean power frequency; MPOS = mean position; MVEL = mean velocity. * indicates variables which had significant main effects of trial ($p < 0.05$); # and ## indicate significant simple contrasts at $p < 0.0167$ and $p < 0.001$, respectively.

Table 4-1: Correlation matrix used to identify COP outcomes with exceedingly high shared variance (r ≥0.9)

	Ellipse area	RMS_{AP}	$Range_{AP}$	MPF_{AP}	$95\%F_{AP}$	$MVEL_{AP}$	TPL	$MPOS_{AP}$	
		0.83	0.79	-0.24	-0.149	0.65	0.67	0.10	Ellipse area
Ellipse area			**0.90**	-0.43	-0.367	0.53	0.49	0.12	RMS_{AP}
RMS_{ML}	0.87			-0.29	-0.247	0.57	0.52	0.09	$Range_{AP}$
$Range_{ML}$	0.86	**0.94**			0.858	0.36	0.33	0.22	MPF_{AP}
MPF_{ML}	-0.39	-0.48	-0.37			0.45	0.43	0.12	$95\%F_{AP}$
$95\%F_{ML}$	-0.28	-0.35	-0.26	**0.91**			**0.96**	0.34	$MVEL_{AP}$
$MVEL_{ML}$	0.57	0.62	0.62	0.30	0.441			0.29	TPL
TPL	0.67	0.63	0.66	0.17	0.283	**0.90**			$MPOS_{AP}$
	Ellipse area	RMS_{ML}	$Range_{ML}$	MPF_{ML}	$95\%F_{ML}$	$MVEL_{ML}$	TPL	$MPOS_{AP}$	

Note. AP = anteroposterior; ML = mediolateral; MPF = mean power frequency; MPOS = mean position; MVEL = mean velocity; RMS = root mean square; TPL = total path length; 95%F= 95% frequency; Pearson correlations coefficients exceeding 0.9 have been boldfaced.

Table 4-2: Summary of statistics for repeated measures ANOVAs and planned contrasts examining the effect of trial for psychological and autonomic state and centre of pressure outcomes

	ANOVA	T_1 vs. T_4	T_2 vs. T_4	T_3 vs. T_4
	Psychological and autonomic outcomes			
Confidence	**$F_{(2.1, 158.8)}$=12.67, p<0.001, η^2_p=0.15**	**t=-4.44, p<0.001, d=-0.51**	**t=-2.97, p=0.004, d=-0.34**	t=-0.15, p=0.884, d=-0.02
Worry	**$F_{(3, 222)}$=16.08, p<0.001, η^2_p=0.18**	**t=-5.22, p<0.001, d=-0.60**	t=-1.36, p=0.179, d=-0.16	t=-0.50, p=0.620, d=-0.06
Somatic anx.	**$F_{(2.5, 182.7)}$=24.84, p<0.001, η^2_p=0.25**	**t=-6.70, p<0.001, d=-0.77**	**t=-2.61, p=0.011, d=-0.30**	t=-0.31, p=0.758, d=-0.04
EDR.freq	**$F_{(2.6, 191.2)}$=47.55, p<0.001, η^2_p=0.39**	**t=-10.16, p<0.001, d=-1.17**	**t=-3.30, p=0.001, d=-0.38**	**t=-2.84, p=0.006, d=-0.33**
Att. MP	**$F_{(2.5, 183.8)}$=7.04, p<0.001, η^2_p=0.09**	**t=-3.37, p=0.001, d=-0.39**	t=-2.21, p=0.030, d=-0.26	t=-0.76, p=0.452, d=-0.09
Att. TRS	$F_{(2.5, 186.9)}$=2.43, p=0.077, η^2_p=0.03	-	-	-
Att. SRS	**$F_{(2.3, 171.1)}$=8.94, p<0.001, η^2_p=0.11**	**t=-3.13, p=0.003, d=-0.36**	t=-0.80, p=0.427, d=-0.09	t=0.09, p=0.393, d=0.10
Att. TO	**$F_{(2.3, 166.7)}$=29.08, p<0.001, η^2_p=0.28**	**t=-7.05, p<0.001, d=-0.82**	**t=-3.53, p=0.001, d=-0.41**	**t=-3.24, p=0.002, d=-0.37**
Att. TI	$F_{(2.5, 187.9)}$=0.70, p=0.532, η^2_p=0.01	-	-	-
	Centre of pressure outcomes			
$MPOS_{AP}$	**$F_{(2.6, 194.2)}$=7.57, p<0.001, η^2_p=0.09**	**t=2.61, p=0.011, d=0.30**	t=-0.95, p=0.348, d=-0.11	t=-1.35, p=0.182, d=-0.16
Ellipse area	$F_{(3, 222)}$=1.84, p=0.141, η^2_p=0.02	-	-	-
RMS_{AP}	$F_{(3, 222)}$=1.56, p=0.199, η^2_p=0.02	-	-	-
RMS_{ML}	$F_{(2.7, 197.7)}$=1.69, p=0.176, η^2_p=0.02	-	-	-
MPF_{AP}	$F_{(3, 222)}$=0.44, p=0.726, η^2_p=0.01	-	-	-
MPF_{ML}	**$F_{(3, 222)}$=5.28, p=0.002, η^2_p=0.07**	t=-2.04, p=0.045, d=-0.24	**t=-2.57, p=0.012, d=-0.30**	t=0.99, p=0.327, d=0.11
$MVEL_{AP}$	$F_{(2.5, 188.9)}$=0.01, p=0.996, η^2_p<0.001	-	-	-
$MVEL_{ML}$	**$F_{(3, 222)}$=4.23, p=0.006, η^2_p=0.05**	**t=-2.69, p=0.009, d=-0.31**	**t=-3.17, p=0.002, d=-0.37**	t=-1.93, p=0.057, d=-0.22

Note. AP = anterioposterior; Att. = attention toward; EDR.freq = frequency of non-specific electrodermal responses; ML = mediolateral; MP = movement-related processes; MPF = mean power frequency; MPOS = mean position; MVEL = mean velocity; RMS = root mean square; SRS = self-regulatory strategies; TI = task-irrelevant information; TO = task objectives; TRS = threat-related stimuli. Significant main effects of trial (p < 0.05) and significant contrasts (p < 0.0167) are boldfaced. When the assumption of sphericity was violated, Greenhouse-Geisser degree of freedom corrections were used.

Chapter 5: Study 4 - Changes in cortical and subcortical descending drive with initial and repeated postural threat exposure

5.1 Introduction

Postural threat manipulations have been used to study how emotional factors, such as fear and anxiety, influence the control of balance. Common manipulations involve raising the height of the surface on which individuals stand (height-induced threat) or having individuals stand at ground level with the expectation that their balance will be suddenly and unpredictably perturbed (threat of perturbation; Adkin and Carpenter, 2018). When standing under such threatening conditions, individuals demonstrate increases in sympathetic activation (estimated from electrodermal activity; EDA), and self-report greater fear and anxiety and lower balance-specific efficacy (Hauck et al. 2008; Horslen et al. 2013; Zaback et al. 2019; Johnson et al. 2019a). These changes in psychological and autonomic state are accompanied by changes in standing balance control that appear to be, at least in part, dependent on the nature of the threat (Adkin and Carpenter, 2018).

With a height-induced threat, individuals tend to lean away from the platform edge and demonstrate smaller amplitude and higher frequency centre of pressure (COP) oscillations (Adkin and Carpenter, 2018). The normally quiescent tibialis anterior (TA) shows increased activation, while the soleus (SOL) only shows slight reductions in its mean level of activity (Carpenter et al. 2001; Cleworth et al. 2016); this results in increased agonist/antagonist coactivation. Interestingly, only some of these changes in standing balance control appear correlated with psychological and autonomic state changes induced by the threat (Zaback et al. 2019). In addition, when individuals are repeatedly exposed to a height-induced threat, there is progressive attenuation of their psychological and autonomic response to threat, yet some standing balance changes are invariant (Zaback et al. 2019; Zaback et al. in press). Specifically, individuals tend to maintain their backward lean and reduced COP amplitude, while high frequency (>0.5 Hz) COP power, TA activation, and plantar/dorsiflexor coactivation show clear habituation over repeated threat exposures (Zaback et al. 2019; Zaback et al. 2021a). A similar pattern of change has also been observed when individuals are repeatedly exposed to the threat of perturbation (Johnson et al. 2019b). Collectively, this suggests that only some threat-induced changes in standing balance are closely linked to individuals' psychological and autonomic response, although what remains unclear are the neural mechanisms underlying these balance changes.

One potential mechanism could be a change in descending drive to muscles that are engaged in the control of balance. Individuals consistently report directing more attention toward their movement when standing under conditions of threat (Huffman et al. 2009; Zaback et al. 2016; 2019; Johnson et al. 2019ab), suggesting there may be greater cortical involvement in the control of standing balance in this particular context. Previous work has shown that when individuals are instructed to consciously intervene in the control of standing balance, there is increased plantar/dorsiflexor co-activation (Reynolds, 2012) and high-frequency COP oscillations (Vuillerme and Nafati, 2007). Furthermore, dual-task manipulations used to minimize the use of such conscious control strategies have been shown to reduce high frequency COP oscillations when standing with the threat of perturbation (Johnson et al. 2020). Thus, greater cortical involvement has the potential to contribute to specific changes in standing balance control typically observed under conditions of threat.

Previous studies have used transcranial magnetic stimulation (TMS) to examine how corticospinal tract excitability is influenced by height-induced threat. The results of these studies have been inconsistent, as motor-evoked potentials of trunk flexor muscles appear to be facilitated (Tanaka et al. 2013), while those of the lower leg are either suppressed or unaffected (Tokuno et al. 2018). This suggests that while corticospinal control of trunk muscles may be facilitated under conditions of postural threat, muscles of the lower leg, which are considerably more involved in the control of standing balance, do not receive greater corticospinal input. However, because TMS preferentially excites fast-conducting monosynaptic corticospinal projections and not the slower conducting projections which make up the majority of the corticospinal tract (Lemon, 2002; Porter and Lemon, 1995; Rathelot and Strick, 2006), these results do not conclusively suggest corticospinal control of postural muscles is unaffected by threat.

It is also likely that there is greater involvement from descending motor tracts originating in the brainstem under conditions of increased threat. Previous work has shown that short- and medium latency responses to vestibular stimulation are facilitated under conditions of threat (Horlsen et al. 2014; Naranjo et al. 2015; 2016) and the vestibulospinal system is actively engaged during standing balance control (Luu et al. 2012). The facilitation of vestibular-evoked responses is thought to largely be the result of increased excitability at the level of the vestibular nuclei. However, it is possible that increased excitability of the reticular formation also contributes, as vestibular-evoked responses are thought to be partially mediated by the reticulospinal tract (Wilson, 1993). Both the vestibular nuclei and reticular formation receive excitatory input from the amygdala and parabrachial nucleus (Balaban, 2002; Staab et al. 2013) which are activated in states of fear and arousal (Balaban and Thayer, 2001). Thus, it is likely that there is increased vestibulo- and reticulospinal drive to postural muscles when standing under conditions of postural threat.

Collectively, there is evidence to suggest that there may be greater contribution from corticospinal and brainstem motor tracts to the control of standing balance under conditions of postural threat. However, the nature of this involvement has not been well studied, nor is it clear how these changes influence balance control. One way this can be studied is by examining changes in corticomuscular (CMC) and intermuscular coherence (IMC). CMC reflects synchronization of electrical field potentials recorded from electrodes on the scalp and muscle fibre action potentials recorded using surface or intramuscular EMG. CMC is typically observed in the beta-band (15-30 Hz) during tonic isometric contractions, although it has also been reported in the low gamma-band (31-40 Hz) during more forceful and/or phasic contractions (Grosse et al. 2002; Omlor et al. 2007). However, previous studies have shown that CMC with muscles tonically active during standing balance is minimal (Masakado et al. 2008; Luu, 2010; Murnaghan et al. 2014; Jacob et al. 2015). Part of this may be related to between-subject variability in the ability to generate detectable CMC during any type of contraction, with some studies suggesting CMC for muscles of the lower leg is only detectable in 45-65% of healthy individuals (Luu, 2010; Ushiyama et al. 2011). However, even in studies that have limited their analyses to participants capable of generating detectable CMC during an isometric contraction, CMC is still relatively low during standing (Luu, 2010; Murnaghan et al. 2014). This may simply reflect that there is limited corticospinal control of postural muscles during unperturbed standing under normal conditions. However, under conditions of threat, where conscious effort is directed to the control of sway (Zaback et al. 2016), stronger CMC may be observed.

In contrast to CMC, IMC provides an estimate of common synaptic input to different motor pools. While multiple afferent and efferent sources can contribute to IMC, the frequencies at which coherence occurs can provide some insight into the possible source of the neural drive (Grosse et al. 2002). For example, startling acoustic stimuli have been found to evoke increases in bilateral 10-20 Hz IMC that cannot be replicated by voluntary contractions (Grosse and Brown 2003; Blouin et al. 2006). Since the startle response is thought to be mediated by the reticulospinal tract, it has been suggested that 10-20 Hz IMC may have a reticulospinal component (Grosse and Brown 2003). Likewise, corticospinal drive to muscle can be inferred from higher frequency IMC, as both beta- and gamma IMC are reduced in disorders affecting corticospinal tract neurons (i.e., primary lateral sclerosis; Fisher et al. 2012) and are highly correlated with changes in motor-evoked potentials over the course of rehabilitation in individuals with incomplete spinal cord injuries (Norton and Gorassini, 2006). Previous work has shown that IMC within these frequency bands can be observed between muscles of the lower leg while standing, particularly during more challenging standing conditions (Boonstra et al. 2009; Nandi et al. 2019) or in individuals with poorer balance control (Obata et al. 2014; Watanabe et al. 2018). Thus, estimates of CMC and IMC can be used as neural correlates of descending drive to muscles engaged in the control of standing balance.

The primary aim of this study was to determine how estimates of CMC and IMC are influenced by height-induced postural threat. These analyses focused primarily on the SOL bilaterally since this muscle has a consistent level of background activity when standing at both low and high threat conditions (Carpenter et al. 2001; Zaback et al. in press). Based on previous work that has shown individuals attempt to consciously control their movement when standing under conditions of increased postural threat, high frequency IMC (>20 Hz) and beta- (15-30 Hz) and gamma- (31-40 Hz) CMC were expected to be facilitated by postural threat. Furthermore, based on known neuroanatomical connections between fear and arousal networks and the reticular formation (Balaban, 2002; Staab et al. 2013), 10-20 Hz IMC was also expected to be facilitated by postural threat. A secondary aim of this study was to examine how estimates of CMC and IMC adapt over the course of repeated threat exposure. Since previous work has shown that only specific components of the behavioural response to threat attenuate over the course of repeated threat exposure (i.e., high frequency COP oscillations and plantar/dorsiflexor coactivation), examining how estimates of CMC and IMC adapt can provide insight into how changes in descending drive affect specific components of the behavioural response to threat. Since estimates of corticospinal and reticulospinal drive are expected change as a function of attention and fear/arousal, respectively, each are expected to show attenuation after repeated threat exposure.

5.2 Methods

5.2.1 Participants

Twenty-eight healthy young adults (mean age ±SD = 23.8 ±4.6 years; 17 males) participated in this study. Participants were free of neurological and musculoskeletal disorders that could impair their balance. No participants reported having an extreme fear of heights. All procedures were reviewed and cleared by the University of British Columbia's Clinical Research Ethics Board and participants provided written informed consent prior to completing the experiment.

5.2.2 *Procedures*

Since significant CMC for muscles of the lower leg is only obtainable in 45-65% of healthy individuals (Luu, 2010; Ushiyama et al. 2011), participants completed a screening protocol prior to the experimental procedures. This involved performing a 2-minute seated isometric plantarflexion contraction against a 23 kg load (Murnaghan et al. 2014). This type of contraction was selected as beta-band coherence is strongest during weak to medium force isometric contractions (Ushiyama et al. 2012). Only those participants who demonstrated measurable CMC during this test contraction (see Figure 5-1) were included in analyses of CMC (Murnaghan et al. 2014).

Participants completed a series of 90-s trials of quiet standing at two different conditions of height-induced postural threat. Throughout each trial, participants stood barefoot on a force plate (BP400600, AMTI, USA) positioned at the edge of a hydraulic lift (1.52 m × 2.13 m; Pentalift, Canada) with their toes aligned to the anterior edge of the plate and a stance width equal to the length of their foot. The borders of participants' feet were marked on the force plate to ensure consistent foot position across trials. For the LOW threat condition, the platform was positioned at its lowest height (0.8 m above ground) and a table (1.6 m × 0.6 m) was positioned in front of the platform, creating 60 cm of continuous support surface in front of the participant. Previous work has shown that these standing conditions are comparable to standing at ground level (Carpenter et al. 2001). For the HIGH condition, the platform was raised to 3.2 m above the ground and participants stood directly at the platform edge.

Participants completed 3 quiet standing trials at the LOW condition before (LOW_{pre}) and after (LOW_{post}) a block of 15 quiet standing trials at the HIGH condition. This blocked presentation order was selected to maximize the rate of within-session habituation (Rowe and

Craske, 1998; Lang and Craske, 2000). Previous work has shown that 15 trials at the HIGH condition is sufficient to substantially reduce and plateau the psychological and autonomic response to threat (Zaback et al. 2021a). Prior to completing the first block of LOW trials, participants completed a single 90-s practice trial to minimize possible first trial effects (Adkin et al. 2000; Zaback et al. 2021b). Participants were instructed to stand quietly with their arms at their sides while fixating their gaze on a visual target (9cm^2 red square on a white wall 3.87m away at eye level). Participants were given the additional instruction to avoid excessive blinking and/or contractions of facial, head, or neck muscles which may introduce artifacts into the EEG. One to two minutes of seated rest were provided between trials to minimize fatigue. Throughout the experimental procedures, participants wore a safety harness that was secured by climbing rope to an overhead beam. The tension of the rope was adjusted such that it did not provide any support during standing, but would support the participant's body weight above the platform if a fall occurred. A spotter was seated directly behind the participant and was trained to provide support if the participant ever appeared unsteady. No participants fell or required support from the spotter during any trials.

5.2.3 Data collection

Muscle activity was recorded bilaterally from the soleus (SOL) and tibialis anterior (TA) from pairs of Ag/AgCl surface electrodes (2 cm inter-electrode distance). Electroencephalography (EEG) was recorded from a 32-channel elasticized cap with electrodes positioned according to the International 10-20 system (ANTWG32, ANT Neuro, Netherlands). Data were recorded from electrodes positioned over Fp1, Fp2, Fz, Cz, Pz, and Oz referenced to digitally-linked mastoids. A ground electrode for both EEG and EMG recordings was placed at AFz. EEG electrode impedances were maintained below 5 kΩ throughout the experiment. EMG and EEG data were analog filtered (0-553Hz), amplified, and A-D sampled at 2048 Hz (Porti7, ANT Neuro, Netherlands). Ground reaction forces and moments were amplified and A-D sampled at 100 Hz from the force plate. Skin conductance was recorded from Ag/AgCl electrodes placed on the thenar and hypothenar eminences of the left hand (Model 2502SA, CED, UK) and A-D sampled at 100 Hz.

Self-reports of emotional and cognitive state were probed at pre-defined points over the course of the experimental procedure. This included the first trial of the LOW_{pre} and LOW_{post} blocks, and every third trial across the HIGH condition (i.e., 1, 4, 7, 10, 13). Before each of these trials, participants were asked to rate how confident they were that they could maintain their balance and avoid a fall during the upcoming balance task. After each trial, participants completed single-item questionnaires which assessed their cognitive and somatic anxiety and fear of falling. Responses to each of these items were rated on a 0-100 point visual analog scale, with higher scores reflecting greater balance confidence, cognitive and somatic anxiety, and fear of falling. Scores on the questions of cognitive and somatic anxiety were averaged to create a state anxiety score (Zaback et al. 2019; Johnson et al. 2019a). An additional five-item questionnaire was completed to assess how much participants directed their attention toward specific information during each trial (Johnson et al. 2019a). Single questions asked participants to report how much they focused on: 1) movement processes (i.e., conscious control or monitoring of movement); 2) threat-related stimuli (i.e., feelings of anxiety or worry); 3) self-regulatory strategies (i.e., coping strategies); 4) task-objectives (i.e., specific goals or instructions related to the task); 5) task-irrelevant information (i.e., thoughts unrelated to the balance task). Responses to each of these items were rated on a 9-point Likert scale, with higher scores indicating more attention directed toward that specific information.

5.2.4 Data analysis

5.2.4.1 EEG and EMG pre-processing

EMG data were band-pass (10-250 Hz) filtered offline using a 4th order dual-pass Butterworth filter and then full-wave rectified. Rectification was considered necessary for calculation of IMC and CMC in order to capture the temporal pattern of grouped motor unit discharge (Boonstra and Breakspear, 2012; Dakin et al. 2014).

EEG data were band-pass filtered (1-50 Hz) offline using a 4th order dual-pass Butterworth filter. Large blink artifacts were identified using a threshold algorithm. Data from the two electrodes closest to the eyes (Fp1 and Fp2) were averaged and one of two possible thresholds was selected: ±4 SDs of this averaged time series data or ±50 µV. Large artifacts were identified as voltage deflections which exceeded the lower of the two thresholds for at least 80 ms. The data were then segmented into 1-s epochs, and epochs containing large artifacts were removed. These same epochs were also removed from the EMG data when completing analyses of CMC. This was done to ensure EEG and EMG signals remained aligned after artifact rejection.

5.2.4.2 Intermuscular coherence

To examine the strength of oscillatory coupling between right and left SOL, coherence was calculated using methods developed by Halliday and colleagues (1995). Coherence reflects the linear dependence or correlation between two signals in the frequency domain. To calculate coherence, data are first separated into 1-s, non-overlapping segments (resulting in 1 Hz frequency resolution). Coherence ($C_{xy}(f)$) was then calculated using the following equation:

$$\left|C_{xy}(f)\right| = \frac{|P_{xy}(f)|^2}{P_{xx}(f) \cdot P_{yy}(f)}$$

where $P_{xy}(f)$ is the averaged cross-power spectral density (PSD) function between the two muscle pairs across all segments at a given frequency, and $P_{xx}(f)$ and $P_{yy}(f)$ are the averaged auto-PSD functions of each muscle across all segments at a given frequency. To improve the reliability of coherence estimates, data were concatenated across consecutive blocks of 3 trials. For example, data from the first 3 LOW trials were concatenated ($LOW_{1,\ 2,\ and\ 3} = LOW_{pre}$) creating a block of data 270-s in duration. Figure 5-2 illustrates the trials that were concatenated into specific blocks and details the naming conventions used for these conditions.

IMC coherence values are presented in two ways. First, data for the right and left SOL for LOW_{pre}, $HIGH_{pre,}$ and $HIGH_{post}$ were concatenated across all participants. IMC was then calculated for these pooled data. 95% confidence limits were calculated based on the number of disjoint segments used to derive estimates of pooled IMC (Halliday et al. 1995). IMC at a given frequency was considered statistically significant when it exceeded the 95% confidence limit. These estimates of pooled IMC were compared across threat conditions using pairwise difference of coherence tests. These pooled analyses were used to determine the frequencies where significant IMC occurred and provide a visual representation of how it changed as a function of threat and repeated threat exposure. For the main statistical analyses, IMC within pre-defined frequency bands (10-20 Hz and 21-40 Hz) was calculated for individual participant data across each block of trials outlined in Figure 5-2. Prior to calculating mean coherence, the variance of coherence was stabilized by transforming the square root coherence (a complex valued function termed coherency) using an arctanh transformation (Halliday et al. 1995).

5.2.4.3 Corticomuscular coherence

Analyses of CMC focused exclusively on coupling between Cz and both SOL muscles. Cz was selected because CMC is typically strongest at this site for muscles of the lower leg

(Salenius et al. 1997; Luu, 2010; Ushiyama et al. 2011). Since there was no reason to expect differences in CMC between left and right sides, data from the right and left SOL were pooled. For participants to be included in the analyses of CMC, they needed to demonstrate significant CMC across at least 4 of 6 consecutive frequency bins (frequency resolution: 1 Hz) within the beta-band during the isometric screening contraction (described in Figure 5-1).

CMC was analyzed and reported using the same approach outlined above for IMC. However, for individual participant data, mean CMC was calculated within beta- (15-30 Hz) and gamma-bands (31-40 Hz). Furthermore, unlike estimates of mean IMC, which were always derived from 270, 1-s disjoint segments, the number of segments from which estimates of CMC were derived were not consistent across trials or participants due to variance in EEG artifact rejection. While the number of segment removals did not systematically differ between blocks of trials (see Table 5-1), the number of segments used can influence estimates of coherence. Thus, mean coherence values for estimates of CMC were normalized to segment number using the following equation:

$$Z = (\text{atanh}\left(\sqrt{C}_{xy}(f)\right) * (\sqrt{2 * L})$$

where $C_{xy}(f)$ is coherence between Cz and SOL at each frequency and L is the number of segments used to estimate the spectrum.

5.2.4.4 Mean muscle activation and coactivation

Tonic muscle activity of SOL and TA were calculated as mean rectified EMG averaged between both legs. To calculate SOL-TA coactivation, SOL and TA data were normalized to maximal voluntary contractions and then low-pass filtered (3 Hz, 5^{th} order dual-pass Butterworth filter). SOL-TA coactivation was then determined for each leg by calculating the absolute overlap of the SOL and TA linear envelopes (Crenna et al. 1992; Frost et al. 1997). Estimates of coactivation for both legs were then averaged for each participant.

5.2.4.5 Sympathetic activation

To provide an estimate of sympathetic activation, non-specific electrodermal response frequency (EDR.freq) was calculated from electrodermal data. EDA data were first low-pass filtered (2 Hz cutoff, 5th order dual-pass Butterworth filter) and then a customized, semi-automated algorithm identified and counted all electrodermal responses with peak amplitudes greater than 0.05 μS (Boucsein et al. 2012). All identified EDRs were visually inspected and any false positive due to movement artifacts or other noise contaminants were manually rejected (Boucsein, 2012).

5.2.4.6 Centre of pressure outcomes

Ground reaction forces and moments were first low-pass filtered (10 Hz cutoff, 2nd order dual-pass Butterworth filter). Since the effect of height-induced threat is greatest in the anterior-posterior direction when individuals are facing the platform edge (Adkin and Carpenter, 2018), only anterior-posterior COP was calculated. From these data, the mean COP position (MPOS-COP) was calculated to provide an estimate of how far individuals leaned toward or away from the edge. The COP signal was then debiased and a linear detrend was applied. From these data, root mean square (RMS-COP) and mean power frequency (MPF-COP) were calculated to provide an estimate of the average amplitude and frequency content of COP oscillations, respectively. Relevant changes in COP frequency content were further quantified by calculating mean power within three specific frequency bands that have been shown to be uniquely affected by initial and repeated threat exposure: 0-0.05 Hz (low), 0.5-1.8 Hz (medium), and 1.8-5 Hz (high; Zaback et al. 2019; 2021a).

5.2.5 Statistical analyses

Prior to conducting statistics on the COP, EDA, and EMG outcomes, each variable was averaged across consecutive blocks of three trials (Figure 5-2). This allows these data to be analyzed at the same time points as estimates of IMC and CMC, which were calculated from data concatenated across the same blocks of trials. This has the added benefit of reducing variability for each of these outcomes.

To examine how psychological and autonomic state, standing balance, and estimates of mean IMC and CMC were affected by threat and repeated threat exposure, a series of two-way (Threat: LOW vs HIGH; Trial: Pre vs Post) repeated measures ANOVAs were conducted. Significant threat × trial interactions were followed-up with Bonferroni corrected paired-samples t-tests that examined the effect of threat across both levels of trial, and the effect of trial across both levels of threat (alpha = 0.0125).

Several outcomes were positively skewed; this included: low- and high-frequency COP power, mean TA EMG, mean gamma CMC, and mean 21-40 Hz IMC. To reduce this skewness and minimize the influence of extreme cases, $\log_{10}$ transformations were applied to these data prior to statistical analyses. All figures present the non-transformed data.

5.3 Results

5.3.1 Psychological and autonomic state

Significant threat × trial interactions were observed for measures of confidence, anxiety, fear of falling, EDR.freq, and attention toward threat-related stimuli (p-values $\leq$0.001; Table 5-2). Follow-up comparisons (summarized in Table 5-3) revealed that when participants were initially exposed to the threat, they were less confident, more anxious, fearful, and physiologically aroused, and they directed more attention toward threat-related stimuli. For each of the aforementioned outcomes, the effect of threat was significantly reduced after repeated threat exposure. This resulted from each measure showing significant attenuation across the block of HIGH trials, with either limited or non-significant change occurring across the LOW blocks (Figure 5-3; Table 5-3). While the effect of threat was reduced, each of these outcomes remained significantly different from LOW_{post} values (Table 5-3), indicating there was still a residual effect of threat.

For the remaining psychological and autonomic state measures, significant main effects of threat were observed for attention toward movement processes and self-regulatory strategies (p-values ≤ 0.001). Individuals directed more attention toward this information at the HIGH compared to LOW condition independent of trial. Significant main effects of trial were also observed for attention toward movement processes, self-regulatory strategies, task objectives, and task-irrelevant information. Individuals directed less attention toward their movement, self-regulatory strategies, and task objectives, and more attention toward task-irrelevant information as a function of time independent of threat condition (p-values ≤ 0.001) (Table 5-2).

5.3.2 Centre of pressure outcomes

Significant threat × trial interactions were observed for MPF-COP and medium- (0.5-1.8 Hz) and high- (1.8-5 Hz) frequency COP power (p-value range: <0.001 - 0.018; Table 5-2). Follow-up comparisons (summarized in Table 5-3) revealed that when participants were initially exposed to height-induced threat, they demonstrated significantly greater MPF-COP and medium- and high-frequency COP power. For each of the aforementioned outcomes, the effect of threat was significantly reduced after repeated threat exposure. The reduced effect of threat for MPF-COP and high-frequency COP power resulted from significant reductions in both of these outcomes occurring from the Pre to Post blocks of the HIGH condition only. For medium-frequency COP power, the effect of threat was no longer significant by the Post block of the HIGH condition (Table 5-3, Figure 5-4).

Significant main effects of threat were observed for all remaining COP outcomes. In particular, at the HIGH condition, participants shifted their MPOS-COP significantly backward and demonstrated significant reductions in RMS-COP and low-frequency COP power (p-values <0.001; Table 5-3). Significant main effects of trial were also observed for MPOS-COP and RMS-COP, such that individuals shifted their MPOS-COP forward (p=0.003) and increased RMS-COP (0.043) as a function of time independent of threat condition (Table 5-2, Figure 5-4).

5.3.3 Mean EMG and plantar/dorsiflexor coactivation

Significant threat × trial interactions were observed for mean TA EMG and SOL-TA coactivation (p-values ≤0.001; Table 5-2). Follow-up comparisons revealed that when individuals were initially exposed to height-induced threat, there were significant increases in mean TA EMG and SOL-TA coactivation (p <0.001; Table 5-3). For each of these outcomes, the effect of threat was significantly reduced after repeated threat exposure. The reduced effect of threat resulted from mean TA EMG and SOL-TA coactivation showing greater reductions from the Pre to Post levels of the HIGH condition compared to the LOW condition (Table 5-3; Figure 5-4). For mean SOL EMG, a significant main effect of threat was observed (p <0.001), such that mean SOL EMG was reduced at the HIGH condition independent of trial (Table 5-2; Figure 5-4).

5.3.4 Corticomuscular coherence (Cz-SOL)

Fourteen participants in this study had detectable CMC based on the results of the screening protocol; analyses of CMC were limited to these participants. Pooled coherence estimates showed that there was significant Cz-SOL CMC during quiet standing at both the LOW and HIGH threat conditions (Figure 5-5A). During the first block of LOW trials, CMC was significant primarily within the beta-band (~19-31 Hz). During the first block of HIGH trials, there was a broadening of the bandwidth of CMC, with significant CMC seen in both beta and gamma bands (~14-16 Hz and 20-45 Hz). A difference of coherence test revealed that CMC was significantly greater at the $HIGH_{pre}$ compared to LOW_{pre} condition at 16, 32, 34, 36, and 38 Hz and significantly smaller at 24 Hz. After being repeatedly exposed to the threat, significant CMC was again confined primarily to the beta-band. A difference of coherence test revealed that from that Pre to Post block of the HIGH condition, CMC decreased primarily in the gamma-band, with significant reductions occurring at 30, 33, 35, and 36 Hz (Figure 5-5A).

Analyses of mean CMC revealed a significant threat × trial interaction for gamma-band CMC (p=0.013; Table 5-2; Figure 5-5B). Follow-up comparisons revealed that this interaction was the result of two statistical trends. Specifically, gamma-band CMC increased when individuals were first exposed to the threat (p=0.062) and subsequently decreased from Pre to Post blocks of the HIGH (p=0.019), but not LOW condition (p=0.981; Table 5-3). No significant interactions or main effects were observed for beta-band CMC (Table 5-2).

5.3.5 Intermuscular coherence (SOL_R – SOL_L)

Pooled coherence estimates showed that there was significant SOL_R-SOL_L IMC across a broad frequency range (~1-32 Hz) when standing at the LOW condition, with the strongest coherence occurring below 5 Hz. During the $HIGH_{pre}$ block, significant coherence was observed across approximately the same frequency band, distinct peaks were also observed at 8, 15, and 28 Hz. Difference of coherence tests revealed that when individuals were first exposed to the threat, IMC decreased between 1-3 Hz and increased between 5-19 Hz and approximately 22-31

Hz (Figure 5-6A). After being repeatedly exposed to threat, significant IMC was observed across approximately the same frequency band, but the distinct peaks at 8, 15, and 28 Hz appeared to level off. Difference of coherence tests revealed that from the Pre to Post block of the HIGH condition, IMC significantly increased between 1-3 Hz and decreased between 5-10, 13-19 Hz, and 22-31 Hz (Figure 5-6A).

Since significant IMC was observed between 1-9 Hz and was shown to be influenced by threat such that IMC decreased at and below 3 Hz and increased at and above 5 Hz, mean IMC for each participant was calculated between 1-3 Hz and 5-9 Hz in addition to the two other pre-defined frequency bands (i.e., 10-20 and 21-40 Hz).

Analyses of mean coherence revealed a significant threat × trial interaction for 21-40 Hz IMC (p=0.010). Follow-up comparisons revealed that when individuals were initially exposed to height-induced threat, 21-40 Hz IMC was significantly increased (p=0.001). The effect of threat for IMC in this frequency band was reduced over the course of repeated threat exposure due to significant reductions from the $HIGH_{pre}$ to $HIGH_{post}$ condition (p<0.001), but not the LOW condition (p=0.452; Figure 5-6B). A significant threat × trial interaction was also observed for 1-3 Hz IMC (p=0.030). Follow-up comparisons revealed that this interaction was the result of two statistical trends. Specifically, 1-3 Hz IMC decreased when individuals were first exposed to threat (p=0.089) and subsequently increased from Pre to Post blocks of the HIGH (p=0.073; Table 5-2; Figure 5-6B). There were no significant threat × trial interactions for 5-9 Hz or 10-20 Hz IMC, although there were significant main effects of threat and trial. IMC in both frequency bands were increased at the HIGH condition and decreased as a function of time independent of threat condition (p-value range: <0.001 - 0.006; Table 5-2; Figure 5-6B).

5.4 Discussion

This study investigated how exposure to a height-related postural threat affects descending drive to muscle engaged in the control of standing balance, inferred through estimates of CMC (Cz-SOL) and IMC (SOL_R-SOL_L). When standing under non-threatening conditions, CMC was confined largely to the beta-band (15-30 Hz), while IMC was observed primarily at lower frequencies (<5 Hz). Exposure to threat induced significant changes in both CMC and IMC. Specifically, CMC increased within the gamma-band (31-40 Hz), while IMC tended to decrease across lower frequencies (<3 Hz) and increase across higher frequencies (>5 Hz). Following repeated threat exposure, individuals' psychological and autonomic response to threat was attenuated, and this was accompanied by reductions in gamma-band CMC and high frequency (21-40 Hz) IMC, and increases in low frequency IMC (<3 Hz). These results suggest that postural threat increases descending drive to muscles that are continually engaged in the control of standing balance, and components of this altered drive are prone to habituation following repeated threat exposure.

5.4.1 Evidence for increased corticospinal drive under conditions of postural threat

Corticospinal drive to the SOL was indirectly assessed from estimates of beta- and gamma-band CMC and high-frequency (21-40 Hz) IMC. Analyses of CMC were limited to those participants who demonstrated detectable CMC during a seated and sustained isometric plantarflexion contraction, while IMC was examined across the entire cohort of participants. Regardless, both set of analyses yielded convergent results. Under non-threatening conditions, participants demonstrated significant, albeit very low, levels of beta-band CMC and high frequency IMC. This finding is consistent with previous evidence suggesting that there is direct, but relatively weak, corticospinal control of balance when performing relatively simple postural tasks such as quiet standing (Luu, 2010; Jacobs et al. 2015). Once individuals were exposed to threat, both estimates of corticospinal drive were facilitated. However, the effect of threat on CMC was frequency-specific, as only gamma-band CMC tended to increase under these conditions.

Increased gamma-band CMC has been observed during very forceful contractions (Brown et al. 1998), phasic contractions (Marsden et al. 2000; Omlor et al. 2007; Andrykiewicz et al. 2007; Gwin and Ferris, 2012), and isometric contractions when a phasic motor response is planned (Schoffolen et al. 2005; 2011). It is unlikely that the increases in gamma-band CMC observed in the present study were related to differences in the forcefulness of the plantarflexion contraction, since the mean level of SOL activity tended to decrease under conditions of threat (Figure 5-4; Carpenter et al. 2001; Zaback et al. 2021a). It is possible that increases in gamma-band CMC were related to changes in the dynamics of standing balance control, since the amplitude of high frequency (>0.5 Hz) COP oscillations increased with postural threat and changed in parallel with estimates of gamma-band CMC after repeated threat exposure. These changes in high frequency COP oscillations are likely to be accompanied by more phasic contractions of the SOL, potentially contributing to the emergence of gamma-band CMC (Gwin and Ferris, 2012). An altered state of motor preparation may have also contributed (Schoffelen et al. 2005; 2011), since individuals reported directing more attention toward their movement when threatened (Figure 5-3) and may have been more primed to respond to any perceived postural instability in this context.

Unlike estimates of CMC, the effects of threat and repeated threat exposure on high-frequency IMC were not confined to the gamma-band (Figure 5-6A). In fact, when mean IMC is calculated within beta (21-30 Hz) and gamma (31-40 Hz) regions of the high-frequency bandwidth, both estimates of IMC demonstrate a similar effect of threat and repeated threat exposure (Figure 5-7). While estimates of high-frequency IMC are highly correlated with estimates of corticospinal excitability (Power et al. 2006; Norton and Gorassini, 2006; Fisher et al. 2012), they do not always show an identical pattern of change relative to corresponding estimates of CMC (Jensen et al. 2019; McClelland et al. 2020). This suggests that IMC and CMC within the same bandwidths may reflect separate cortical processes (e.g., mono- vs. polysynaptic corticospinal input; corticospinal input to single vs. multiple motor pools, etc.). It is also possible that high-frequency IMC is not a pure surrogate of corticospinal drive and may be influenced by common synaptic input from subcortical or spinal sources (Grosse et al. 2002; Thompson et al. 2019). Nevertheless, threat-induced changes in CMC and high-frequency IMC were largely consistent, strongly suggesting that threat induces greater corticospinal involvement in the control of balance. In addition, the observation that each of these estimates tended to habituate over the course of repeated threat exposure suggests that threat-related increases in corticospinal drive are coupled with psychological and autonomic state changes induced by the threat. It is unclear whether cognitive or physiological changes associated with threat are responsible for this increased corticospinal involvement. Since cognitive factors, such as attention toward movement (Kristeva-Feige et al. 2002; Stepp et al. 2011) and motor readiness (Schoffelen et al. 2005) have been shown to increase beta- and gamma-band CMC and IMC, and arousal state has been shown to influence corticospinal excitability (Hajcak et al. 2007; Coelho et al. 2010), changes in both attention and arousal likely contribute to threat-related increases in corticospinal drive to the SOL.

5.4.2 Evidence for increased reticulospinal drive under conditions of postural threat

Bilateral SOL IMC between 10-20 Hz was calculated in the present study to provide an indirect estimate of reticulospinal drive (Grosse and Brown, 2003; Blouin et al. 2006). Since the reticular formation receives excitatory inputs from the amygdala and parabrachial nucleus directly or indirectly via the vestibular nuclei (Balaban, 2002; Staab et al. 2013), and these nuclei are more active in states of fear and arousal, it was expected that IMC within this frequency band would be facilitated by postural threat and covary with changes in emotional state over the course of repeated threat exposure. The results of this study partially supported this hypothesis, as 10-20 Hz IMC was facilitated under conditions of threat, but the effect of threat was not significantly reduced after repeated threat exposure. These results may suggest that reticulospinal input to the SOL is facilitated under conditions of postural threat, but this change in descending drive is somewhat independent of individuals' psychological and autonomic response to threat. It is unclear why IMC between 10-20 Hz showed relatively limited habituation over the course of repeated threat exposure. Something that could have contributed to this is the threat-induced backward lean. Previous work has shown that forcing individuals to adopt a backward lean induces bilaterally coherent lower-limb muscle activity between 13-18 Hz (Sharott et al. 2003). Since the threat-induced backward lean is largely preserved over the course of repeated threat exposure to heights, this may have contributed to the limited habituation of IMC between 10-20 Hz. It must also be acknowledged that IMC within the 10-20 Hz bandwidth is not likely a pure surrogate of reticulospinal drive, as other cortical (Fisher et al. 2012), subcortical (Dakin et al. 2007), and spinal mechanisms (Christakos et al. 2006; Williams et al. 2010) can generate motor oscillations which overlap with this frequency band and it is unclear how these other potential inputs may vary with emotional state.

5.4.3 *Other changes in common synaptic input induced by postural threat*

While this study made specific hypotheses related to IMC within 10-20 Hz and 21-40 Hz frequency bands, postural threat was also found to reduce IMC at and below 3 Hz and increase IMC between 5-9 Hz. The neural origin of IMC within each of these lower frequency bandwidths are not well established. The 5-9 Hz band roughly corresponds to the frequency of the physiological force tremor (6-12 Hz) that is observed during steady contractions (McAuley and Marsden, 2000). Potential mechanisms contributing to force tremor include olivary-cerebellar (Llinas and Pare, 1995) and cerebello-thalamo-cortical networks (Schnitzler et al. 2006), and muscle spindle feedback loops (Christakos et al. 2006; Erimaki and Christakos, 2008). Since postural threat is thought to increase muscle spindle dynamic sensitivity (Davis et al. 2011; Horslen et al. 2013; 2018), changes in muscle spindle feedback may have contributed to the observed increases in 5-9 Hz IMC. It is also possible that the vestibulospinal system contributed, since previous work has shown that electrical vestibular stimulation elicits coherent responses in muscles of the triceps surae which peak between 5-7 Hz (Dakin et al. 2007) and are facilitated under conditions of threat (Horslen et al. 2014; Lim et al. 2017). However, vestibular-evoked responses have been found to change as a function of arousal state (Collins and Poe, 1960; Yardley et al. 1995) and have been positively correlated with threat-related changes in fear and anxiety (Naranjo et al. 2015; Lim et al. 2017). Since the effect of threat on 5-9 Hz IMC was not significantly reduced after repeated threat exposure despite significant reductions in fear and arousal, it is unlikely that vestibulospinal changes alone can explain this change in IMC.

IMC between muscles of the lower leg at and below 3 Hz has been consistently observed during quiet standing (Mochizuki et al. 2006; Saffer et al. 2008; Boonstra et al. 2008; 2009; Obata et al. 2014; Nandi et al. 2019). IMC in this band is thought to be driven by comodulation of muscle activity related to postural sway (Saffer et al. 2008; Boonstra et al. 2009). The results of the present study are partly in line with this hypothesis, since RMS amplitude of COP displacement and low-frequency IMC both decreased when individuals were exposed to threat. However, threat-related reductions in RMS-COP did not change as a function of repeated threat exposure, while low frequency IMC increased and returned to LOW threat values after repeated threat exposure. This could suggest that while low-frequency IMC is related to postural sway in some capacity, it does not scale linearly with changes in sway amplitude (Danna-Dos-Santos et al. 2015; Watanabe et al. 2018; Nandi et al. 2019). It is possible that threat-related changes in low frequency SOL IMC may have been influenced by bilateral activation of the TA. When standing at non-threatening conditions, the TA is typically quiescent (Day et al. 2013) and the SOL is primarily responsible for the control of sway (Heroux et al. 2014). However, the TA becomes active under conditions of threat, which may reflect a change in the muscle synergies used for the control of sway. With the observed shift toward a coactivation synergy with threat, bilateral SOL activation may become decoupled from the control of sway, potentially contributing to a reduction in low frequency SOL IMC. The increase in low frequency SOL IMC over the course of repeated threat exposure coincides with concurrent reductions in TA activation and SOL-TA coactivation (Figure 5-4), providing further support for this speculation.

5.4.4 How might changes in descending drive influence standing balance control?

The observed changes in CMC and IMC indicate that postural threat induces a shift toward synchronous, high frequency grouped motor unit discharge of the SOL during stance. Previous work has provided evidence that such changes in grouped motor unit discharge affect the variability of muscle force. Ushiyama and colleagues (2017) showed a strong, positive association between the magnitude of beta-band CMC and force variability within and below the beta-band during an isometric dorsiflexion contraction. Physiological force tremor of the SOL (calculated as 8-12 Hz mechanical oscillations of the SOL) during standing has also been associated with high-frequency COP power and COP velocity in older adults (Kouzaki and Masani, 2012). Patients with primary orthostatic tremor, a movement disorder characterized by coherent lower limb muscle activity between 13-18 Hz, also demonstrate larger amplitude COP oscillations at and below the tremor frequency (Yarrow et al. 2001). Thus, irrespective of the source of neural drive, more synchronous, high-frequency grouped motor unit discharge may increase muscle force variability, potentially contributing to the increased average frequency content of COP oscillations observed with threat.

In the present study, estimates of corticospinal drive (i.e., gamma-band CMC and high-frequency (21-40 Hz) IMC) were facilitated by threat and habituated after repeated threat exposure. These changes in descending drive, therefore, paralleled changes in high-frequency (>0.5 Hz) COP power and plantar/dorsiflexor coactivation. Previous work has shown that increases in corticospinal excitability are associated with higher velocity COP oscillations during challenging balance tasks (Nandi et al. 2018; 2019). In addition, attention toward postural control, which is presumably associated with increased corticospinal involvement, has been related to increases in the amplitude of high-frequency COP oscillations (Vuillerme and Nafati, 2007; Wuehr et al. 2017; Johnson et al. 2019c) and coactivation of muscles acting at the ankle joint (Reynolds, 2010; Wuehr et al. 2017). Thus, it seems very likely that threat-related changes in corticospinal drive may contribute to threat-related changes in high-frequency COP power and plantar/dorsiflexor coactivation. It is unlikely that changes in corticospinal drive to the SOL contributed to the posterior lean or reductions in COP amplitude and low frequency COP power, since none of these outcomes showed a reduced effect of threat after repeated exposure despite both estimates of corticospinal drive returning to LOW threat values. In contrast, estimates of subcortical drive (5-9 Hz and 10-20 Hz IMC) to the SOL were facilitated by threat, yet showed limited habituation after repeated threat exposure. This suggests that descending drive to the SOL from subcortical sources may not contribute strongly to threat-related increases in high-frequency COP power. However, given that synchronous grouped motor unit discharge between 5-20 Hz is likely to have a mechanical consequence (Yarrow et al. 2001; Enoka et al. 2003; Kouzake and Masani, 2011) and both 5-9 Hz and 10-20 Hz IMC showed some reduction over time, it is difficult to rule out the possibility that subcortical drive to the SOL has no influence on high-frequency COP power. On the other hand, it is possible that common input to the SOL from subcortical sources contributed to, or is at least related to, some threat-related changes in balance control which did not habituate. As discussed earlier, the backward lean that individuals adopt under conditions of threat may contribute to bilaterally coherent EMG within the 10-20 Hz bandwidth (Sharrot et al. 2003). While the lean itself may not be caused by altered reticulospinal drive, it is possible that the reticulospinal system is more involved in the control of balance in this particular posture.

5.4.5 Limitations

This study limited its analyses of CMC and IMC to the SOL. This was done because the SOL has some level of background activation at both LOW and HIGH threat conditions and, therefore, permits comparisons of descending drive to the same muscle engaged in the control of balance. However, it must be acknowledged that the SOL is not the only muscle acting at the ankle that is engaged in the control of standing balance at the HIGH condition. While the TA is typically quiescent at the LOW condition, it shows prominent, bilateral activation at the HIGH condition (Figure 5-4). Since the TA is known to receive greater corticospinal projections than the SOL (Brouwer and Ashby, 1992) and its activation is prone to habituation over the course of repeated threat exposure, it is possible that common input to the TA may contribute substantially to threat-related changes in standing balance control, particularly those which appear most prone to habituation.

In the present study, electrical field potentials over the sensorimotor cortex were analyzed from a single scalp electrode (Cz). While estimates of CMC for muscles of the lower leg are typically strongest at Cz (Salenius et al. 1997; Ushiyama et al. 2011), this varies slightly between individuals and may have limited our ability to optimally record relevant activity of cortical neurons across all participants (Mima et al. 2001). Furthermore, the neural origin of the electrical field potentials coherent with lower limb EMG cannot be determined when relying on a single scalp electrode (Luck, 2014). Previous work has shown that beta-band CMC can originate from either side of the central sulcus (Witham et al. 2010) and is influenced by both descending (corticospinal) and ascending (reafference) pathways (Baker et al. 2007; Witham et al. 2011). While it is unclear if this also applies to estimates of gamma-band CMC, it must be acknowledged that changes in sensory feedback known to occur under conditions of threat (Horslen et al. 2017; 2018) may have contributed to changes in CMC observed in the current study.

To minimize artifacts in the EEG, participants were encouraged to avoid excessive blinking and/or contraction of head, neck, or facial muscles while standing. This arguably introduces a secondary task which may influence how individuals direct their attention and maintain balance control (Woollacott and Shumway-Cook, 2002). However, this dual-task effect was likely inconsequential, as these instructions were consistent across conditions and participants demonstrated threat-induced changes in attention and balance control similar to those previously reported (Zaback et al. 2019; 2021a).

5.5 Conclusions

The present study provides evidence that corticospinal and subcortical descending drive to the SOL, inferred through estimates of CMC and IMC, are facilitated when standing under conditions of height-related threat. Estimates of corticospinal drive habituated in parallel with estimates of psychological and autonomic state after repeated threat exposure, while estimates of subcortical drive appear more resistant to habituation. These results suggest that postural induces a shift toward more supraspinal control of balance and that neural drive from cortical and subcortical sources may influences separate components of the behavioural response to threat.

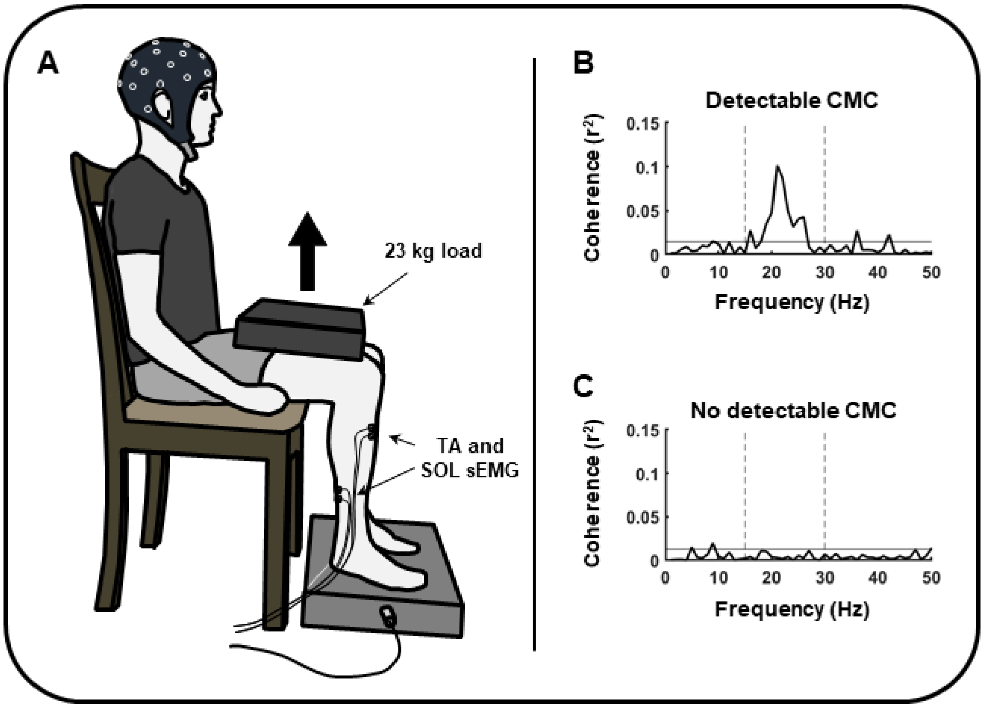

Figure 5-1: Screening protocol for identifying participants with detectable corticomuscular coherence (CMC). Participants completed a 120-s isometric plantar flexion contraction against a 23 kg load (A). For participants to be included in analyses related to CMC they needed to demonstrate significant Cz-SOL CMC (pooled across left and right legs) at no less than 4 of 6 consecutive frequency bins (frequency resolution: 1 Hz) within the beta-band (15-30 Hz). Exemplar coherence spectra for participants with (B) and without (C) detectable CMC are illustrated. Vertical dashed lines denote the bounds of the beta-band; horizontal black lines represent 95% confidence limits, with any coherence estimates exceeding these limits representing frequencies of significant CMC.

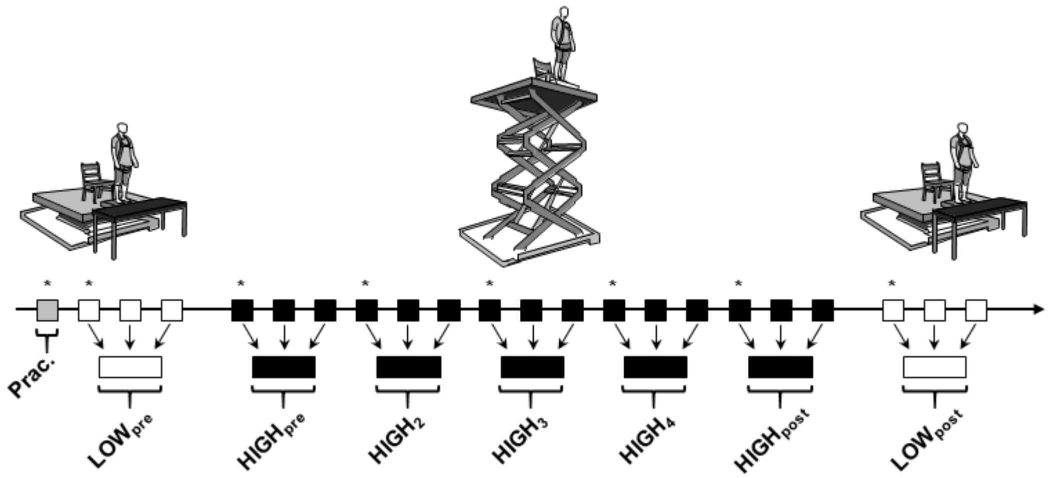

Figure 5-2: Schematic outlining the experimental protocol and grouping of trials. Participants completed a series of 90-s trials of quiet standing at LOW (open squares) and HIGH (filled black squares) conditions. A block of 3 LOW trials were completed before and after a block of 15 HIGH trials. Data from consecutive blocks of 3 trials were combined for analytical purposes; arrows indicate the blocks of trials that were combined. * indicate trials where self-reports of emotional and cognitive state were probed.

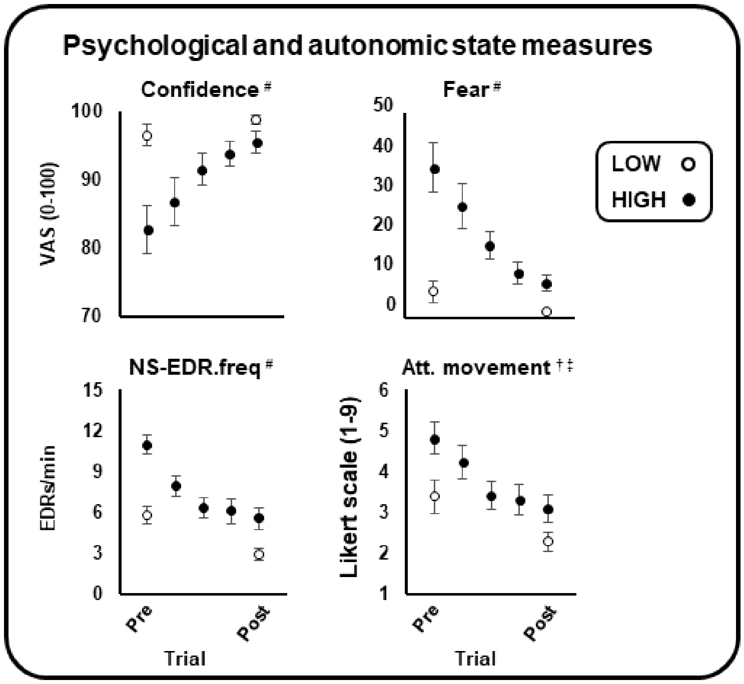

Figure 5-3: Psychological and autonomic state measures across blocks of LOW and HIGH trials. For NS-EDR.freq, each point reflects the average from the 3 trials comprising respective blocks of trials outlined in Figure 2. VAS = visual analog scale; NS-EDR.freq = non-specific EDR frequency; Att. = attention toward. # = significant threat × trial interaction; † = significant main effect of threat; ‡ = significant main effect of trial; alpha = 0.05.

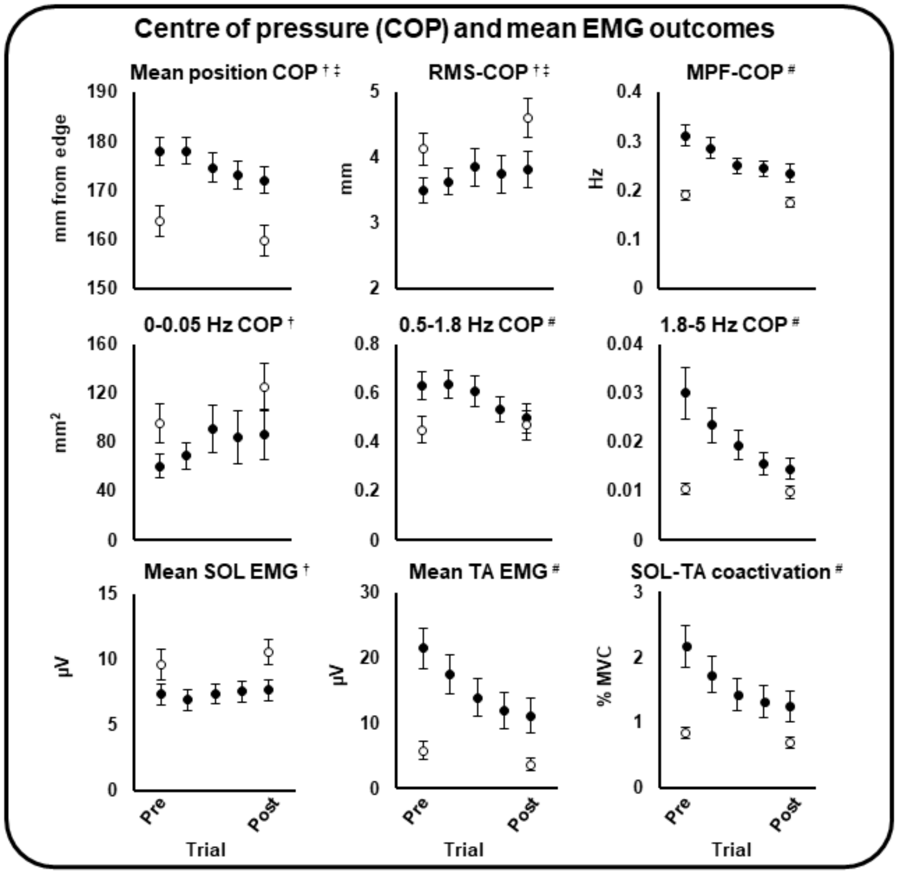

Figure 5-4: Centre of pressure (COP) and mean EMG outcomes for blocks of LOW (○) and HIGH (●) trials. Each point reflects the average from the 3 trials comprising respective blocks of trials outlined in Figure 2. RMS = root mean square; MPF = mean power frequency; SOL = soleus; TA = tibialis anterior; # = significant threat × trial interaction; † = significant main effect of threat; ‡ = significant main effect of trial; alpha = 0.05.

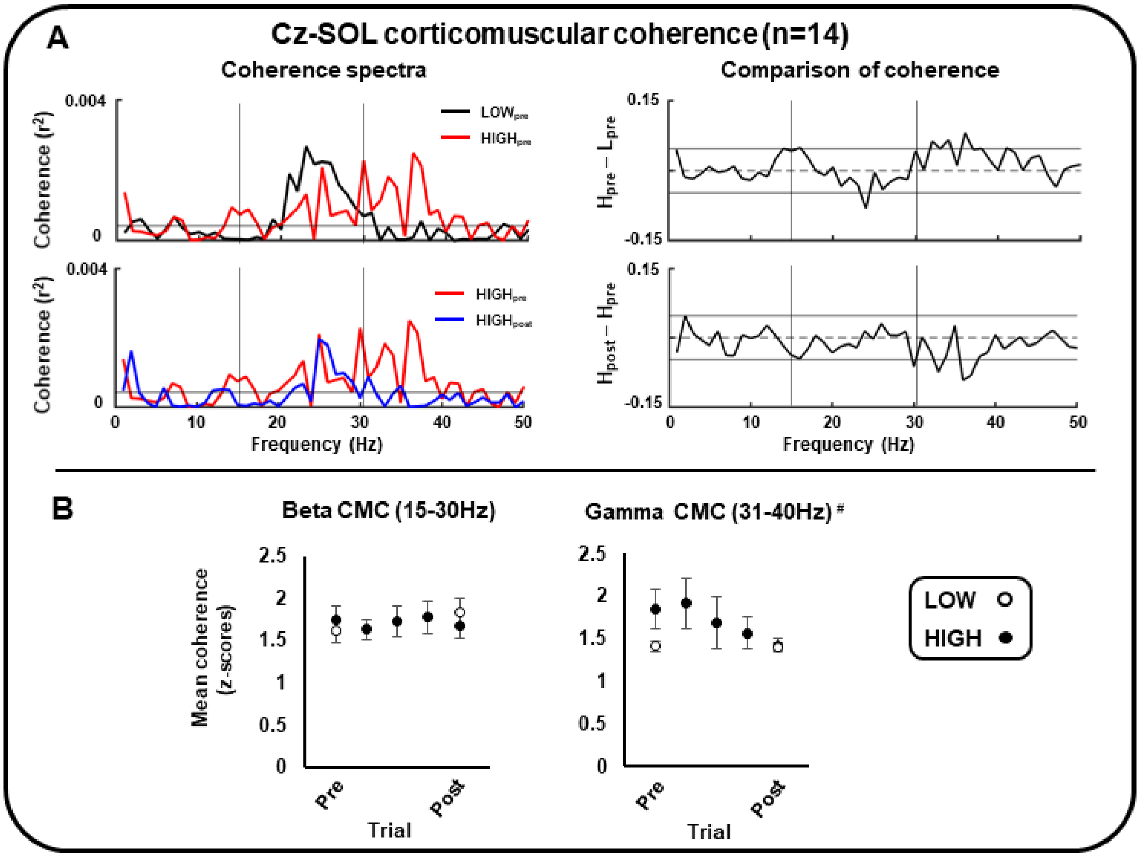

Figure 5-5: Coherence spectra and mean coherence for Cz-SOL corticomuscular coherence (CMC). Panel A presents the coherence spectra from data concatenated across all participants with detectable CMC for LOW_{pre} and $HIGH_{pre}$ (top left) and $HIGH_{pre}$ and $HIGH_{post}$ (bottom left) conditions. Solid horizontal lines reflect 95% confidence limits; vertical dashed lines indicate the boundaries of the beta-band (15-30 Hz). When standing at the LOW condition, significant CMC was limited to the beta-band, but this expanded into the gamma band when participants were first exposed to the HIGH condition. Over the course of repeated threat exposure, CMC in the gamma band was abolished. Statistical comparisons of coherence (top and bottom right of Panel A) indicate the frequencies at which coherence differs between conditions. Horizontal solid lines reflect 95% confidence limits of the difference of coherence. Panel B presents group mean data

for mean CMC calculated within the beta and low gamma bands. # = significant threat × trial interaction; alpha = 0.05.

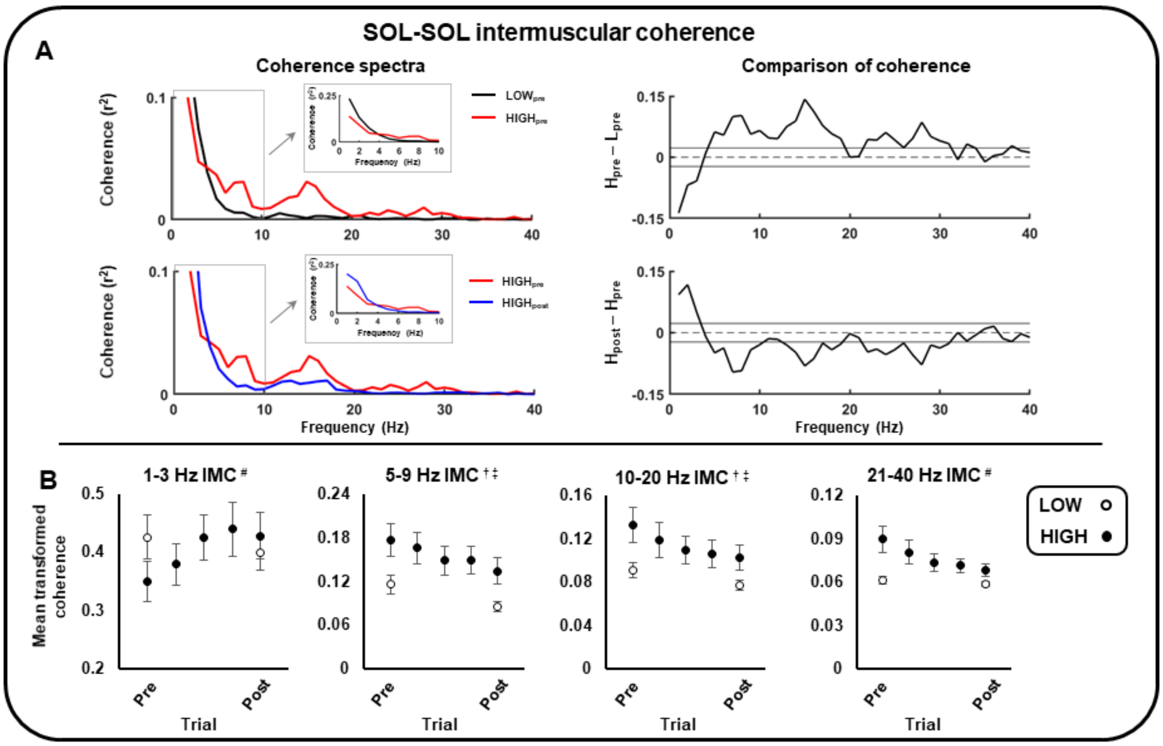

Figure 5-6: Coherence spectra and mean coherence for SOL$_R$-SOL$_L$ intermuscular coherence (IMC). Panel A presents the coherence spectra for LOW$_{pre}$ and HIGH$_{pre}$ (top left) and HIGH$_{pre}$ and HIGH$_{post}$ (bottom left). Solid horizontal lines reflect 95% confidence limits. Insets present the same data from 0-10 Hz on a larger scale to show the stronger IMC at lower frequencies. Statistical comparisons of coherence (top and bottom right of Panel A) indicate the frequencies at which coherence differs between conditions. Horizontal solid lines reflect 95% confidence limits of the difference of coherence. Panel B presents group mean data for mean IMC calculated within 0-3 Hz, 5-10 Hz, 10-20 Hz, and 20-40 Hz. # = significant threat × trial interaction; † = significant main effect of threat; ‡ = significant main effect of trial; alpha = 0.05.

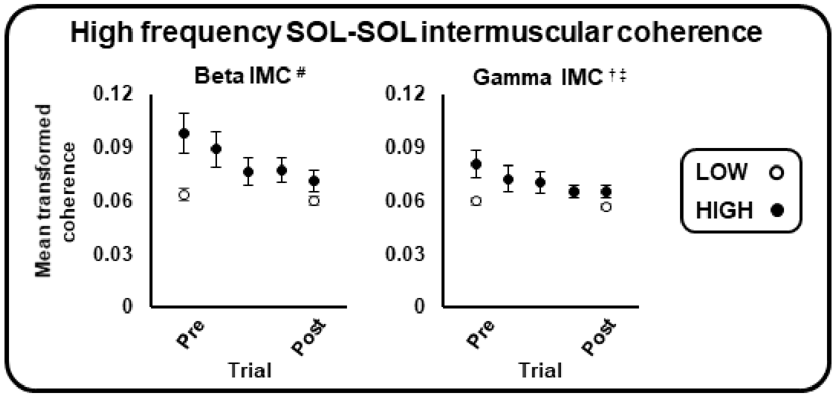

Figure 5-7: High frequency SOL-SOL intermuscular coherence (IMC; 21-40 Hz) split into beta- (21-30 Hz) and gamma (31-40 Hz) regions. Unlike estimates of corticomuscular coherence, SOL-SOL IMC is facilitated by threat exposure at both beta- and gamma-frequencies. # = significant threat × trial interaction; † = significant main effect of threat; ‡ = significant main effect of trial; alpha = 0.05.

Table 5-1: Number of segments removed from each block of trials for estimates of CMC due to EEG artifacts

LOW_{pre}	$HIGH_{pre}$	$HIGH_2$	$HIGH_3$	$HIGH_4$	$HIGH_{post}$	LOW_{post}
13.8 (±13.5)	17.6 (±19.3)	22.1 (±30.7)	19.3 (±19.4)	17.7 (±14.6)	14.4 (±12.3)	13.9 (±12.5)

Values reflect means (± standard deviations) of the total number of segments removed within a block of trials composed of a total of 270 segments.

Table 5-2: RM-ANOVAs for measures of psychological and autonomic state, standing balance, and mean IMC and CMC

	Threat × trial interaction			Threat main effect			Trial main effect		
	$F_{(1,27)}$	p-value	η^2_p	$F_{(1,27)}$	p-value	η^2_p	$F_{(1,27)}$	p-value	η^2_p
Psychological and autonomic state measures									
Confidence	13.433	**0.001**	0.332	18.457	**<0.001**	0.406	23.118	**<0.001**	0.461
Anxiety	19.778	**<0.001**	0.423	29.410	**<0.001**	0.521	31.662	**<0.001**	0.540
Fear	26.462	**<0.001**	0.495	34.491	**<0.001**	0.561	28.420	**<0.001**	0.513
EDR.freq	12.939	**0.001**	0.324	74.036	**<0.001**	0.733	147.075	**<0.001**	0.845
Att. MP	1.477	0.235	0.052	14.214	**0.001**	0.345	33.414	**<0.001**	0.553
Att. TRS	28.588	**<0.001**	0.514	39.706	**<0.001**	0.595	28.024	**<0.001**	0.509
Att. SRS	0.254	0.618	0.009	36.789	**<0.001**	0.577	18.468	**<0.001**	0.406
Att. TO	2.009	0.168	0.069	1.947	0.174	0.067	17.185	**<0.001**	0.389
Att. TI	0.034	0.855	0.001	0.144	0.707	0.005	12.560	**0.001**	0.317
Standing balance measures									
MPOS-COP	1.162	0.291	0.041	54.464	**<0.001**	0.669	10.552	**0.003**	0.281
RMS-COP	0.586	0.451	0.021	21.355	**<0.001**	0.442	4.609	**0.041**	0.146
MPF-COP	6.389	**0.018**	0.191	33.253	**<0.001**	0.552	13.539	**0.001**	0.334
LF power	0.076	0.785	0.003	16.736	**<0.001**	0.383	3.408	0.076	0.112
MF power	7.981	**0.009**	0.228	7.093	**0.013**	0.208	3.242	0.083	0.107
HF power	21.366	**<0.001**	0.442	31.704	**<0.001**	0.540	36.099	**<0.001**	0.572
Tonic SOL	1.111	0.301	0.040	24.608	**<0.001**	0.477	1.551	0.224	0.054
Tonic TA	20.155	**<0.001**	0.427	24.627	**<0.001**	0.477	27.550	**<0.001**	0.505
SOL-TA coactivation	14.217	**0.001**	0.345	30.856	**<0.001**	0.533	46.680	**<0.001**	0.634
Mean corticomuscular coherence									
Beta (15-30Hz)[a]	3.798	0.073	0.226	0.004	0.949	<0.001	1.340	0.268	0.093
Gamma (31-40Hz)[a]	8.295	**0.013**	0.390	1.772	0.206	0.120	3.408	0.088	0.208
Mean intermuscular coherence									
SOL-SOL 0-3 Hz	5.272	**0.030**	0.163	0.535	0.471	0.019	0.747	0.354	0.027
SOL-SOL 5-10 Hz	1.210	0.281	0.043	14.419	**0.001**	0.348	13.985	**0.001**	0.341
SOL-SOL 10-20 Hz	2.654	0.115	0.089	11.958	**0.002**	0.307	13.592	**0.001**	0.335
SOL-SOL 20-40 Hz	7.754	**0.010**	0.223	13.036	**0.001**	0.326	9.608	**0.003**	0.262

Note. EDR.freq = frequency of non-specific electrodermal responses; Att. = attention toward; MP = movement processes; TRS = threat-related stimuli; SRS = self-regulatory strategies; TO = task objectives; TI = task-irrelevant information; COP = centre of pressure; MPOS = mean position; RMS = root mean square; MPF = mean power frequency; LF = low frequency (0-0.05 Hz); MF = medium frequency (0.5-1.8 Hz); HF = high frequency (1.8-5 Hz); SOL = soleus; TA = tibialis anterior. [a] = $F_{(1,13)}$.

Table 5-3: Follow-up comparison p-values for all dependent outcomes that demonstrated significant threat × trial interactions

	$HIGH_{pre}$ vs LOW_{pre}	$HIGH_{pre}$ vs $HIGH_{post}$	$HIGH_{post}$ vs LOW_{post}	LOW_{pre} vs LOW_{post}
		Psychological and autonomic state measures		
Confidence	**<0.001**	**<0.001**	**0.011**	0.047
Anxiety	**<0.001**	**<0.001**	**<0.001**	0.015
Fear of falling	**<0.001**	**<0.001**	**0.001**	0.063
EDR.freq	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Att. TRS	**<0.001**	**<0.001**	**0.001**	0.018
		Standing balance measures		
MPF-COP	**<0.001**	**0.002**	**0.001**	0.110
MF power	**0.006**	0.020	0.351	0.481
HF power	**<0.001**	**<0.001**	**0.001**	0.144
Tonic TA	**<0.001**	**<0.001**	**<0.001**	**0.004**
SOL-TA coactivation	**<0.001**	**<0.001**	**0.005**	**0.011**
		Mean corticomuscular and intermuscular coherence		
Gamma CMC	0.062	0.019	0.926	0.981
SOL-SOL 0-3 Hz	0.089	0.073	0.449	0.442
SOL-SOL 20-40 Hz	**0.001**	**<0.001**	0.026	0.452

Note. EDR.freq = frequency of non-specific electrodermal responses; Att. = attention toward; TRS = threat-related stimuli; COP = centre of pressure; MPF = mean power frequency; MF = medium frequency (0.5-1.8 Hz); HF = high frequency (1.8-5 Hz); SOL = soleus; TA = tibialis anterior; CMC = corticomuscular coherence. Significant differences (p<0.0125) are bolded.

Chapter 6: Study 5 - Changes in cortical potentials time-locked to discrete postural events with initial and repeated postural threat exposure

6.1 Introduction

Postural threat manipulations have been used to investigate how emotional factors, such as fear and anxiety, influence the control of balance. The most commonly used threat manipulation involves having individuals stand at the edge of an elevated surface (Adkin and Carpenter, 2018). When standing under these conditions, individuals demonstrate increases in sympathetic activation (estimated from changes in electrodermal activity; EDA) and self-report greater anxiety and fear of falling and lower balance-specific efficacy (Carpenter et al. 2006; Hauck et al. 2008). These changes in psychological and autonomic state are accompanied by changes in standing balance control. In particular, individuals lean away from the platform edge, coactivate muscles acting at the ankle, reduce the amplitude of low frequency centre of pressure (COP) oscillations, and increase the amplitude of high frequency COP oscillations (Zaback et al. 2019; 2021a). While this postural control strategy has been consistently observed, only some features of this behaviour appear related to the psychological and autonomic state changes induced by the threat. This has been demonstrated recently by work that has repeatedly exposed individuals to postural threat (Zaback et al. 2019; 2021a). With repeated threat exposure, individuals' psychological and autonomic response to threat demonstrates rapid attenuation, yet only some threat-induced standing behaviours show a similar pattern of change. Specifically, the amplitude of high frequency (>0.5 Hz) COP oscillations and plantar/dorsiflexor coactivation decrease over time, while the backward lean and reduced amplitude of low frequency COP oscillations (<0.05 Hz) are largely preserved (Zaback et al. 2019; 2021a). This observation suggests that specific threat-induced balance changes are mediated by distinct neural mechanisms.

One potential mechanism that could contribute to threat-induced balance adaptations is shift toward greater cortical involvement in balance control. Previous work has shown that the N1 component of the perturbation-evoked cortical potential (PEP) is facilitated under conditions of threat (Adkin et al. 2008; Sibley et al. 2010). This component of the PEP peaks approximately 85-165 ms after the onset of the postural perturbation and is widely distributed over fronto-central cortical regions (Bolton, 2015; Varghese et al. 2017). The neural processes underlying the PEP-N1 are not entirely clear. Early interpretations suggested it may reflect sensory processing related to the balance disturbance (Dietz et al. 1985; Quant et al. 2004a) that may also be influenced by attention (Quant et al. 2004b). However, since the amplitude of the N1 is substantially reduced when perturbations are either predictable (Adkin et al. 2006) or self-initiated (Dietz et al. 1985; Mochizuki et al. 2009), others have suggested that it may reflect an error signal with a more general role in detecting instability (Adkin et al. 2006; Mochizuki et al. 2009). More recently, work using dipole source localization techniques has shown an N1 source generator in the supplementary motor area, suggesting it may have a role in planning and generating later components of compensatory postural responses (Marlin et al. 2014). Regardless of its specific function, its facilitation under conditions of threat suggests there is increased cortical involvement in *reactive* balance control under these conditions (Adkin et al. 2008; Sibley et al. 2010). However, it is less clear if there are similar increases in cortical engagement during the control of *unperturbed* standing balance.

Previous work using transcranial magnetic stimulation (TMS) has shown that motor-evoked potentials for muscles of the lower limb are either unchanged or reduced when standing under conditions of height-related threat, suggesting there is little change in corticospinal excitability (Tokuno et al. 2018). However, recent work using analyses of corticomuscular and intermuscular coherence has suggested there may be greater corticospinal drive to muscles engaged in the control of standing balance under conditions of threat (Chapter 5). Other work which has examined somatosensory-evoked potentials (SEPs) following non-destabilizing stimuli of the lower leg has shown that while early components of the SEPs are unaffected by threat (Davis et al. 2011; Horslen, 2016), later components, which reflect higher-level sensory processing, show evidence of facilitation (Horslen, 2016). Thus, while there is some evidence of increased cortical involvement in the control of standing balance under conditions of threat, the findings are not entirely consistent. One possible explanation for these inconsistent results is that cortical networks may only become more engaged during discrete moments of instability which occur intermittently during the control of sway.

Recently, it has been shown that a cortical potential time-locked to natural moments of instability can be recorded during unperturbed standing balance (Varghese et al. 2015). This cortical potential has been shown to peak approximately 90 ms prior to COP displacement peaks in the mediolateral (ML) plane, and its scalp distribution and frequency modulation are similar to the PEP-N1, suggesting it may be generated by a similar cortical network. Unlike the PEP-N1, this so called ‘natural instability’ N1 is very small in amplitude, and was shown to only exceed the level of background EEG when ML stability was challenged by having individuals adopt a tandem Romberg stance (Varghese et al. 2015). However, given that individuals often report greater subjective instability (Davis et al. 2009; Cleworth and Carpenter, 2016) and attention toward their movement (Huffman et al. 2009; Zaback et al. 2016) when standing at the edge of an elevated surface, it is possible this cortical potential may be detectable during unperturbed stance under these conditions. Furthermore, if this cortical potential is generated by a similar cortical network as the PEP-N1, it may be subject to the same threat-induced facilitation observed by others (Adkin et al. 2008; Sibley et al. 2010).

Since the effects of height-induced postural threat on standing balance control are primarily observed in the anteroposterior (AP) plane, the present study limited its analyses to AP COP events. Since previous work has only examined instability-evoked potentials in response to ML COP events and it is known that sway is controlled by independent mechanisms in the AP and ML planes (Winter et al. 2003), it is unclear if similar cortical potentials will be observed in response to AP COP events. Thus, the primary objective of this study was to determine if cortical potentials time-locked to discrete postural events are 1) detectable during quiet, unperturbed standing and 2) modulated by exposure to a height-related threat. It was hypothesized that cortical potentials would only be detectable once individuals are exposed to the height-related threat. If these cortical potentials were found to be affected by postural threat, a secondary aim was to determine how they change as individuals are repeatedly exposed to threat. Since previous work has shown that only some threat-induced standing balance changes habituate over the course of repeated threat exposure (Zaback et al. 2019; 2021a) examining how these cortical potentials habituate can provide insight into how this change in cortical processing might influence threat-induced balance changes. Since previous work has shown that threat-related increases in PEP-N1 amplitude is significantly correlated with subjective fear and anxiety (Adkin et al. 2008), it was hypothesized that the amplitude of cortical potentials time-locked to discrete COP events would habituate after repeated threat exposure.

6.2 Methods

Data for this study were collected in conjunction with another study presented as part of this thesis (Chapter 5). However, the primary analyses described herein have not been previously reported and all relevant methodological details are provided.

6.2.1 Participants

Twenty-eight healthy young adults participated in this study. One participant's data could not be included due to technical issues synchronizing force plate and EEG data, reducing the total sample to 27 (mean age ±SD = 23.7 ±4.7 years; 16 males). Participants were free of neurological and/or musculoskeletal disorders that could affect their balance. All procedures were reviewed and cleared by the University of British Columbia's Clinical Research Ethics Board and participants provided written informed consent.

6.2.2 Procedures

Participants completed a series of 90-s quiet standing trials at two conditions of height-induced postural threat. During these trials, participants stood barefoot on a force plate (AMTI, BP400600, AMTI, USA) which was positioned at the edge of a hydraulic lift (1.52 m × 2.13 m; Pentalift, Canada). Participants stood with a stance width equal to their foot length and their toes aligned to the anterior edge of the force plate. The borders of their feet were marked on the surface of the force plate to ensure the same foot position was maintained between trials. For the LOW threat condition, the platform was positioned at its lowest height (0.8 m above ground level) and an additional support surface (1.6 m × 0.6 m) was positioned in front of the lift, creating 60 cm of continuous support surface in front of the participant. For the HIGH condition, the additional support surface was removed and the platform was elevated 3.2 m above the ground.

Participants completed 3 quiet standing trials at the LOW condition before (LOW_{pre}) and after (LOW_{post}) a block of 15 trials at the HIGH condition. The total number of trials and presentation order was selected for two reasons. First, this allowed for data from blocks of 3 consecutive trials to be collapsed. This ensured that a sufficient number of discrete COP events (described in *Data Analysis* section) could be pooled together at relevant time points throughout the experiment to examine the effects of initial and repeated threat exposure. Figure 6-1 illustrates the trials that were collapsed together into specific blocks and details the naming conventions used for these conditions. The specific conditions of interest were LOW_{pre}, LOW_{post}, $HIGH_{pre}$, and $HIGH_{post}$. The blocked presentation of the HIGH trials was also selected to maximize within-session habituation of the psychological and autonomic response to threat (Rowe and Craske, 1998; Lang and Craske, 2000). A total of 15 HIGH trials were selected since previous work has shown that this is sufficient to substantially reduce and plateau the psychological and autonomic response to threat (Zaback et al. 2021a). Prior to completing the first block of LOW trials, participants completed a single 90-s practice trial to minimize anxiety-mediated first trial effects (Adkin et al. 2000; Zaback et al. 2021b). Participants were instructed to stand quietly with their arms at their sides and gaze fixated on an eye-level visual target (9 cm^2 red square) adhered to the wall ~3.8 m in front of them. Participants were given the additional instruction to avoid excessive blinking and/or contractions of facial, head, or neck muscles which may introduce artifacts into the EEG. Throughout all trials, participants wore a harness that was secured by climbing rope to an overhead beam. The tension of the rope was adjusted such that it would not provide support to the participant while standing, but would support their weight above the platform in the event of a fall. A spotter was seated directly behind participants throughout all trials and was trained to provide additional support if the participant ever appeared unsteady. However, no participants fell or required the spotter's assistance during any trials.

6.2.3 Data collection

Muscle activity was recorded bilaterally from the soleus (SOL) and tibialis anterior (TA) from bipolar pairs of Ag/AgCl surface electrodes (2 cm inter-electrode distance). Electroencephalographic (EEG) recordings were made from a 32-channel elasticized cap with electrodes positioned according to the International 10-20 system (ANTWG32, ANT Neuro, Netherlands). Data were recorded from electrodes positioned over Fp1, Fp2, Fz, Cz, Pz, and Oz referenced to digitally linked electrodes positioned over the mastoid processes. A ground electrode for both EEG and EMG recordings was placed at AFz. EEG electrode impedances were checked before, during, and after the experiment and were maintained at or below 5 kΩ. EEG and EMG data were analog filtered (DC-553 Hz), amplified, and A-D sampled at 2048 Hz (Porti7, ANT Neuro, Netherlands). Skin conductance was recorded from two Ag/AgCl electrodes adhered to the thenar and hypothenar eminences of the non-dominant hand; these data were amplified and A-D sampled at 100 Hz. Ground reaction forces and moments were amplified and A-D sampled from the force plate at 100 Hz. Self-report measures of emotional and cognitive state were probed at pre-defined points over the course of the experimental procedure (Figure 6-1). Details of the timing and nature of these questionnaires are described in detail in Chapter 5.

6.2.4 Data analysis

6.2.4.1 Identification of discrete COP events

Ground reaction forces and moments were resampled from 100 to 2048 Hz, low-pass filtered offline at 5 Hz (5^{th} order, dual-pass Butterworth filter), and COP was calculated in the anteroposterior (AP) plane. Identification of discrete COP events was limited to the AP plane since previous work has shown that the effect of height-induced postural threat on standing balance control is greatest in this direction when individuals are facing the platform edge (Adkin and Carpenter, 2018). Since it is unclear which kinetic events the cortical response is most sensitive to, events were identified separately from COP velocity and displacement data, the former of which was generated by taking the first derivative of the COP displacement. Since there are known edge effects associated with height-related postural threat (Adkin and Carpenter, 2018), events were further distinguished based on their direction toward or away from the platform edge. Therefore, a total of four different event types were identified and analyzed separately: forward peak displacement, backward peak displacement, forward peak velocity, and backward peak velocity.

To identify COP events from the *velocity* data, peaks exceeding a participant-specific threshold were identified. To determine each participant-specific threshold, ±2 standard deviations (SD) of the COP velocity data were calculated for each of the trials comprising the Pre and Post levels of the LOW and HIGH conditions (LOW_{1-6}, $HIGH_{1-3}$, and $HIGH_{13-15}$). The lowest ±2 SD value across these trials for each participant was selected as their threshold. This ensured 1) that the same threshold criterion for event-identification was applied to each trial for a given participant and 2) a sufficient number of events could be identified even in trials with slower velocity COP oscillations. For a velocity peak to be identified, it had to exceed the ± 2 SD threshold in terms of peak height and height relative to adjacent peaks (prominence), and not occur within 500 ms of a larger peak. This ensured that only the most prominent velocity peaks were identified.

Unlike COP velocity, COP *displacement* does not typically oscillate around a zero mean within a short-time interval, but instead contains many discrete adjustments superimposed on larger low-frequency oscillations. Therefore, discrete COP peaks from the displacement data were identified using only a prominence threshold. To minimize the influence of low-frequency oscillations when calculating each participant-specific threshold, a linear detrend and high-pass filter (cut off: 0.1 Hz; 5^{th} order dual-pass Butterworth filter) were first applied to the COP displacement data before the standard deviation of the time series data was calculated. This was done for all 12 trials comprising the Pre and Post levels of the LOW and HIGH conditions and the lowest ±1 SD value was selected as the participant-specific threshold.

The different threshold criteria for identifying COP events from velocity and displacement data were selected because they yielded a sufficient number of the most prominent COP events (75-150 events per block of trials; Table 6-1). Since event-related potentials (ERPs) associated with discrete COP adjustments are known to be small in amplitude (Varghese et al. 2015), it was necessary to optimize the threshold used to ensure that a large number of only the most relevant COP events were used for waveform averaging. Figure 6-2 illustrates representative COP displacement and velocity time series data with respective *forward* event markers highlighted.

6.2.4.2 Event-related potential (ERP) analyses

Previous work has shown that the PEP-N1 and natural instability-evoked N1 are maximal at Cz (Varghese et al. 2015; 2017), therefore analyses of ERPs were limited to this electrode site. EEG data were band-pass filtered offline from 1-50 Hz (5^{th} order, dual-pass Butterworth filter) and a customized algorithm (described in section 5.2.4.1) identified large blink artifacts and deleted any event markers which occurred within 400 ms of these artifacts (Figure 6-2). Since

ERPs in response to discrete COP events are not always detectable from individual participant waveform averages, the amplitude of ERP components for individual participant data were calculated using a fixed window analysis. To determine the timing and width of the fixed windows, grand averages for each condition of interest (i.e., LOW_{pre}, LOW_{post}, $HIGH_{pre}$, $HIGH_{post}$) were generated separately for each event type (i.e., forward and backward peak COP velocity and displacement). From these grand averages, the onsets and offsets of positive and/or negative ERP components occurring within a ±300 ms search window, centred on the event trigger, were identified. To determine the timing of the onsets and offsets, a mean ± 2 SD threshold was calculated from the baseline period of each grand average (1500 to 1000 ms before the event trigger). The onset of an ERP component was identified as the point when the grand averaged EEG data exceeded and remained outside of the threshold for at least 60 ms within a 100 ms sliding window. For any onsets identified, the subsequent offset was identified as the point where the averaged EEG data returned and remained within the respective threshold for at least 60 ms within a 100 ms sliding window. This procedure was performed on the four grand averages (i.e., LOW_{pre}, LOW_{post}, $HIGH_{pre}$, $HIGH_{post}$) separately for each event type. The fixed window used for an ERP component of a given event type was determined as the earliest onset and latest offset identified for that component across the four conditions of interest (see Figure 6-3 for a schematic illustrating these procedures applied to forward peak COP velocity events). Once the timing and width of the fixed windows were identified for each event type, ERP amplitude within these regions was calculated on individual participant waveform averages for each block of trials. ERP amplitude was calculated as mean EEG from the baseline period (1500 ms to 1000 ms before the event trigger) subtracted from mean EEG within the respective fixed windows. Mean amplitude, as opposed to peak amplitude, was used in the current study since the number of events, and therefore noise level, differed across conditions. Unlike mean amplitude, estimates of peak amplitude are systematically biased toward larger values with noisier data, and is therefore an inappropriate measure of ERP amplitude when comparing waveforms derived from a different number of events (Luck, 2014).

6.2.4.3 Event-related EMG analyses

EMG data were band-pass filtered offline from 10-250 Hz (5^{th} order, dual-pass Butterworth filter) before full-wave rectification. Individual participant waveform averages for bilateral SOL and TA EMG responses were generated for the conditions of interest (LOW_{pre}, LOW_{post}, $HIGH_{pre}$, $HIGH_{post}$) using the same event markers and procedures that were used for generating individual participant ERP waveform averages. An additional 50 Hz low-pass filter (5^{th} order dual-pass Butterworth) was applied to these data to improve detection of response onsets and offsets. To identify the onset and offset of an EMG response to a discrete COP event, a mean ± 2 SD threshold was calculated from the baseline period of each individual participant waveform average (1500 ms to 1000 ms before the event trigger). The onset of the EMG response was identified as the point when the EMG exceeded either threshold for at least 60 ms within a 100 ms sliding window within a search period ranging from -1000 ms to 0 ms relative to the event trigger. The offset was determined as the point when the EMG return and remained within the respective threshold for at least 60 ms within a 100 ms sliding window. Since EMG response onsets could not always be detected across all conditions, participant-specific fixed windows were defined based on the earliest onset and latest offset across the conditions of interest for a given event type and muscle (see Figure 6-4 for schematic illustrating these procedures). To determine the amplitude of the EMG response, baseline EMG (mean activity from 1500 ms to 1000 ms before the event trigger) was subtracted from the waveform average and the area of the EMG response within the participant-specific fixed window was calculated. In the rare event (n=5/216 trials) when no EMG onset could be identified across the four conditions of interest for a given event type and muscle, area values of zero were assigned.

6.2.5 Statistics

Prior to statistical analyses, all variables were checked for normality and screened for statistical outliers. TA EMG response amplitudes for all event types demonstrated significant skewness, therefore log transformations were applied to these data. Any data points identified as statistical outliers were converted to the closest, non-outlying value.

To examine how psychological and autonomic state and event-related cortical and EMG response amplitudes were affected by threat and repeated threat exposure, a series of two-way (Threat: LOW vs HIGH; Trial: Pre vs Post) repeated measures ANOVAs were conducted (alpha = 0.05). Significant threat × trial interactions were followed-up with Bonferroni corrected paired-samples t-tests that examined the effect of threat across both levels of trial, and the effect of trial across both levels of threat (alpha = 0.0125).

6.3 Results

6.3.1 Psychological and autonomic state measures

The influence of initial and repeated threat exposure on measures of psychological and autonomic state for this cohort of participants has been previously reported in Chapter 5. Despite the removal of one participant from the current analyses, the same effects were observed. In general, when individuals were first exposed to the threat, they demonstrated increased sympathetic arousal and reported less confidence and more fear and anxiety. Participants also reported directing more attention toward their movement, threat-related stimuli, and self-regulatory strategies. After repeated exposure, individuals' psychological and autonomic response to threat demonstrated significant attenuation. Specifically, individuals demonstrated reduced sympathetic arousal, greater confidence, and less anxiety, fear, and attention toward threat-related stimuli (see section 5.3.1 for a detailed summary of these results).

6.3.2 ERP amplitude

Analysis of the grand averaged ERPs revealed at least one ERP component that exceeded background EEG variability for all four event types. However, these components were typically only detectable at the HIGH conditions, as forward peak COP velocity and forward and backward peak COP displacement events did not elicit clear ERPs across either the LOW_{pre} or LOW_{post} conditions. Only backward COP velocity events elicited a detectable ERP at the LOW_{post} condition.

6.3.2.1 ERP amplitude for peak COP displacement events

Two distinct ERP components were observed when Cz EEG was trigger-averaged to *forward peak COP displacement* events (Figure 6-5a). Grand averages revealed an initial negative component which occurred between -174.8 ms and +11.7 ms relative to forward peak COP displacements, and a later positive component which occurred between +146.5 ms and +300.3 ms. Only one ERP component was observed when Cz EEG was trigger-averaged to *backward peak COP displacement* events. Grand averages revealed a late positive component which occurred between -25.4 ms and +128.4 ms relative to backward peak COP displacements (Figure 6-5c).

Two-way repeated measures ANOVAs revealed significant main effects of threat for mean amplitude of all identified ERP components triggered from both forward and backward peak COP displacement events. The amplitude of each ERP component was significantly larger at the HIGH compared to LOW threat conditions independent of trial (p-values = 0.004 – 0.035; Figure 6-5b and 6-5d). A significant main effect of trial was also observed for the later positive component triggered from forward COP displacement events, with mean ERP amplitude decreasing as a function of trial independent of threat condition (p=0.004; Figure 6-5b). No significant interactions were observed for mean amplitude of any of the identified ERP components (Table 6-2).

6.3.2.2 ERP amplitude for peak COP velocity events

Two distinct ERP components were observed when Cz EEG was trigger-averaged to *forward peak COP velocity* events (Figure 6-6a). Grand averages revealed an early positive component which occurred between -249.0 ms and -93.3 ms relative to forward peak COP velocity, and a later negative component which occurred between -56.6 ms and +142.1 ms (Figure 6-6a). Similar ERP components were observed when Cz EEG was trigger-averaged to *backward peak COP velocity* events, although these were of opposite polarity relative to forward events (Figure 6-6c). Grand averages revealed an initial negative component which occurred between -278.3 ms and +31.7 ms relative to backward peak COP velocity and a later positive component which occurred between +88.9 ms and +186.0 ms (Figure 6-6c).

For forward peak COP velocity triggered ERPs, two-way repeated measures ANOVAs revealed a significant main effect of threat on mean ERP amplitude of the late negative component (p = 0.005), with ERP amplitude being significantly greater (more negative) at the HIGH compared to LOW threat conditions independent of trial (Figure 6-6b; Table 6-2). A similar effect was observed for the early positive component, although this effect only trended toward significance (p = 0.054). A main effect of trial was observed for the early positive component (p = 0.036), with mean ERP amplitude decreasing as a function of trial independent of threat condition. No other main effects or interactions were observed (Table 6-2).

In contrast, for backward peak COP velocity triggered ERPs, two-way repeated measures ANOVAs revealed no significant interactions or main effects of threat or trial on mean amplitude for either of the components identified (Figure 6-6d; Table 6-2).

6.3.3 Event-related EMG response

The SOL and TA demonstrated reciprocal patterns of activation in response to each type of COP event (Figure 6-7). Prior to forward peak COP displacement and velocity events, the SOL demonstrated increased activation while the TA was suppressed. An opposite pattern of activation was observed in response to backward peak COP displacement and velocity events. Descriptive statistics of the participant-specific EMG response onsets and offsets which were used for calculating the amplitude of each participants' EMG response are presented in Table 6-3.

Significant threat × trial interactions were observed for SOL response amplitude for all four event types (p-value range: 0.045 to 0.008; Table 6-4). Follow-up comparisons revealed that when individuals were initially exposed to the threat, there was significantly less modulation of SOL activity prior to discrete COP events, with less facilitation observed prior to forward peak COP displacement and velocity events (p-values <0.001; Figure 6-8a) and less suppression prior to backward peak COP displacement and velocity events (p-values <0.001). This effect of threat was significantly reduced after individuals were repeatedly exposed to the threat, with greater modulation of SOL activity observed at the Post compared to Pre block of the HIGH condition for all event types (p-value range ≤ 0.001), while no change occurred across the LOW blocks (p-value range = 0.064 to 0.329).

No significant threat × trial interactions were observed for TA response amplitude for any of the COP events. However, significant main effects of threat were observed for all four event types (p-values <0.001), with the TA demonstrating significantly greater modulation in response to each type of COP event at the HIGH compared to LOW condition, independent of trial (Figure 6-8b). Specifically, greater facilitation was observed prior to backward peak displacement and velocity events (p-values < 0.001) and greater suppression prior to forward COP events (p-values < 0.001). Significant main effects of trial were also observed for all four event types, with the TA demonstrating less modulation in response to each event type over time independent of threat condition (p-values ≤ 0.001; Table 6-4).

6.4 Discussion

The primary objective of this study was to determine if cortical potentials time-locked to discrete postural events are detectable during unperturbed stance and modulated by exposure to a height-related threat. Consistent with what has been observed in response to similar COP events in the ML plane (Varghese et al. 2015), ERPs were generally small, or not detectable when standing at non-threatening conditions regardless of the type (i.e., peak COP velocity or displacement) or direction (i.e., forward or backward) of the triggering event. These findings are consistent with previous work which has demonstrated the cerebral cortex is involved in the control of standing balance, although its level of excitability is relatively low during tasks which pose little challenge or threat to stability (Luu, 2010; Varghese et al. 2015; Jacobs et al. 2015).

As hypothesized, clear ERPs only became evident once individuals were standing at the HIGH condition. This finding is consistent with previous work which has demonstrated that balance-related cortical potentials only exceed the level of background EEG once balance is challenged by having participants stand in a more unstable tandem stance (Varghese et al. 2015). The timing of the cortical potentials observed in the current study were similar to those previously reported. In particular, a clear negative potential was observed approximately 100 ms prior to forward peak COP displacement events. Since previous work has shown this early cortical potential has similar spatial and frequency characteristics to the PEP N1, it has been suggested that it may reflect similar cortical processes (Varghese et al. 2014; 2015). While no such potential was observed prior to backward peak COP displacements, this was likely because the effect of threat was greater for forward compared to backward events. Nevertheless, when displacement events are collapsed across directions, this same negative potential can still be observed, although it is smaller in amplitude (Figure 6-9).

Later positive potentials, which occurred after peak displacement events, were also observed in this study. The timing of these positive potentials differed depending on the direction of the event, with peaks occurring approximately 50 ms after backward displacement events and approximately 200 ms after forward displacement events. While these later positive potentials have not been previously described or analyzed in detail, some evidence of a later positive peak can be observed in the ERP of the fronto-central component illustrated by Varghese and colleagues (2015; see Figure 3c). The functional significance of these later potentials is not entirely clear and a full explanation is beyond the scope of this study. However, there are several possible explanations which warrant further investigation. First, assuming the early negative potential is similar to the PEP N1, it is possible that the later potential could be related to the P2 component which is known to occur between 100-300 ms after the N1 (Quant et al. 2004a; 2005). Another possibility is that the later cortical potentials reflect monitoring or reafference of the balance corrective response. Alternatively, the later potentials could reflect similar cortical processes to separate postural events. In the present study, cortical potentials were observed in response to both peak COP displacement and velocity events. Since a peak COP displacement event is invariably followed by an increase in COP velocity in the opposite direction, the later potential could reflect the cortical response to this subsequent event. The timing of the early and late potentials relative to when peak COP displacement and velocity events would occur is consistent with this speculation (Figure 6-7). This raises an important question about which sensory or motor event is most closely associated with the cortical activity observed in this study.

The results of this study contribute to the growing body of evidence which suggests there is a shift toward more cortical involvement in balance control when individuals are presented with a threat to stability. Previous work has shown that perturbation-evoked N1 potentials are facilitated under conditions of height-related threat, providing evidence of increased cortical involvement in reactive balance control (Adkin et al. 2008; Sibley et al. 2010). Recently, analyses of corticomuscular and intermuscular coherence also provided evidence of greater direct corticospinal control of postural muscles when individuals stand under conditions of threat (Chapter 5). The results of the current study extend this work, demonstrating that there is cortical activity associated with discrete postural events which occur continuously during unperturbed standing under conditions of threat. This cortical activity is largely absent when standing under normal conditions, suggesting that there is the recruitment of additional cortical networks for the intermittent control of postural sway when balance is threatened.

There are a number of threat-related mechanisms that could potentially contribute to the observed increase in the cortical response. If the cortical potentials observed in this study are closely related to the PEP N1, they could be influenced by threat-related changes in attention (Quant et al. 2004a; Little and Woollacott, 2015) or ability to detect errors in stability (Adkin et al. 2006; Mochizuki et al. 2009). In this study, individuals reported directing significantly more attention toward their movement when standing at the HIGH threat condition. Other work has also shown that perceptions of balance-relevant movements are amplified under conditions of threat (Cleworth et al. 2018; 2019) and individuals perceive themselves to be less stable (Hauck et al. 2008; Huffman et al. 2009; Cleworth et al. 2012). Facilitation of cortical potentials may also be related to known increases in proprioceptive and vestibular gain when standing under threatening conditions (Horslen et al. 2013; 2014; 2018; Naranjo et al. 2015). However, there is evidence that this altered sensory inflow is gated before reaching the cortex (Davis et al. 2011). Changes in the muscle synergies responsible for the control of sway may have also influenced the ERPs. When standing at the LOW conditions, postural sway is primarily regulated through modulation of ongoing SOL activation. However, analysis of event-related EMG revealed that once individuals are exposed to threat there is less modulation of the SOL and more modulation of the TA coupled to each COP event (Figure 6-7 and 6-8). Since the TA is known to receive a greater number corticospinal projections than the SOL (Brouwer and Ashby, 1992; Brouwer and Qiao, 1995), greater cortical activation may be expected to accompany discrete postural events at the HIGH condition.

Previous work has shown that only a subset of threat-induced changes in standing balance control habituate when individuals are repeatedly exposed to threat (Zaback et al. 2019; 2021a; Johnson et al. 2019b). Therefore, in an effort to provide insight into how altered cortical processing of balance-relevant events is related to specific threat-induced behaviours, this study also examined how these cortical potentials changed as individuals were repeatedly exposed to threat. While the amplitude of ERPs tended to decrease as a function of time, there were no significant threat by trial interactions, indicating that the effect of threat was not significantly reduced after repeated threat exposure; although ERP components in response to some events showed trends toward attenuation (Figure 6-5d and 6-6b). This was observed despite substantial habituation of individuals' psychological and autonomic response to threat and clear changes in standing balance control (see section 5.3.2 for analyses of COP summary measures). This contrasts previous work which has suggested that corticospinal drive to postural muscles, inferred through estimates of corticomuscular and intermuscular coherence, shows clear habituation following repeated threat exposure. This suggests that ERP facilitation was not simply a consequence of increased corticospinal drive. It is unclear why the effect of threat on ERP amplitude was not significantly reduced following repeated threat exposure. As discussed above, one factor which may have contributed to threat-related increases in ERP amplitude was a shift in attention toward balance-relevant movements (Quant et al. 2004b; Little and Woollacott, 2015). While individuals tended to direct less attention toward their movement over the course of the experiment, this difference was similar across the Pre and Post blocks of the LOW and HIGH conditions, so the effect of threat did not significantly change. Since individuals continued to direct more attention toward their movement at the HIGH compared to LOW condition, this may have limited changes in cortical activation.

Regardless of the mechanisms contributing to the limited attenuation of mean ERP amplitude, this observation provides some clues as to how this intermittent pattern of cortical activation might influence threat-related behaviours. In particular, it is unlikely that this altered cortical activation contributes to those threat-related changes in standing balance control which show rapid habituation with repeated threat exposure. This includes threat-related increases in high-frequency COP power and ankle muscle coactivation (Zaback et al. 2019; 2021a; Chapter 5). Instead, it is more likely that this altered cortical processing contributes to threat-related balance changes which show limited habituation. This includes the posterior lean and threat-related reductions in COP amplitude and low frequency power (<0.05 Hz). The observation that cortical potentials were increased to a greater extent for forward COP events provides some insight into how these variables may be related. Previous work has provided evidence that the anterior edge of individuals' perceived limits of stability shrinks when standing under conditions of threat (Cleworth et al. 2018). Since the forward COP events identified in this study function to accelerate the centre of mass backward, away from the platform edge, the tendency for the cortical response to be greater for these types of events could reflect an instability detection mechanism which is primed for detecting forward movement of the centre of mass that encroaches on the anterior stability limits. Such a mechanism would reinforce the posterior lean and may also contribute to reductions in COP amplitude and low frequency COP power, as it would be operating to control the centre of mass within a smaller stability range (van Emmerik and van Wegen, 2000). It should also be noted that one of the two ERP components which showed some sign of attenuation was in response to backward COP displacement events, which accelerate the centre of mass forward (or arrest backward COM movement). Thus, habituation of this cortical potential would not impact the preservation of the backward lean.

It is worth noting that there was a tendency for mean ERP amplitude to decrease as a function of time independent of threat condition. This continuous reduction in mean ERP amplitude was potentially due to reductions in alertness which are known to occur over the course of repeated testing and have been shown to influence later components of ERPs (Humphrey et al. 1994; Oken et al. 2006). These order effects were also observed for estimates of the posterior lean, COP amplitude, and low-frequency COP power, providing additional support that these variables may be related.

6.4.1 Limitations

Since there was insufficient pre-existing research to inform the location and width of appropriate measurement windows, the current study used the grand averaged ERPs in response to the different COP events to establish these windows. Since the number of COP events varied considerably across participants for specific conditions (Table 6-1), some participants would have had a disproportionate influence on the shape of the grand average ERP and, ultimately, the location the measurement windows. However, we opted to weight all events, as opposed to participant-specific waveform averages, equally at this phase of the analysis to maximize the signal-to-noise ratio of the grand averaged ERPs so the widest possible measurement windows could be established.

This study recorded data from a small number of electrodes and the analyses were limited to the Cz electrode. This was done since the cortical potential of interest has been previously shown to be maximal at Cz (Varghese et al. 2015) and we sought to minimize participant burden since the experimental protocol was already extensive and time-consuming (2-2.5 hours after preparation). However, since activity from multiple electrocortical sources contribute to the shape of an ERP observed from a single electrode, this study is unable to provide insight into the specific neural generator(s) contributing the various ERP components that were observed (Luck, 2014). While this information was beyond the scope of the current study, future work could investigate this by using high-density EEG and independent component analyses to undercover the different electrocortical generators contributing to each ERP component in response to different event types (Lau et al. 2012). Another limitation of this study is that it is unclear whether the cortical activity associated with discrete COP events represents reactions to natural moments of instability or feedforward control events (Loram et al. 2002). Nevertheless, recent work has suggested that a similar cortical network contributes to both reactive and anticipatory control events (Varghese et al. 2014; 2016).

To minimize artifacts in the EEG, participants were encouraged to avoid excessive blinking and/or contraction of head, neck, or facial muscles while standing. This arguably introduces a secondary task which may influence how individuals direct their attention and maintain balance control (Woollacott and Shumway-Cook, 2002). However, this dual-task effect was likely inconsequential, as these instructions were consistent across conditions and participants demonstrated threat-induced changes in attention and balance control similar to those previously reported (Zaback et al. 2019; 2021a).

6.5 Conclusions

This study provides evidence of increased cortical engagement in the control of standing balance when individuals stand under conditions of height-related threat. This altered cortical engagement is not likely the result of a generalized increase in cortical excitability or corticospinal drive, but likely reflects changes in processing of contextually-relevant postural events. This increased cortical engagement appears resistant to habituation following repeated threat exposure and may be related to specific threat-induced changes in standing balance which also show little habituation or association with psychological and autonomic state changes induced by threat.

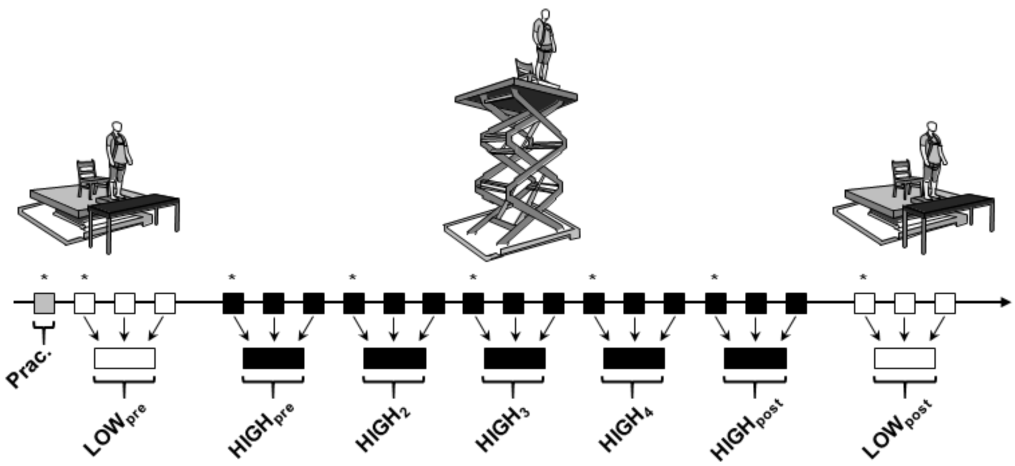

Figure 6-1: Schematic outlining the experimental protocol and grouping of trials. Participants completed a series of 90-s trials of quiet standing at LOW (open squares) and HIGH (filled black squares) conditions. A block of 3 LOW trials were completed before and after a block of 15 HIGH trials. Data from consecutive blocks of 3 trials were combined for analytical purposes; arrows indicate the blocks of trials that were combined. * indicate trials where self-reports of emotional and cognitive state were probed.

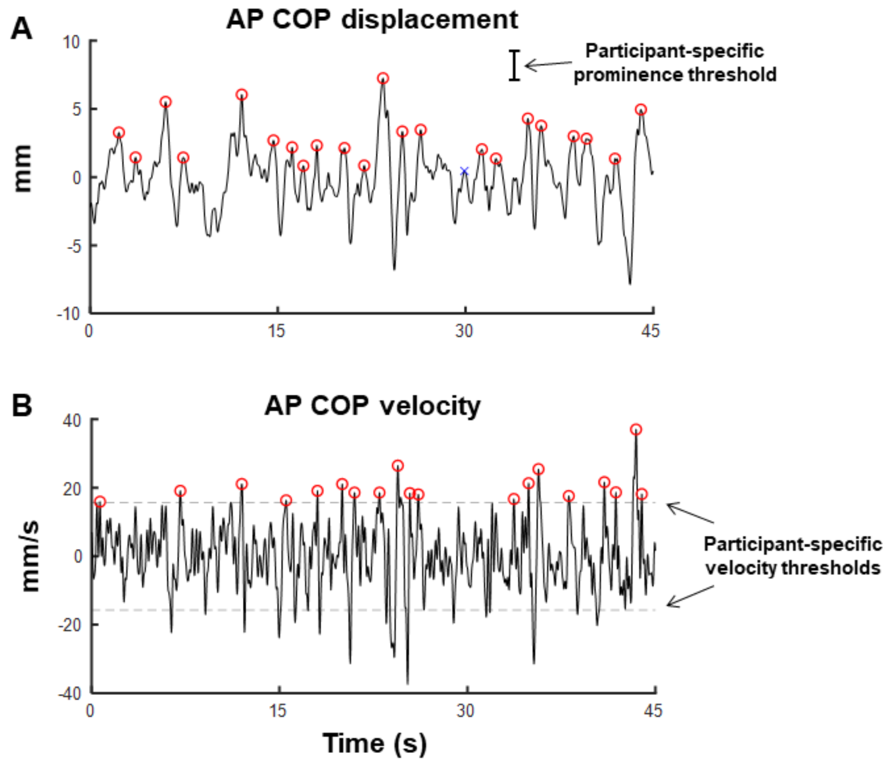

Figure 6-2: Schematic illustrating the methods used for identifying discrete COP displacement and velocity events. Panel A illustrates the detection of *forward peak displacement* events. Forward COP peaks with prominence values which exceeded the participant-specific displacement threshold were identified (red circles). Any events which occurred within ±400 ms of a blink artifact were deleted prior to waveform averaging (blue x's). Panel B illustrates the detection of forward peak COP velocity events. Forward velocity peaks with peak amplitude and prominence values exceeding the participant-specific threshold were identified (red circles).

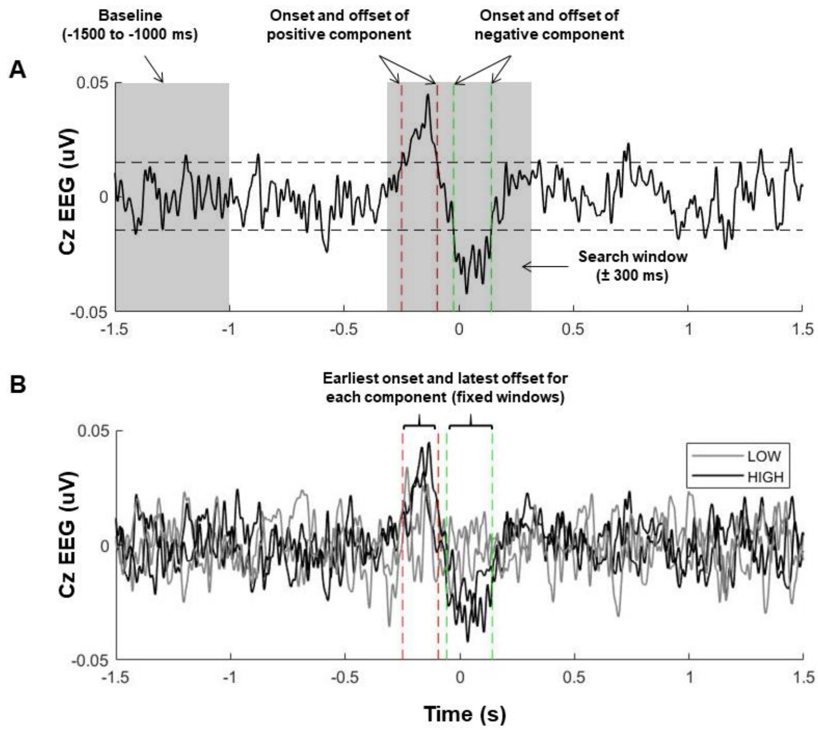

Figure 6-3: Schematic illustrating the methods used for identifying the fixed windows for the ERP analyses. Panel A shows the grand averaged ERP (n=27) for all events triggered from forward COP velocity peaks during the $HIGH_{pre}$ condition. The onsets (and offsets) of ERP components were identified as the points in time when the grand averaged EEG exceeded (and returned within) the level of background EEG (mean ± 2 standard deviations of grand averaged EEG from 1500 to 1000 ms prior to the events) for at least 60 ms within a 100 ms sliding window. These identification procedures were applied to the grand averages for each of the conditions of statistical interest (LOW_{pre}, LOW_{post}, $HIGH_{pre}$, $HIGH_{post}$) separately for each type of COP event. For each type of event, the fixed windows used for calculating mean amplitude of each ERP component were set as the earliest onset and latest offset identified for each ERP component across the conditions of statistical interest. Panel B illustrates highlights the fixed windows that were applied to each ERP component of forward COP peak velocity events. All four grand averages from which these windows were generated are superimposed.

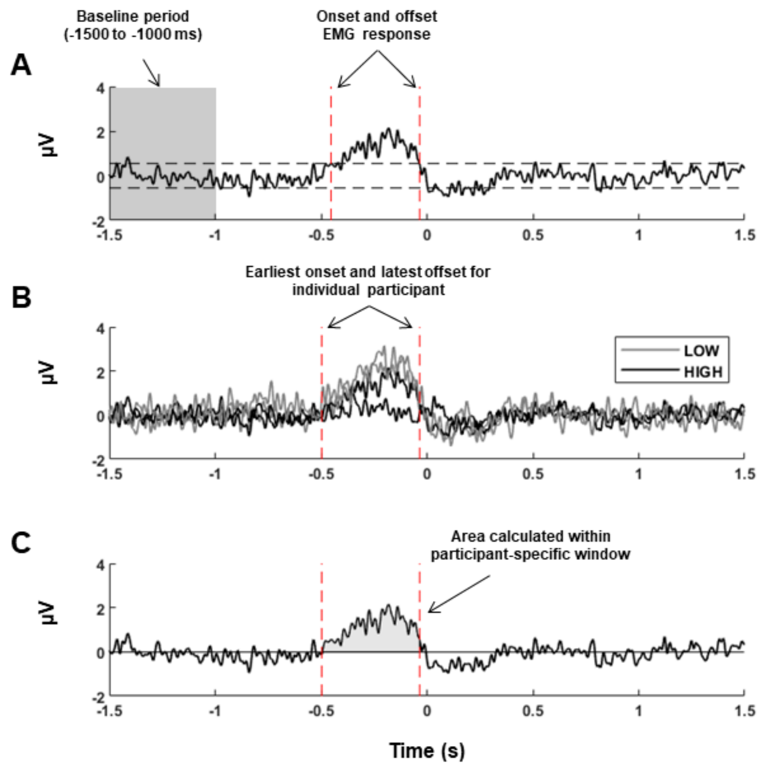

Figure 6-4: Schematic illustrating the methods used for calculating participant-specific EMG response amplitude. Panel A shows a representative participant SOL EMG trigger-averaged to forward peak COP displacement events at the $HIGH_{post}$ condition. The onset of the EMG response was calculated as the point where EMG data exceeded a positive or negative threshold (±2 SD of baseline period) for at least 60 ms within a 100 ms sliding window. The offset was identified using similar procedures. For each participant, the same procedures were applied for each of the waveform averages of the same event type and muscle. A participant-specific measurement window was determined as the earliest onset and latest offset across each of the four conditions of interest (B). Area of the EMG response within the participant-specific window was calculated across each of the conditions of interest to quantify the amplitude of the EMG response (C).

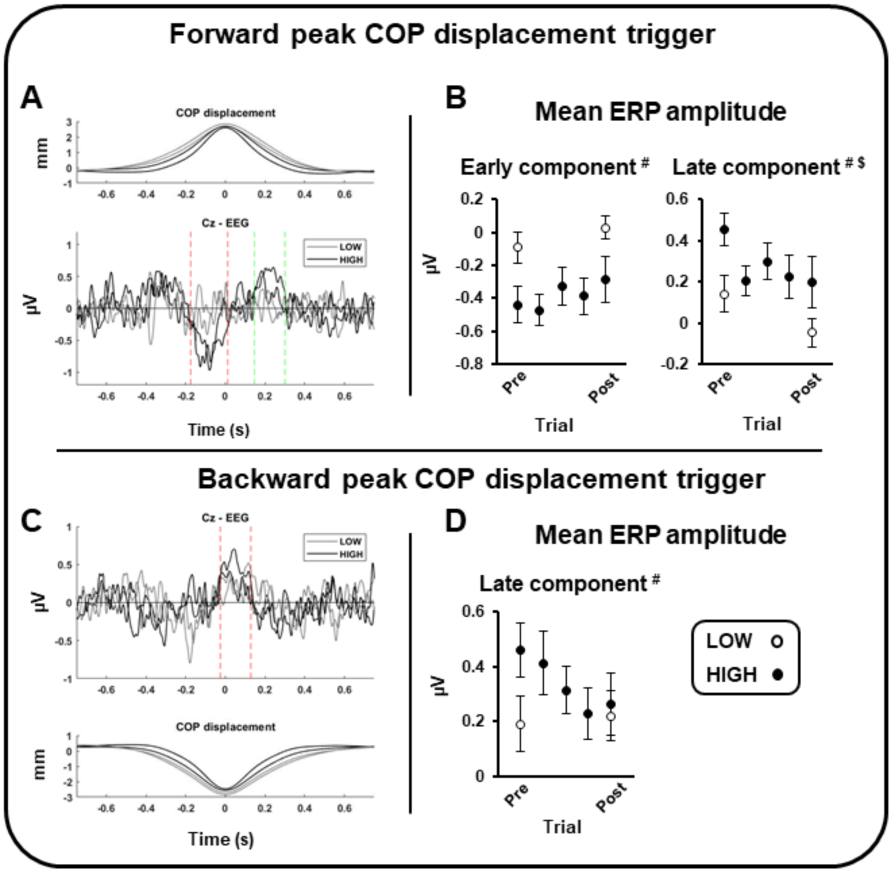

Figure 6-5: Influence of threat and trial on ERP amplitude in response to forward (A, B) and backward (C, D) peak COP displacement events. Panels A and C depict grand averages (n=27) of COP displacement and Cz EEG across all four conditions of interest (LOW_{pre}, LOW_{post}, $HIGH_{pre}$, and $HIGH_{post}$). The location and width of identified fixed windows are highlighted by vertical dashed lines. Panels B and D summarize the results of the two-way RM-ANOVA which examined the influence of threat and trial on mean ERP amplitude for each of the identified components. Data provided represent means and standard errors of mean ERP amplitude for individual participant data. # = significant main effect of threat; $ = significant main effect of trial (alpha = 0.05).

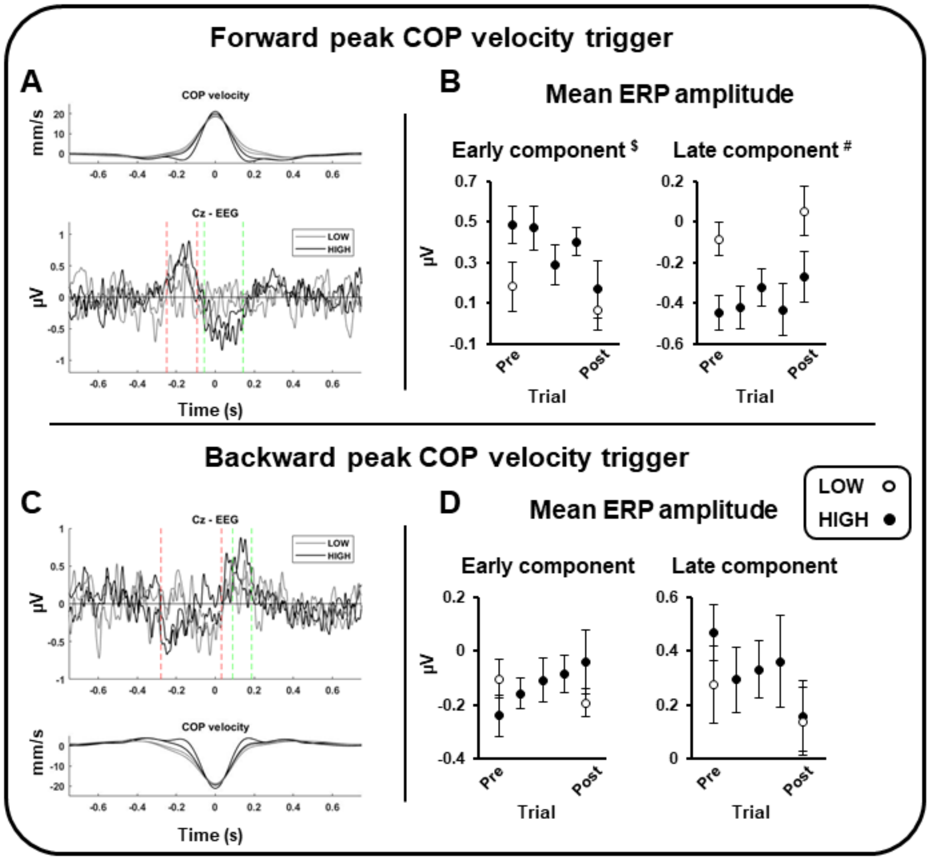

Figure 6-6: Influence of threat and trial on ERP amplitude in response to forward (A, B) and backward (C, D) peak COP velocity events. Panels A and C depict grand averages (n=27) of COP velocity and Cz EEG across all four conditions of interest (LOW_{pre}, LOW_{post}, $HIGH_{pre}$, and $HIGH_{post}$). The location and width of identified fixed windows are highlighted by vertical dashed lines (early components = red; late components = green). It should be noted that while two distinct ERP components are observed for forward and backward peak COP velocity events, these components are of opposite polarity. Panels B and D summarize the results of the two-way RM-ANOVA which examined the influence of threat and trial on mean ERP amplitude for each of the identified components. Data provided represent means and standard errors of mean ERP amplitude for individual participant data. # = significant main effect of threat; $ = significant main effect of trial (alpha = 0.05).

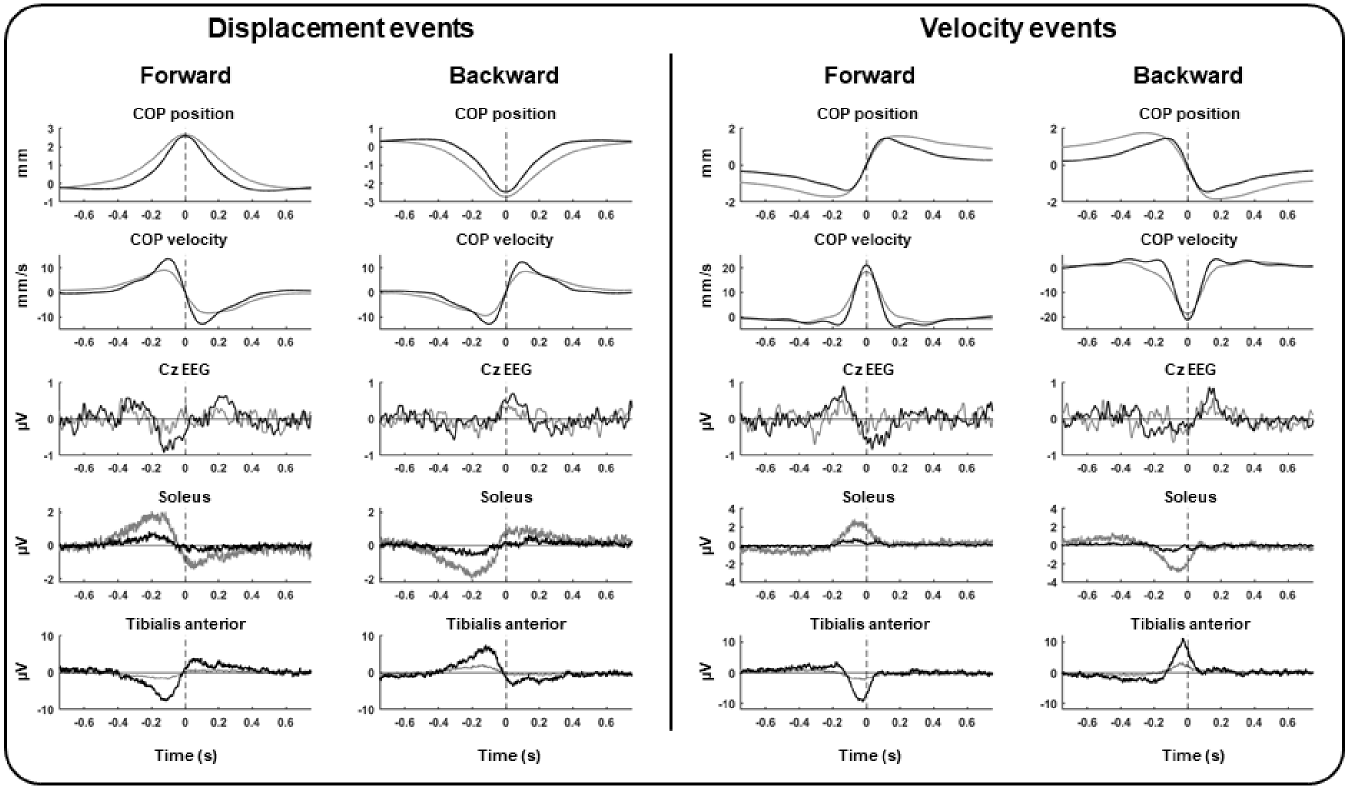

Figure 6-7: Grand averages for COP position and velocity, Cz EEG, and soleus and tibialis EMG for all event types across LOW_{pre} (grey) and $HIGH_{pre}$ (black) conditions. Respective events are aligned to 0-s and are indicated by a vertical dashed line. These figures are presented for descriptive purposes, as they illustrate the relative timing of COP velocity peaks for displacement events and vice versa. Likewise, they illustrate the timing and polarity of the EMG responses relative to cortical potentials and COP displacement and velocity peaks.

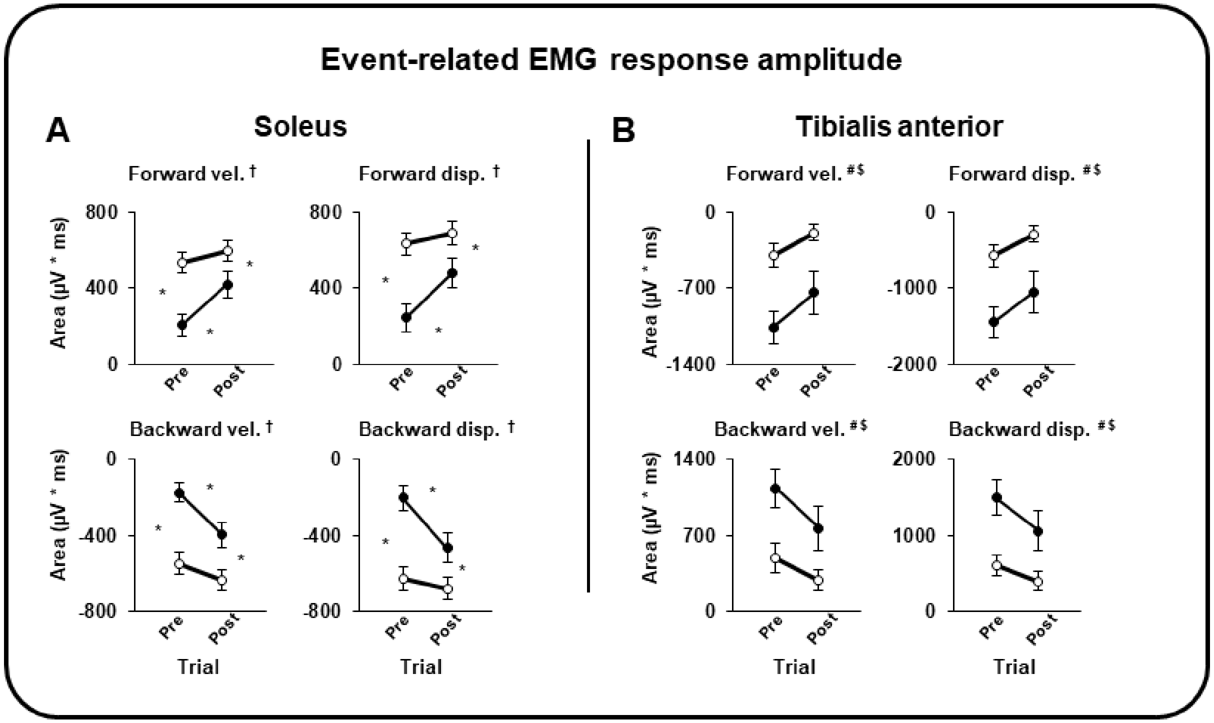

Figure 6-8: Influence of threat and trial on SOL (A) and TA (B) response amplitude to each type of discrete COP event. Values presented reflect mean and standard errors. Open circles represent data at the LOW condition; filled black circles represent data at the HIGH condition. † = significant Threat × Trial interactions; # = significant main effect of threat; $ = significant main effect of trial (alpha = 0.05). * indicate significant follow-up comparisons ($p < 0.0125$) for significant Threat × Trial interactions.

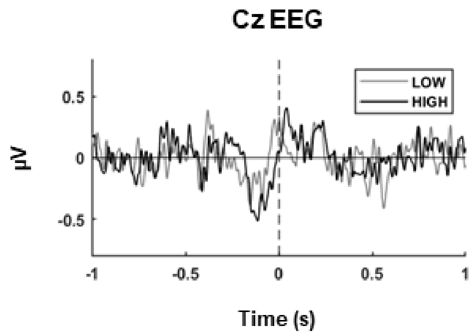

Figure 6-9: Grand averaged EEG for COP displacement events triggered across forward and backward directions. The vertical dashed line indicates the time of peak COP displacements events. A clear negativity can be seen peaking ~100 ms before these events.

Table 6-1: Average number of events identified for each condition of interest

		LOW_{pre}	LOW_{post}	$HIGH_{pre}$	$HIGH_{post}$
Forward peak velocity	Mean (±SD)	75.1 (±23.3)	65.9 (±20.9)	157.9 (±94.5)	96.7 (±48.9)
	Range	42 to 129	35 to 136	67 to 383	48 to 277
Backward peak velocity	Mean (±SD)	73.3 (±23.6)	68.4 (±19.1)	148.3 (±94.0)	92.4 (±44.8)
	Range	38 to 119	45 to 128	51 to 360	47 to 257
Forward peak displacement	Mean (±SD)	108.8 (±23.3)	105.3 (±19.2)	149.8 (±46.9)	120.8 (±29.3)
	Range	72 to 160	73 to 155	87 to 260	84 to 217
Backward peak displacement	Mean (±SD)	109.9 (±22.7)	105.9 (±19.7)	150.9 (±45.9)	121.2 (±29.5)
	Range	73 to 160	72 to 153	86 to 257	83 to 220

Table 6-2: Effect of threat and repeated threat exposure on event-related cortical potential amplitude

	Threat × trial interaction			Threat main effect			Trial main effect		
	$F_{(1,26)}$	*p*	η_p^2	$F_{(1,26)}$	*p*	η_p^2	$F_{(1,26)}$	*p*	η_p^2
Forward peak velocity trigger									
Peak 1 (+)	1.046	0.316	0.039	4.081	0.054	0.136	4.879	**0.036**	0.158
Peak 2 (-)	0.034	0.855	0.001	9.507	**0.005**	0.268	3.214	0.085	0.110
Backward peak velocity trigger									
Peak 1 (-)	3.474	0.074	0.118	0.067	0.798	0.003	1.234	0.277	0.045
Peak 2 (+)	0.994	0.328	0.037	1.088	0.307	0.040	2.903	0.100	0.100
Forward peak displacement trigger									
Peak 1 (-)	0.157	0.695	0.006	9.958	**0.004**	0.277	2.053	0.164	0.073
Peak 2 (+)	0.275	0.604	0.010	9.671	**0.005**	0.271	9.673	**0.004**	0.271
Backward peak displacement trigger									
Peak 1 (+)	1.934	0.176	0.069	4.934	**0.035**	0.159	0.499	0.486	0.019

Note. Significant p-values for interactions and main effects are boldfaced.

Table 6-3: Descriptive statistics summarizing participant-specific fixed windows used for analysis of event-related EMG response amplitude

		Soleus		Tibialis anterior	
		Onset (ms)	Offset (ms)	Onset (ms)	Offset (ms)
Forward peak displacement	Mean (±SD)	-512.0 (±105.8)	-45.7 (±22.7)	-483.6 (±199.8)	23.1 (±112.7)
	Range	-720.2 to -287.6	-90.8 to -2.0	-1000 to -206.1	-104.5 to 376.0
Backward peak displacement	Mean (±SD)	-510.2 (±85.5)	-48.1 (±20.8)	-469.9 (±157.8)	35.6 (±165.5)
	Range	-706.5 to -344.7	-94.7 to 0.5	-956.1 to -263.12	-137.7 to 608.9
Forward peak velocity	Mean (±SD)	-207.4 (±48.9)	91.0 (±63.5)	-165.6 (±38.8)	79.8 (±56.3)
	Range	-328.6 to -129.9	-16.1 to 271.5	-256.3 to -95.2	24.9 to 203.6
Backward peak velocity	Mean (±SD)	-231.1 (±35.6)	64.5 (±41.1)	-172.7 (±47.7)	142.8 (±)151.9
	Range	-305.7 to -142.6	22.5 to 167.5	-267.6 to -92.3	-20.5 to 660.6

Table 6-4: Effect of threat and repeated threat exposure on event-related EMG response amplitude

	Threat × trial interaction			Threat main effect			Trial main effect		
	$F_{(1,26)}$	*p*	η_p^2	$F_{(1,26)}$	*p*	η_p^2	$F_{(1,26)}$	*p*	η_p^2
				Forward peak velocity trigger					
SOL	7.263	**0.012**	0.218	26.358	**<0.001**	0.503	14.703	**0.001**	0.361
TA	1.472	0.236	0.054	46.402	**<0.001**	0.641	32.258	**<0.001**	0.554
				Backward peak velocity trigger					
SOL	4.419	**0.045**	0.145	37.804	**<0.001**	0.593	17.289	**<0.001**	0.399
TA	0.939	0.342	0.035	45.725	**<0.001**	0.638	15.960	**<0.001**	0.380
				Forward peak displacement trigger					
SOL	4.925	**0.035**	0.159	26.548	**<0.001**	0.505	10.161	**0.004**	0.281
TA	0.316	0.579	0.012	51.113	**<0.001**	0.663	22.151	**<0.001**	0.460
				Backward peak displacement trigger					
SOL	8.212	**0.008**	0.240	33.570	**<0.001**	0.564	12.397	**0.002**	0.323
TA	0.587	0.450	0.022	34.855	**<0.001**	0.573	18.564	**<0.001**	0.417

Note. SOL = soleus; TA = tibialis anterior; significant p-values for interactions and main effects are boldfaced.

Chapter 7: General discussion

The link between fear of falling and fall-risk has sparked considerable interest in understanding how emotional factors influence balance control. Over the past 20 years, research has explored this relationship using a variety of postural threat manipulations (Adkin and Carpenter, 2018). Exposure to different types of postural threats elicit changes in psychological and autonomic state which would be expected in individuals experiencing a fear of falling. These are consistently accompanied by changes in balance control which appear to be moderated by the context of the threat. While this research has been instrumental in improving our understanding of how emotions influence the control of balance, there is mounting evidence that some threat-related balance changes may not be a consequence of the psychological and autonomic state changes induced by the threat, but instead may be shaped primarily by the context of the threat (Adkin and Carpenter, 2018). This raises questions as to how fear and related psychological processes impact the control of balance and what are the neural mechanisms mediating these relationships? The studies outlined in this thesis attempted to explore these questions using a novel, repeated threat exposure model. Using this model, psychological and autonomic state can be manipulated within a threatening context, thereby decoupling these state-related changes from the context of the threat.

7.1 Summary of results

All studies in this thesis, with the exception of Study 3, involved repeated exposure to a height-related postural threat while standing unperturbed. While the duration of the threat exposure protocols differed across studies, each study successfully manipulated individuals' psychological and autonomic state. When individuals first stood at the edge of the elevated surface, they demonstrated increases in sympathetic activation (indexed by non-specific electrodermal response frequency) and reported lower balance confidence and greater fear and anxiety. Participants also reported changes in attention, as they focused more on their movement, the constraints of the task, threat-related stimuli, and self-regulatory strategies, and less on task-irrelevant information. After individuals were repeatedly exposed to threat, their psychological and autonomic response was substantially reduced, although some changes in attention were not consistently attenuated across studies. The extent of psychological and autonomic adaptation was dependent on the duration of the exposure period. However, because the greatest adaptation occurred during the early trials of the threat exposure block, the psychological and autonomic response to threat was still significantly reduced in all studies.

The first two studies of this thesis focused primarily on how threat-related changes in standing balance control changed as a function of repeated threat exposure. Study 1 used a relatively short exposure protocol consisting of five 120-s standing trials. When individuals were first exposed to the threat, they leaned backward and demonstrated smaller amplitude and higher frequency COP oscillations. Despite significant reductions of the psychological and autonomic response to threat following repeated exposure, threat-related changes to standing balance control were largely invariant. Only threat-related changes in high-frequency COP power (>1.8 Hz) and plantar/dorsiflexor coactivation showed significant attenuation across the HIGH condition. Multiple regression analyses demonstrated that significant variance in these two outcomes were accounted for by a linear combination of psychological and autonomic state changes. By contrast, these same regression models accounted for less variance in other threat-related balance outcomes, especially RMS-COP and low-frequency COP power. These results suggested that only some threat-related changes in standing balance control are closely related to the psychological and autonomic response to threat. However, this study used a relatively short exposure protocol and most psychological and autonomic outcomes were still moderately elevated relative to the LOW threat condition. If there was a non-linear relationship between some threat-related balance changes and individuals' emotional response to threat, it was possible that adaptations to the threat-related postural strategy may only become apparent after complete or near-complete attenuation of the emotional response.

Therefore, the second study of this thesis used an extended threat exposure protocol to determine if threat-related changes to standing balance control persist after complete or near complete attenuation of individuals' emotional response to threat. The exposure protocol used in this study resulted in much greater attenuation of the psychological and autonomic response to threat, with complete adaptation back to LOW threat values observed in a subset of participants ('Adaptors'). Nevertheless, similar effects to Study 1 were still observed. In particular, the posterior lean and threat-related reductions in COP amplitude and low frequency power were maintained. By contrast, threat-related increases in the average frequency content of COP oscillations, medium (0.5-1.8 Hz) and high (1.8-5 Hz) COP power, and plantar/dorsiflexor coactivation decreased in parallel with measures of psychological and autonomic state. These same effects were observed in the Adaptor subgroup. Collectively, the results from Studies 1 and 2 suggest that only a subset of threat-related changes to standing balance control are tightly coupled to the psychological and autonomic response to threat, whereas others are primarily dependent on the context of the threat and are more resistant to habituation.

Studies 1 and 2 of this thesis demonstrated that anxiety and arousal can influence distinct components of standing balance control; therefore, they have the potential to confound balance assessment. The third study of this thesis investigated whether participants naïve to balance assessment were anxious when their balance was assessed for the first time, and whether these changes in anxiety were sufficient to influence balance control. Despite the absence of any overt threat to balance, individuals were more anxious and aroused when completing the first in a series of quiet standing trials. This anxiety and arousal response declined with repeated testing, with the greatest changes occurring from the first to second trial. These changes in psychological and autonomic state were accompanied by some changes in standing balance control. Most notably, individuals tended to adopt a slight forward lean during the first trial, much like what is observed when arousal is increased by having individuals perform a mental arithmetic task (Maki and McIlroy, 1996). Individuals' also showed evidence of higher frequency and velocity COP oscillations in the ML direction. The results suggest that subtle changes in anxiety can impact standing balance control and should be taken into account when designing experiments or interventions that involve balance assessment.

The pattern of adaptation observed in Studies 1 and 2 of this thesis suggest that distinct neural mechanisms contribute to specific threat-related changes in standing balance control. Examining how sensorimotor changes associated with postural threat adapt as a function of repeated threat exposure can therefore provide insight into how these sensorimotor changes contribute to specific threat-related behaviours. Studies 4 and 5 of this thesis capitalized on this to investigate how descending input from cortical and subcortical networks might contribute to threat-related changes in standing balance control. Study 4 used estimates of CMC and IMC to infer how descending drive to the SOL was influenced by initial and repeated threat exposure. When individuals were first exposed to the height-related threat, there was an emergence of significant gamma-band CMC, and IMC increased at frequencies above 5 Hz. After repeated exposure, threat-related changes in gamma-band CMC and high-frequency IMC (20-40 Hz) demonstrated clear attenuation, while IMC between 5-20 Hz showed limited attenuation. These results provide evidence that postural threat increases corticospinal and subcortical drive to the SOL, but only corticospinal drive attenuates alongside estimates of psychological and autonomic state over the course of repeated threat exposure. These changes in corticospinal drive are therefore unlikely to contribute to threat-related balance changes which show limited habituation, and are instead more likely related to the emergence of high frequency COP oscillations.

Study 5 of this thesis extended these results by examining how cortical processing of balance relevant events are affected by threat and repeated threat exposure. This was done by examining cortical potentials time-locked to large peaks in the COP displacement and velocity data. Under non-threatening conditions, there was little to no cortical activity associated with any type of COP event. However, once individuals were exposed to the threat, clear cortical potentials before and after discrete COP events could be observed. The extent to which these potentials were facilitated depended on the direction of the COP event, with cortical potentials tied to forward COP events demonstrating greater facilitation. Over the course of repeated threat exposure, these cortical potentials demonstrated limited habituation. These results demonstrate that there is an emergence of intermittent cortical processing of contextually-relevant postural events under conditions of threat. The observation that this altered cortical processing is not prone to attenuation following repeated threat exposure suggests it may be related to threat-related balance changes which also show limited habituation.

7.2 Why are some threat-related balance changes resistant to habituation?

The four studies of this thesis which involved exposure to a height-related postural threat demonstrated a clear dissociation between a subset of standing balance changes and measures of psychological and autonomic state. While threat-related increases in MPF-COP, medium- and high-frequency COP power (>0.5 Hz), and plantar/dorsiflexor coactivation decreased in parallel with individuals' psychological and autonomic response to threat over the course of repeated exposure, the posterior lean and reduction in COP amplitude and low-frequency COP power were largely invariant. This is consistent with previous work which has shown weak and inconsistent correlations between changes in psychological and autonomic state measures and COP mean position and RMS when individuals are exposed to a height-related threat (Carpenter et al. 2006; Hauck et al. 2008; Davis et al. 2009; Huffman et al. 2009). A similar dissociation between measures of psychological and autonomic state and threat-related standing behaviours has recently been observed following repeated exposure to the threat of an unpredictable ML perturbation (Johnson et al. 2019b). In particular, threat-related increases in ML MPF-COP and medium frequency COP power (0.5-1.8 Hz) decreased as a function of repeated threat exposure, while threat-related increases in ML RMS-COP were invariant (Johnson et al. 2019b). Unlike a height-related threat, the threat of an ML perturbation does not elicit a lean or a change in low frequency COP power (Johnson et al. 2019b). Individuals do adopt a forward lean in response to the threat of an AP perturbation (Maki and Whitelaw, 1993; Johnson et al. 2019a). In contrast to what is observed with a height-related threat, there is some evidence that this forward lean habituates with decreases in arousal as individuals repeatedly experience this type of threat (Maki and Whitelaw, 1993). Similar adaptations in leaning were observed in Study 3 of this thesis, as the slight forward lean individuals adopted during their first trial of balance assessment decreased in parallel with changes in anxiety and arousal with repeated testing (Zaback et al. 2021b). This could suggest that the extent to which some threat-related balance changes covary with psychological and autonomic state depends on the context of the threat and direction of imposed instability.

It is unclear why some threat-related balance changes do not attenuate in parallel with psychological and autonomic state over the course of repeated threat exposure. From a functional point of view, the suite of threat-related behaviours which appear resistant to habituation have one major distinction – that being, their potential protective role. When standing and facing the edge of an elevated surface, adopting a slight backward lean and reducing sway amplitude reduces the likelihood of a fall in the direction of the threat. The same cannot be definitively said for increases in the amplitude of high-frequency COP oscillations and increases in ankle joint coactivation. High-frequency COP oscillations may have little influence on the control of sway due to the body's large moment of inertia (Gage et al. 2004). If anything, these unnecessary oscillations interfere with or mask balance-relevant somatosensory inputs (Collins et al. 1997; Mildren and Bent, 2016). In addition, plantar/dorsiflexor coactivation is energetically costly (Peterson and Martin, 2010) and may interfere with voluntary and reactive balance control (Nagai et al. 2013; 2017; Le Mouel and Brette, 2019). Activation of the TA also disrupts the normally orthodox relationship between TA fascicle length and postural sway (Day et al. 2013), potentially impairing proprioceptive coding of postural sway. Thus, it appears that potentially maladaptive behaviours potentially linked with the emotional response to threat are prone to habituation, while other context-appropriate behaviours are preserved despite changes in emotional state.

It should be noted that the measures of psychological and autonomic state used throughout this thesis may not have fully captured individuals' emotional response to threat. There is evidence that emotions like fear and anxiety involve both conscious and unconscious processing of threat-stimuli (Pessoa and Adolphs, 2010; Sylvers et al. 2011; Adolphs, 2013). The self-report questionnaires used throughout this thesis can only quantify individuals' retrospective assessment of their conscious experience of fear and anxiety. It is possible that unconscious processing of threat-stimuli triggered specific defensive behaviours which were less prone to habituation. It is also possible that our studies did not adequately distinguish the effects of fear and anxiety. While fear and anxiety are both negatively valenced affective states, they are generally considered distinct emotions which have distinct neurobiological underpinnings (Sylvers et al. 2011). One factor which distinguishes fear from anxiety is its duration and susceptibility to habituation. A fear response is short-lived and prone to habituation, whereas an anxiety response is characterized by sustained hypervigilance which is less prone to habituation (Walker and Davis, 1997). While separate self-reports of fear and anxiety were used throughout this thesis, it is possible that individuals rated their subjective experience of aversive arousal on each of these questionnaires, which may be more closely related to the subjective experience of fear (Sylvers et al. 2011). Thus, while speculative, it is possible that the components of the behavioural response to threat which are prone to habituation are tied to a fear response, while those components which are resistant to habituation are tied to an anxiety response.

7.3 Neural mechanisms contributing to threat-related changes to standing balance control

The unique pattern of adaptation in standing balance control observed when individuals were repeatedly exposed to threat suggests that distinct neural mechanisms mediate different components of the behavioural response to threat. While a number of sensorimotor changes known to occur with height-related threat could influence balance control, this thesis focused on possible changes in corticospinal and subcortical descending drive (Study 4) and cortical processing of balance relevant events (Study 5) since these potential mechanisms have received the least attention to date.

Threat-related increases in gamma CMC and high-frequency IMC (Study 4) suggest there is greater connectivity between sensorimotor cortical areas and muscles engaged in the control of balance. While it is unclear what neural processes the cortical potentials identified in Study 5 represent, the observation that they are facilitated by threat provides additional evidence of increased cortical engagement in standing balance control. The cortical changes examined in Studies 4 and 5 likely represent distinct neural processes, as they demonstrated a different pattern of adaptation following repeated threat exposure. Threat-related increases in gamma CMC and high-frequency IMC were significantly attenuated, while cortical potentials to discrete postural events, particularly those events which pushed the COM away from the platform edge, were resistant to attenuation. Thus, the cortical potentials observed in Study 5 are not likely a manifestation of increased corticospinal drive, but may reflect higher level cortical processing of balance relevant events (Varghese et al. 2015). The disparate pattern of adaptation also suggests that these different cortical processes influence distinct components of threat-related behaviour.

Threat-related increases in corticospinal drive are more likely to be related to changes in high-frequency COP oscillations and plantar/dorsiflexor coactivation, as these variables share a similar pattern of adaptation over the course of repeated threat exposure. The changes in CMC and IMC also reflect a shift toward more high-frequency, synchronous grouped motor unit discharge of SOL. Such changes in motor unit firing behaviour may contribute to greater force variability (Ushiyama et al. 2017). Gamma-band CMC has been related to increased corticospinal excitability (Keil et al. 2014) and greater corticospinal excitability of lower limb muscles has been associated with higher velocity COP oscillations during challenging balance tasks (Nandi et al. 2018; 2019). By contrast, threat-related changes in cortical processing of discrete postural events are more likely to be related to the posterior lean and reductions in COP amplitude and low-frequency COP power, as these variables both show limited attenuation over the course of repeated threat exposure. Cortical potentials were most facilitated when associated with forward COP events, which serve to accelerate the COM away from the platform edge. While speculative, the tendency for greater cortical engagement tied to these types of events could reflect a cortical mechanism which reinforces the backward lean when individuals are standing under conditions of threat. A consequence of reinforcing this behaviour is that the range over which the COM can oscillate becomes smaller, particularly in the direction of the threat (van Emmerik and van Wegen, 2000), potentially contributing to reductions in COP amplitude and low-frequency power.

Estimates of SOL_R-SOL_L IMC in Study 4 of this thesis also suggest that postural threat increases descending drive from other brainstem motor tracts. Of particular interest were threat-related changes in reticulospinal drive which were estimated from 10-20 Hz IMC (Grosse and Brown, 2003; Blouin et al. 2006). This was found to be facilitated by postural threat, but the effect of threat only showed slight decreases after repeated exposure. It was surprising that IMC within this band did not tightly covary with changes in psychological and autonomic state, since the reticular formation is known to receive excitatory inputs from neural substrates activated in states of fear (Balaban, 2002; Staab et al. 2013). One factor which potentially contributed to the modest preservation of 10-20 Hz IMC was the posterior lean, as this has been shown to induce bilaterally coherent lower limb muscle activity between 13-18 Hz (Sharott et al. 2003). Because of this potential confound and the observation that there was a slight trend toward habituation, it is difficult to infer how changes in reticulospinal drive contribute to threat-related balance changes. A limitation which further complicates this interpretation is that IMC is influenced by multiple afferent and efferent sources and 10-20 Hz IMC is not a pure surrogate of reticulospinal drive (Grosse and Brown, 2003; Grosse et al. 2002). To better understand how threat influences contributions from the reticulospinal system, future work may endeavour to use other techniques to probe the reticulospinal system, such as the StartReact paradigm (for review, see Nonnekes et al. 2015).

A limitation of Study 4 is that CMC and IMC were only examined for the SOL. This was done because the SOL has some level of tonic activity at both LOW and HIGH conditions (Carpenter et al. 2001; Zaback et al. 2021) and, therefore, permits comparisons of descending drive to the same muscle engaged in the control of standing balance. However, while the SOL is primarily responsible for the control of sway under normal conditions (Heroux et al. 2014), this is not always the case when standing at a HIGH condition, as the TA takes on a larger role (Carpenter et al. 2001; Zaback et al. 2021). This was highlighted in Study 5 of this thesis, as EMG responses to discrete COP events were accompanied predominantly by modulation of the SOL at the LOW condition, while modulation of the TA was dominant at the HIGH condition

(Figure 6-7). Thus, examining changes in SOL CMC and IMC provides only a limited view as to how threat influences descending drive to all muscles engaged in the control of balance and, by extension, how these changes in neural drive impact specific threat-related standing behaviours. Since the TA receives greater corticospinal input than the SOL (Brouwer and Ashby, 1992) and its activation is prone to attenuation over the course of repeated threat exposure, it is possible that common input to the TA contributes to threat-related changes in standing balance control which are also prone to habituation. However, unique approaches need to be considered to provide accurate estimates of CMC and IMC for the TA, which is only periodically active during stance.

7.4 Other sensorimotor changes associated with threat and their potential influence on threat-related balance changes

Previous work has shown that balance-relevant reflexes in response to proprioceptive and vestibular stimuli are facilitated under conditions of threat. The lower-limb stretch reflex has been examined using Achilles T-reflexes (Davis et al. 2011; Horslen et al. 2013; 2018) and rapid ramp-and-hold surface rotations (Horlsen et al. 2018). Since Achilles T-reflexes are facilitated independent of changes in the SOL H-reflex (Horslen et al. 2013) and there is increased velocity scaling of short-latency responses to ramp-and-hold stretch reflexes (Horslen et al. 2018), it has been suggested that postural threat increases muscle spindle dynamic sensitivity. Vestibular-evoked responses have been probed using electrical (SVS) and mechanical (VEMPs) stimuli. Short- and medium-latency responses to SVS are facilitated by height-related threat (Horslen et al. 2014) and the threat of perturbation (Lim et al. 2017). VEMPs of the SOL have also been shown to be facilitated under conditions of threat and are positively correlated with self-reported fear and anxiety (Naranjo et al. 2015). It has been suggested that facilitation of vestibular-evoked responses is due to increased excitatory inputs at the vestibular nuclei from neural substrates responsible for processing emotional and affective stimuli (Balaban, 2002; Staab et al. 2013).

This work suggests that postural threat induces a multi-sensory adaptation process, whereby balance-relevant input from muscle and vestibular sources are tuned, possibly to facilitate reactive responses and/or monitoring of postural state (Horslen et al. 2013; 2017; 2018; Naranjo et al. 2015; 2016; Lim et al. 2017). Future studies could explore how this altered sensorimotor processing contributes to threat-related changes in standing balance control by examining how vestibular-evoked responses and/or short-latency stretch reflexes change as a function of repeated threat exposure. To undertake these studies, it would be necessary to use a stimulus that can applied multiple times without causing harm to the participant and can elicit a reliable response in a short enough period of time to provide adequate resolution of adaptation. VEMPs would be inappropriate since approximately 250 tone bursts (4ms, 500Hz stimuli at 125dB) are needed to evoke reliable VEMPs in muscles of the lower limb (Naranjo et al. 2015). Only 750 stimuli at this noise intensity can be delivered within a single session before putting an individual at risk of hearing damage due to harmful noise exposure (as per safety limits determined by the Canadian Center for Occupational Health and Safety). On the other hand, SVS can be administered indefinitely without causing harm to the participant. Using linear systems analyses, the frequency characteristics of the kinetic or EMG response can be examined in terms of coherence and gain, and clear responses can be observed with as little as 2-minutes of stimulation (Dakin et al. 2010). The short-latency stretch reflex can be examined using a similar approach. Mildren and colleagues (2017) recently developed a technique that involves applying a random, aperiodic vibratory stimulus to the Achilles tendon during standing balance. This stimulus does not noticeably perturb balance and can elicit reliable responses in as little as 40-s (Mildren et al. 2017). By contrast, transient stimuli, such as T-reflexes, need to be delivered with an inter-stimulus interval of at least 10-s to avoid attenuation due to homosynaptic post-activation depression, and therefore would require much longer periods of time to obtain reliable ensemble averages (Mildren et al. 2016).

Recent work has also shown that postural threat amplifies conscious perceptions of balance relevant movements (Cleworth and Carpenter, 2016; Cleworth et al. 2018; 2019). Conscious perceptions are influenced by a combination of sensory and cognitive processes. The perceptual changes associated with threat are likely the result of altered high-level cortical processing of balance relevant inputs, since perceptual thresholds to cutaneous or proprioceptive stimuli are either unaffected or increased by threat (Cleworth, 2018) and early components of somatosensory-evoked potentials are unaffected by threat (Davis et al. 2011; Horslen, 2016). Study 5 of this thesis demonstrated there is altered cortical processing of balance-relevant events, particularly those which function to push the COM away from the platform edge. It is possible that this altered cortical processing is related to changes in conscious perceptions and these factors may contribute to reductions in sway amplitude and a tendency for individuals to lean away from the platform edge.

7.5 Clinical implications and future directions

Cognitive-behavioural interventions have been used to reduce fear of falling in individuals who are at risk of falling (Zijlstra et al. 2007; Dorresteijn et al. 2016). A potential concern when implementing these types of interventions is that they could instill a false sense of confidence and motivate individuals to engage in risky behaviours or approach a given threat without an appropriate level of caution (Delbaere et al. 2006; Lamarche et al. 2013). This is a legitimate concern, and cognitive-behavioural interventions should take into consideration individuals' physiological fall-risk prior to their implementation. However, the results from this thesis reveal a promising pattern of behavioural adaptation when individuals are repeatedly exposed to a threat. That is, potentially maladaptive components of the behavioural response to threat are attenuated in parallel with estimates of fear and arousal, while protective components are largely preserved. Thus, attenuating an individual's emotional response to a given threat may not adversely affect their tendency to employ context-appropriate postural strategies.

While the changes to standing balance control following repeated threat exposure appear functional, Study 2 of this thesis demonstrated that they are not well retained. This was likely a consequence of using a massed and constant exposure protocol to maximize within-session habituation at the expense of long-term fear reduction (Craske et al. 2008; 2014). Since the maladaptive changes to standing balance control (i.e., increased high frequency COP oscillations and plantar/dorsiflexor coactivation) are tightly coupled to the psychological and autonomic state changes induced by the threat, exposure protocols which maximize long-term fear reduction may result in more effective retention of standing balance adaptations. Thus, an important avenue for future research is explore the effectiveness of different types of exposure protocols to maximize long-term fear reduction and retention of balance adaptations. It should also be acknowledged that the studies outlined in the current thesis only investigated adaptations to standing balance control in healthy young adults in response to a specific threat manipulation. Therefore, the generalizability of these results are limited and their clinical significance should be interpreted with caution. Before repeated threat exposure can be advocated as an effective component of cognitive-behavioural therapies for individuals living or working with a fear of falling, it is critical to investigate how repeated exposure to different perceived threats influences performance on a variety of balance tasks in both healthy and clinical populations. Prospective studies should also investigate whether balance adaptations following repeated threat exposure are associated with a reduced likelihood of falling in at-risk populations.

This thesis also has implications for balance assessment in laboratory and clinical settings. Study 3 demonstrated that when individuals naïve to balance assessment performed a series of quiet standing trials, they were more anxious and aroused during the trials at the beginning of the assessment. While these changes in emotional state were mild, they may have been sufficient to influence balance control, as individuals tended to lean forward and show higher frequency and velocity ML COP oscillation during the first and second trials. Since studies often rely on a single baseline assessment when examining the effects of an intervention or experimental manipulation, emotional state changes have the potential to mask or create the illusion of treatment effects. It should be emphasized that the 'first trial' effects studied in this thesis were observed in healthy adults. Previous work has shown that the presence of an expert evaluator is more likely to adversely affect balance control in older compared to young adults (Geh et al. 2011). It is possible that anxiety-mediated first trial effects may be greater in populations with anxiety or movement disorders. Thus, it is critical to adequately familiarize participants or patients with the postural task prior to balance assessment.

7.6 Limitations and future directions

It is assumed that when healthy individuals stand at the edge of an elevated surface the perceived consequences of falling are analogous to those experienced by fearful elderly individuals when they perform activities of daily living. Thus, this postural threat should induce a similar suite of emotional and cognitive state changes, allowing one to study how these factors influence balance in a controlled environment without possible confounds associated with ageing and pathology (Adkin and Carpenter, 2018). Some of these assumptions seem reasonable, as healthy young adults self-report changes in attention and cognitive appraisals that would be expected in individuals living with a fear of falling (Young and Williams, 2015). However, the extent to which these changes truly match those experienced by individuals living with a fear of falling is unclear since phenomenological research on the experience of fear of falling is currently lacking (Ellmers et al. 2020b).

The results from this thesis highlight a potentially more problematic limitation of the postural threat model as a means for studying how fear of falling influences balance control. That is, major components of the behavioural response to threat appear largely unrelated to the fearfulness experienced by individuals. This suggests that some threat-related balance changes are tailored specifically to the unique challenges imposed by threat and may not accurately reflect how balance control is affected by a general fear of falling. This may explain why changes in standing balance control observed with exposure to a height-related threat do not replicate the differences in standing balance control between fearful and non-fearful older adults (Maki et al. 1991; Lamarche et al. 2013). This limitation is not exclusive to the height-related threat, as context-specific balance changes have also been reported when standing with the threat of perturbation (Johnson et al. 2019ab). In this case, some balance changes may be a consequence of preparing a highly specific motor response independent of the level of anxiety or fear experienced (Johnson et al. 2019ab).

The current thesis attempted to overcome this limitation of the threat model by varying emotional state within a fixed threat context. Using this approach, it was demonstrated that only a subset of threat-related balance changes attenuated in parallel with changes in emotional state, suggesting these factors were closely related. However, the nature of these relationships are not well understood, as multiple physiological and cognitive changes beyond those studied in this thesis are likely to mediate the relationship between specific emotional factors and balance control (see sections 7.3 and 7.4). These relationships may also be bidirectional, as changes to balance control or perceptions of unsteadiness may influence attention in a bottom-up manner and/or increase fear and arousal (Balaban, 2002; Staab et al. 2013). Furthermore, since these relationships were observed within a threatening context, they may still reflect context-specific balance changes that are simply moderated by the emotional response to threat. This possibility was highlighted by Study 3, which demonstrated that when no physical threat was present, changes in emotional state were not accompanied by changes in MPF or mean velocity of AP-COP movement. However, the changes in emotional state in this study were considerably smaller than those seen with a height-related threat and may have been insufficient to influence specific postural outcomes. To fully understand how specific emotional and cognitive factors associated with fear of falling influence balance control, future work should use novel methods to manipulate these factors without the use of a physical threat. This has been done previously by presenting individuals with affective pictures (Azevedo et al. 2005; Horslen and Carpenter, 2011) or using different forms of social evaluative threat (Geh et al. 2011; Doumas et al. 2018; Orcioli-Silva et al. 2021). Other approaches may involve virtual reality or pharmacological interventions which can vary factors like arousal and fear without a balance-relevant threat. Future work could also investigate how specific balance outcomes vary as function of postural or secondary task difficulty, as these manipulations elicit emotional and cognitive changes similar to those observed with postural threats (Maki and McIlroy, 1996; Hauck et al. 2008).

Another caveat of the repeated exposure manipulation is the amount time and/or number of trials required to adequately reduce the emotional response to threat. This need for time and repetition invariably introduces a variety of potential confounds, including fatigue (physical and mental), and/or boredom. Thus, while the goal of this manipulation is to examine how balance and balance-relevant processes change as fear and related psychological processes habituate, there are likely other unintended physiological and cognitive changes related to repeated testing which may also impact behaviour. Evidence of such order effects can be seen in multiple self-report, physiological and behavioural outcomes throughout this thesis. For example, when comparing data from LOW_{pre} to LOW_{post} trials in both Studies 2 and 4, individuals show significant reductions in EDR.freq and attention toward task objectives, and significantly more attention toward task-irrelevant information (p-values ≤ 0.014). Participants may have been more aroused and focused during the first block of LOW trials due to anticipation of the upcoming HIGH trials. However, it seems more plausible that there was a progressive disengagement from the task due to prolonged and repeated testing. While these order effects are difficult to avoid, we attempted to control for them statistically by using 2×2 repeated measures ANOVAs (Threat: LOW vs. HIGH; Trial: Pre vs. Post) to examine how the effect of threat changes at two separate points in time. However, this only serves as an effective control if the order effects are linear and the factors contributing to them have a similar effect at LOW and HIGH conditions.

Each of the studies in this thesis inferred changes in sympathetic arousal from an estimate of tonic EDA. Tonic EDA was inferred from the frequency of non-specific EDRs since this estimate is more sensitive to changes in experimental conditions than the mean level of EDA and varies more linearly as a function of arousal state (Boucsein, 2012). A semiautomated algorithm was used to identify and count all EDRs with an amplitude greater than 0.05 µS. There are several potential caveats to this approach. First, it does not take into consideration the mean amplitude of the identified EDRs. However, it is unclear what additional information this would provide since there is an inverted-U relationship between the amplitude of non-specific EDRs and arousal state (Boucsein et al. 2012). Another potential limitation of this approach is that the same threshold was applied to each participant's data without consideration of individual variability. A minimum amplitude of 0.01 – 0.05 μS is recommended for the identification of EDRs (Boucsein et al. 2012). The decision to set a minimum threshold of 0.05 μS could have led to some EDRs going undetected if participants had particularly small EDRs. However, prior to filtering the data, the amplitude of noise could often exceed values of 0.01-0.02 μS; therefore, lowering the threshold below 0.05 μS could have increased the rate false positives arising from artifacts in the data.

It should be acknowledged that across each of the studies of this thesis there was considerable individual variability for each dependent outcome. This was exemplified in Study 2, as one subgroup of participants demonstrated complete adaptation of their psychological and autonomic response to threat after repeated exposure, while another, albeit relatively small (n=2), group of participants demonstrated further increases in these same outcomes. The factors contributing to this between-subject variability are beyond the scope of this thesis. Previous work has shown that specific personality traits can influence the emotional and behavioural response to threat (Zaback et al. 2015), but it is unclear if these same factors also influence habituation. Further work exploring these interactions is warranted, as it could provide insight into specific individual characteristics that moderate the efficacy of repeated exposure as a possible form of cognitive-behavioural therapy for reducing fear of falling.

7.7 Conclusions

The studies presented throughout this thesis used a novel repeated threat exposure model to investigate how fear and related psychological processes impact standing balance control. These works demonstrated a dissociation between a subset of standing balance changes and measures of psychological and autonomic state. This suggests that some threat-induced standing behaviours are tightly coupled with the psychological and autonomic state changes induced by the threat, while others may reflect context-appropriate adaptations that are resistant to habituation. In the absence of any overt threat, subtle changes in anxiety and arousal were also associated with distinct balance changes, highlighting the potential for these emotional factors to confound balance assessment. The unique pattern of adaptation observed in response to repeated threat exposure suggests that different components of the behavioural response to threat are mediated by separate neural mechanisms. This thesis investigated how changes descending corticospinal and subcortical drive to lower limb muscles and cortical processing of balance-relevant events might contribute to specific threat-related behaviours. It is suggested that alterations in descending drive may contribute to threat-related behaviours prone to adaptation, while altered cortical processing of balance-relevant information may contribute to behaviours resistant to habituation.

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