Cortical Activity Associated With Changes in Sensory Contributions During Standing Balance Control

by Kelly Jean Hebner

A thesis

presented to the University of Waterloo

in fulfillment of the

thesis requirement for the degree of

Master of Science

In

Kinesiology

Waterloo, Ontario, Canada, 2021

©Kelly Jean Hebner 2021

Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Abstract

Maintenance of safe upright static stance regardless of sensory input is imperative for completing activities of daily living required for high quality of life. The current body of work aims to the potential involvement of the cortex in standing balance by examining the frequency of cortical activity associated with manipulation of task challenge and sensory contributions. The current study is focused manipulating sensory input (haptic touch, and vision) to explore if there was evidence of changes at the level fo cortex that may implicate cortical contributions in sensory processing during the control of stationary standing. Since altering sensory inputs will alter challenge it was necessary to determine the impact of changes in cortical activity related to changes in balance challenge independent of sensory status. It was hypothesized that increasing task challenge, by altering base of support, would result in an increase in theta frequency power ratio and a decrease in alpha frequency power ratio, specifically at frontocentral regions of the cortex. It was predicted that by including haptic touch there would be an increase in theta frequency power ratio and a decrease in alpha frequency power ratio, with accompanying increase in power in beta, delta, and gamma frequency bands around the Pz electrode. Finally, it was hypothesized that increasing visual availability would result in an increase in theta frequency power ratio and a decrease in alpha frequency power ratio, with accompanying increase in power in beta, delta, and gamma frequency bands around the Oz electrode. The study tested 12 healthy young subjects who performed 7 different tasks: 1) Tandem stance with eyes closed, 2) Narrow stance with eyes closed, 3) Standard stance with eyes closed, 4) Tandem stance with restricted visual field, 5) Tandem stance with eyes open but vision occluded, 6) Tandem stance eyes open, 7) Tandem stance with haptic touch. Cortical activity was measured using a 32 channel electroencephalography (EEG) system and balance control was measured from ground reaction forces used to calculate centre of pressure (COP). Frequency analysis was conducted and plotted topographically for qualitative evaluation. Mean power, within each band (delta, theta, alpha, beta, gamma) was calculated for specific electrode sites

(Fz, Pz, Oz) and compared across task conditions. Mean ML (mediolateral) and AP (anteroposterior) COP and velocity was compared across task conditions. Overall, the manipulation of task challenge did result in significant changes in COP as a measure of task challenge, but there were only modest changes in cortical excitation that were largely characterized by an increase power of theta and alpha frequency. The main effect seen in frontocentral increase in power was observed for manipulation of task challenge (altered based of support) and changes in sensory inputs. With respect to changes in sensory information, the availability of haptic information was used to determine evidence of unilateral parietal cortical involvement that would have been consistent with the spatial specificity of the sensory input. Results supported the hypothesis of an increase in theta power and decrease in alpha power over the Pz electrode. With respect to visual inputs there was an expectation of varying activity in occipital power of theta and alpha frequency; when vision is available it was expected that theta power would increase and alpha power would decrease in the posterior regions of the cortex. Overall the current study confirms the expected impact of BOS and sensory input changes in on COP sway. However, the changes in cortical activity were more modest. Common across tasks of varying challenge (BOS or sensory) was increase in theta power in frontocentral region which may be associated with the N1 responses that are associated with reactive control. For sensory conditions there was some modest difference frequency of activity for haptic (Pz) and visual (Oz) though these were not statistically significant. The current study reinforces the involvement of the cortex in the control of reactive balance control but does not confirm a potential role for sensory processing. Future studies investigating delta, beta, and gamma frequency bands and sensory manipulation during standard stance should be undertaken to improve statistical power and reduction of potential confounding influence of differences associated with task challenge.

Acknowledgements

I would like to thank my supervisor Dr. William McIlroy and committee members Dr. Richard Staines and Dr. Ewa Niechwiej-Szwedo for their support in producing this thesis. Although a global pandemic side-tracked my original research, you were all supportive in my attempts to move forward and complete my graduate degree, and for that I will be forever grateful.

I would like to thank the NiMBaL lab for their unending support and gentle reminders to stay on track. Special thanks to Dr. Laura Williams and Dr. Sherri Thomson for reminding me why I wanted to complete this degree in the first place and for offering wise guidance when needed. Thank you to Dr. Jessy Parokaran Varghese and Mark Laylor for kindly guiding me through the complicated world of MatLab and EEG and for patiently answering all my questions.

Finally, thank you to my family and friends for always supporting me no matter how many times

I changed my mind about my life path. Please continue that support as I change my mind at least 50

more times.

Table of Contents

Author's Declaration		ii
Abstract		iii
Acknowledgements		V
List of Figures		ix
Chapter 1 Background		1
1.1 Introduction	on	1
1.2 Importanc	e of Balance Control	2
1.3 Classes of	Balance Control	3
1.3.1	Predictive Control	3
1.3.2	Reactive Control	4
	1.3.2.1 Change in Support	5
	1.3.2.2 Fixed Support	5
1.4 Measurem	ents of Static Balance Control	7
1.5 Cortical Co	ontrol of Balance	8
1.5.1	Overview	8
1.5.2	Role of Sensory Information	10
1.6 Sensory Co	ontributions	10
1.6.1	Vestibular	10
1.6.2	Proprioceptive/Somatosensory	11
1.6.3	Visual	12
1.6.4	Adaptable Hierarchy Model	12
1.7 Cortical Pr	ocessing of Visual Information During Balance Control	13
1.8 Postural Se	et	17
1.8.1	Determinants of Postural Set	18

1.9 E	EG Markers of Cortical Processing	21
	1.9.1 Event Related Potentials	22
	1.9.2 Frequency of Cortical Activity	23
	1.9.2.1 Frequency of Cortical Activity and Balance Control	25
1.10	Study Objectives	29
1.11	Hypothesis	30
	ethods	
·		
2.1 P	articipants	32
2.2 P	rotocol Summary	32
2.3 N	leasures	34
	2.3.1 Force Plate	34
	2.3.2 Electroencephalography	34
2.4 D	ata Analysis	34
	2.4.1 Force Plate	34
	2.4.2 Electroencephalography	35
Chapter 3- Re	esults	37
3.1 Ta	ask Related Differences in Centre of Pressure	37
	3.1.1 Stance Width Comparison	37
	3.1.2 Haptic Comparison	40
	3.1.3 Vision Availability Comparison	43
3.2 Ta	ask Related Differences in Cortical Activity	46
	3.2.1 Topography	46
	3.2.1.1 Stance Width Comparison	46
	3.2.1.2 Haptic Comparison	48
	3.2.1.3 Vision Availability Comparison	51
	3.2.2 Peak Amplitude	55
	3 2 2 1 Stance Width Comparison	52

3.2.2.2 Haptic Comparison	54
3.2.2.3 Vision Availability Comparison	56
Chapter 4- Discussion	60
4.1 Discussion	60
4.2 Measure of Balance Control Across Tasks	62
4.3 Frontocentral Activity	63
4.4 Task Challenge	65
4.5 Haptic Touch	67
4.6 Visual Information	68
4.7 Limitations	70
4.8 Conclusions and Future Directions	71
References	76
Annendix	81

List of Figures

Figure 1.0- Average anteroposterior (AP) centre of pressure displacement measured as RMS across task
stance width comparison. Solid bars denote in order: Standard stance eyes closed, narrow stance eyes
open, tandem stance eyes closed. Error bars represent standard deviation and parenthesis represent
statistical significance (p<0.05)38
Figure 2.0- Average mediolateral (ML) centre of pressure displacement measured as RMS across task
stance width comparison. Solid bars denote in order: Standard stance eyes closed, narrow stance eyes
open, tandem stance eyes closed. Error bars represent standard deviation and parenthesis represent
statistical significance (p<0.05)
Figure 3.0- Average anteroposterior (AP) centre of pressure velocity across task stance width
comparison. Solid bars denote in order: Standard stance eyes closed, narrow stance eyes open, tandem
stance eyes closed. Error bars represent standard deviation and parenthesis represent statistical
significance (p<0.05)39
Figure 4.0- Average mediolateral (ML) centre of pressure velocity across task stance width comparison.
Solid bars denote in order: Standard stance eyes closed, narrow stance eyes open, tandem stance eyes
closed. Error bars represent standard deviation and parenthesis represent statistical significance
(p<0.05)40
Figure 5.0- Average anteroposterior (AP) centre of pressure displacement measured as RMS across
haptic touch task comparison. Solid bars denote in order: tandem stance eyes closed, tandem stance
eyes closed with haptic touch. Error bars represent standard deviation and parenthesis represent
statistical significance (n<0.05)

Figure 6.0- Average mediolateral (ML) centre of pressure displacement measured as RMS across haptic
touch task comparison. Solid bars denote in order: tandem stance eyes closed, tandem stance eyes
closed with haptic touch. Error bars represent standard deviation and parenthesis represent statistical
significance (p<0.05).
Figure 7.0- Average anteroposterior (AP) centre of pressure velocity across haptic touch task
comparison. Solid bars denote in order: tandem stance eyes closed, tandem stance eyes closed with
haptic touch. Error bars represent standard deviation and parenthesis represent statistical significance
(p<0.05)
Figure 8.0- Average mediolateral (ML) centre of pressure velocity across haptic touch task comparison.
Solid bars denote in order: tandem stance eyes closed, tandem stance eyes closed with haptic touch
Error bars represent standard deviation and parenthesis represent statistical significance (p<0.05)42
Figure 9.0- Average anteroposterior (AP) centre of pressure displacement measured as RMS across
visual availability task comparison. Solid bars denote in order: Tandem stance eyes open, tandem stance
restricted vision, tandem stance eyes open vision occluded, tandem stance eyes closed. Error bars
represent standard deviation and parenthesis represent statistical significance (p<0.05)44
Figure 10.0- Average mediolateral (ML) centre of pressure displacement measured as RMS across visual
availability task comparison. Solid bars denote in order: Tandem stance eyes open, tandem stance
restricted vision, tandem stance eyes open vision occluded, tandem stance eyes closed. Error bars
represent standard deviation and parenthesis represent statistical significance (p<0.05)44
Figure 11.0- Average anteroposterior (AP) centre of pressure velocity across visual availability task
comparison. Solid bars denote in order: Tandem stance eyes open, tandem stance restricted vision,
tandem stance eyes open vision occluded, tandem stance eyes closed. Error bars represent standard
deviation and parenthesis represent statistical significance (n<0.05)

Figure 12.0- Average anteroposterior (AP) centre of pressure velocity across visual availability task
comparison. Solid bars denote in order: Tandem stance eyes open, tandem stance restricted vision,
tandem stance eyes open vision occluded, tandem stance eyes closed. Error bars represent standard
deviation and parenthesis represent statistical significance (p<0.05)46
Figure 13.0- Grand average topographic representation of delta, theta, alpha, and beta frequency power
(db/Hz) for stance width comparison49
Figure 14.0- Grand average topographic representation of delta, theta, alpha, and beta frequency power
(db/Hz) for haptic touch comparison50
Figure 15.0- Grand average topographic representation of delta, theta, alpha, and beta frequency power
(db/Hz) for visual availability comparison53
Figure 16.0- Peak amplitude representation of delta, theta, alpha, and beta frequency power ratio for
stance width comparison. Solid bars denote in order: Standard stance eyes closed, narrow stance eyes
open, tandem stance eyes closed (p>0.05)55
Figure 17.0- Peak amplitude representation of delta, theta, alpha, and beta frequency power ratio for
haptic comparison. Solid bars denote in order: tandem stance eyes closed, tandem stance eyes closed
with haptic touch (p>0.05)57
Figure 18.0- Peak amplitude representation of delta, theta, alpha, and beta frequency power ratio for
visual availability comparison. Solid bars denote in order: Tandem stance eyes open, tandem stance
restricted vision, tandem stance eyes open vision occluded, tandem stance eyes closed (n>0.05)

Chapter 1 Background

1.1 Introduction

Understanding the control of upright stability is crucial for both practical reasons, such as improving our understanding of causes of falls, as well as for foundational reasons, better understanding how the human central nervous controls complex behaviours. The control of upright posture is particularly complex given the degrees of freedom required to maintain the stability of the multi-segmented body with respect to a typically small base of support. Control requires the complex interaction between anticipatory and reactive motor coordination to elicit static (fixed support) or dynamic (change in support) balance reactions (Maki & McIlroy 1997). Essential to successful control is the reliance on sensory information to provide information about surrounding environment and state of the body with respect to segment and whole-body stability. Necessarily this requires the integration of several systems including vision, somatosensory and vestibular inputs (Horak & Nashner, 1986). The current study is specifically focused on advancing understanding on how the central nervous processes sensory information for the control of upright balance. In particular, the work is focused on the use of vision and in particular the role for cortical processing.

The focus on the potential importance of cortical control of balance has emerged from several lines of inquiry (Maki et al., 1992; Bolton et al., 2015). Cortical contributions have been inferred from dual-task studies but more directly revealed through the use of brain imaging techniques, such as electroencephalography (Maki et al., 1992; Bolton et al., 2015). Studies using electroencephalography revealed significant cortical activity associated with perturbations and during periods of preparation or anticipation of instability (Maki et al., 1992; Bolton et al., 2015). To date the majority of studies have highlighted the potential contribution of the cortex but not explicitly focus on involvement of the sensory processing areas particularly as they relate to the involvement of vision. The current study sets out to determine evidence for changes in cortical activity associated with changes in visual and

somatosensory information during the control of upright standing balance. The study explores task related changes and cortical activity measured using EEG under various task conditions that manipulate the availability of vision and somatosensory information. Consistent with the hypothesis that the cortex plays an important role in the control of balance it is anticipated that there will be regional specific changes and cortical activity, as measured by frequency changes, that coincide with the availability of specific sensory inputs. This study will seek to advance understanding for the role of the central nervous system in the control of upright stability in humans. It is believed that such understanding will be important to advance future approaches to maintain stability and reduce fall risk in individuals with central nervous system and or sensory system challenges.

1.2 Importance of Balance Control

Balance control is crucial not only for the maintenance of upright stability during static stance but for mobility and activity to perform activities of daily living. In order to stand upright the central nervous system must integrate sensory information from vision, proprioception, somatosensory, and vestibular inputs to determine orientation of the head and body as well as detect and react to internally produced postural sway. During locomotion the central nervous system must anticipate taking a step and reposition the centre of mass accordingly, propel the centre of mass forward, then catch the centre of mass and prevent a fall by reposition a lower limb (Bruijn et al., 2010; Meyns et al., 2013; Kibushi et al., 2018). Humans spend a significant amount of time walking or standing in order to perform daily activities, therefore the maintenance of upright posture is crucial to live a normal life. Additionally, the maintenance of upright posture gives insight into how the central nervous system processes multisensory input in order to produce a motor output.

Although central nervous system involvement is imperative for the maintenance of upright stance and therefore locomotion, the underlying mechanisms of how sensory information is processed within the cortex remains unclear (Petsche et al., 1984; Sur & Sinha 2009; Varghese et al., 2015; Sibley

et al., 2010; Buzsáki et al. 2012). Studies conducted utilizing electroencephalography during reactive balance control tasks reveal significant cortical involvement through the appearance of event related potentials (Petsche et al., 1984; Sur & Sinha 2009; Sibley et al., 2010; Buzsáki et al., 2012; Varghese et al., 2015) cortical involvement during static stance is revealed through frequency activity (Stam, 2000; Sipp et al., 2013; Bruijn et al., 2015). Understanding how the nervous system processes incoming sensory data for the purposes of upright stance may provide insight as to why older adults experience decline in postural stability and therefore indicate how this decline can be mitigated through physiotherapy or pharmaceuticals.

1.3 Classes of Balance Control

1.3.1 Predictive control

Predictive balance control is defined as a feedforward method of balance control; the central nervous system anticipates perturbation and adjusts posture accordingly to reduce the impact of the expected perturbation on stability (Laessoe et al., 2008). The most striking example of predictive balance control is the moving bus example; a person who has ridden the same bus route many times knows when stops are approaching. The person is standing and is therefore acutely aware of any possible postural threat (re. postural set, section 1.8.1). The person knows the bus is about to stop, and therefore leans forward, repositioning their centre of mass forward in anticipation of an external perturbation backwards, which reduces the required muscular contraction required to stabilize them post-perturbation (bus decelerating and stopping). Predictive balance control is also uniquely apparent during locomotion, when the CNS repositions the centre of mass in anticipation of raising a leg to initiate a step (Laessoe et al., 2008). Predictive balance control is essential for stability before perturbation, but reactive control is essential for stability post-perturbation.

1.3.2 Reactive control

Reactive balance control is one of the hallmarks of human motor control that allows us to adapt our stance and posture to an unexpected perturbation that may otherwise result in a fall or serious injury; it is considered a feedback method of balance control (Laessoe et al., 2008). Reactive control is the ultimate the line of defense to prevent falls where predictive control serves to maximize stability by reducing the challenges to reactive control. Reactive control is unique in that responses are very rapid (Lakhani et al., 2013) and yet highly adaptable to changes in the environment, initial posture, physical ability, and desired outcome (Horak et al., 2006). These actions require a highly sophisticated network for stimulus detection, response selection, and execution. Responses to perturbation have been classified, based on behaviour, as either a fixed support reaction, in which the base of support (BOS) does not change, or a change in support reaction, in which the BOS moves to accommodate COM disruption. Both optimally result in regained control of the COM with respect to the BOS (Thomas & Whitney, 1959; Gurfinkel et al., 1974; Soames & Atha, 1982; Winter et al., 1990).

The aforementioned postural responses typically begin around 100ms after the onset of perturbation and can take the form of fixed support or change in support reactions (Nashner et al., 1980). These postural responses depend on bottom-up processing for the execution of movement; a perturbation is sensed via visual inputs, vestibular inputs, muscular stretch inputs, and/or tactile sensation inputs from the bottom of the feet (Thomas & Whitney, 1959; Gurfinkel et al., 1974). Once perturbation is sensed, the distributed network of the cortex, cerebellum, brainstem, and spinal cord work to produce compensatory postural responses within 100ms from the onset of perturbation (Maki & McIlroy, 1997). As will be explained further, some of these responses are fixed support, meaning the BOS does not change in space during compensatory reactions to maintain balance, rather forces are generated to maintain the position of the COM within the existing BOS. On the other hand, some of these reactions do involve changing the BOS in space, either through movement of the feet or reaching

of the hands in order to grasp objects to increase BOS size. The next section of this paper will examine fixed support reactions in detail.

1.3.2.1 Change in Support

Change in support reactions are defined as balance stabilization reactions that involve the reorganization of distal limb position to change the physical properties of the BOS in 3D space (Maki & McIlroy, 1997). Change in support reactions generally take two forms; lower body and upper body, where lower body reactions involve the legs and feet and upper body reactions involve the arms, hands, and trunk. The perturbation required to elicit a change in support reaction is typically larger than the perturbation required to elicit a fixed support reaction (Maki & McIlroy, 1997).

1.3.2.2 Fixed Support

Fixed support reactions are defined as balance stabilization reactions elicited without changing the size, shape, or other physical properties of the BOS (Winter et al., 1990). These reactions work with the centre of pressure (COP) in order to "corral" the COM with the end goal of re-establishing the COM within the BOS (Winter et al., 1990). COP is a force vector that is the sum of the forces acting on the body. It is a point on the supporting surface that reflects the sum of the forces generated working to stabilize the COM. Therefore, it is responsible for pushing the COM back within the BOS. Fixed support reactions are elicited during small amplitude perturbation, and although the amplitude required to elicit fixed support reactions differs based on the physical abilities of the subject, the characteristics of the reactions have a stereo typical timing and pattern of muscle activity that is determined by the characteristics of the perturbation (Horak & Nashner, 1978; Maki, 1993).

Fixed support postural reactions typically follow a "distal to proximal" pattern that is characteristic of the postural response (Horak & Nashner, 1978). This means that the first muscles to compensate for perturbation are often muscles of the feet and ankle. The specific muscles that are activated are dependent on the direction of perturbation (Horak & Nashner, 1978). For example, in the

case of mediolateral perturbations to stability, the inverters and everters of the ankle, specifically tibialis posterior and peroneus longus, brevis, and tertius are activated (Horak & Nashner, 1978; Wikstrom et al., 2009). For example, if a subject is physically pushed to the right, the inverters of the right foot will become active, while the everters of the left foot will become active. The purpose of this muscle activation is to reposition the COM back within the BOS. The ankle muscles are activated to facilitate movement of the COP from the right to the left. This regains control of the COM and re-establishes its position within the BOS without changing its spatial characteristics. A similar principle is evoked with anteroposterior perturbation, but the muscles activated are gastrocnemius, soleus, and tibialis anterior. The COM moves outside the BOS and the compensatory muscles of the ankle are active to utilize COP to regain balance (Horak & Nashner, 1978; Tang et al., 1998). The amplitude of muscle activation increases with increased perturbation amplitude until the limit of muscle activation is saturated and the body must move to a more proximal postural reaction (Tang et al., 1998). The activation associated with the fixed support reactions includes contraction across many body segments, as noted, in a typical distal to proximal sequence. As an example, for anteroposterior perturbations the compensatory reaction would include sequence activation of knee, hip, and trunk muscles with the specific involvement of flexors or extensors depending on the direction of perturbation (Gurfinkel et al., 1974; Horak & Nashner, 1978; Soames & Atha, 1982; Winter et al., 1990). In addition to the pattern of the muscle activity being determined by the direction of perturbation, the amplitude of responses is scaled to the amplitude of the imposed instability (Horak & Nashner, 1978). In other words, the larger the perturbation the larger the muscle activation and generated force.

The evoked reactions, including pattern of coordination and muscle activation, is also modified by task conditions. An example of this adaptability is the generation of hip strategies to imposed perturbation that reveal a reversed order of recruitment (proximal to distal) but at the same rapid latency. In addition, rapid arm reactions to generate counter balancing reactions are also possible

depending on task conditions (Horak & Nashner, 1978; Woollacott et al., 1997). Such adaptability of response characteristics influenced by task conditions is a hallmark of these balance reactions and is further demonstrated by the characteristics of change in support reactions discussed in the subsequent section.

Fixed-support compensatory balance responses are also susceptible to differences associated with individuals such as age-related changes. For example, elderly subjects or those with limited lower body strength may experience saturated reactions at lower amplitudes and will therefore require proximal strategies or change in support reactions at lower amplitude perturbations (Tang et al., 1998). It is important to note that the nervous system has the ability to determine which strategy is most likely to regain control of the COM within an average of 100ms (Maki & McIlroy, 1997).

1.4 Measurements of Static balance control

Static balance control is defined as the ability to maintain an upright posture in a fixed position (Winter et al., 1990; Patla, 1997) – measures of static balance control focus on postural sway that can be measured as a kinematic measure (centre of mass sway) or kinetically as change in ground reaction force (centre of pressure sway). COM sway is defined as horizontal movement of the body around the centre of gravity during static stance. COP sway is related to COM sway and is assessed using force plates to provide a measure of the summed forces generated to maintain the position of the COM (Winter et al., 1990). For the purposes of this thesis postural sway will refer to COP sway. As previously noted, fixed support reactions are defined as balance stabilization reactions elicited without changing the size, shape, or other physical properties of the BOS (Winter et al., 1990; Woollacott et al, 1997; Horak et al., 2006). COP is a force vector that is the sum of the forces acting on the body. In essence, it is a point on the supporting surface that reflects the forces working to move the COM. During fixed support reactions, it moves in the same direction of the COM but exceeds the location of the COM in the same direction of movement. Therefore, it is responsible for pushing the COM back within the BOS

(Winter et al., 1990; Woollacott et al., 1997; Horak et al., 2006). Fixed support reactions are elicited during small amplitude perturbation, and although the amplitude required to elicit fixed support reactions differs based on the physical abilities of the subject, the characteristics of the reactions maintain a similar pattern regardless of the person (Winter et al., 1990; Woollacott et al., 1997; Horak et al., 2006).

Postural sway is quantified in many ways. Two conventional approaches are variability of displacement of COP (root mean square (RMS) and velocity of sway. RMS is defined as the average variance of the centre of gravity around its static location, while velocity of postural sway is the average speed of COP sway (Neville et al., 2015). The measures of postural sway during static standing are used to determine the integrity of the balance control system. For example, in elderly participants with age related decline in balance, the RMS will be significantly higher, and the velocity of sway will be significantly lower, indicating postural instability (Lord et al., 2000). This postural instability results in a higher fall risk due to the reduced efficacy of the fixed support reactions (Horak et al., 2006).

Postural sway measures, during stationary standing, have also been used to reveal the important of sensory inputs to balance control. For example, on examination of postural sway in older adults post detailed visual examination, it was found that poor vision was highly correlated with an increase in RMS, indicating a reduction in postural stability (Lord et al., 2000).

1.5 Cortical Control of Balance

1.5.1 Overview

Although postural stability is highly visualized in muscular contractions and force plate analysis, recent evidence has indicated that there is a role for the cortex in postural stability. Varghese and colleagues (2015) examined event related potentials during static stance by timelocking natural postural sway reactions to the collected EEG data. It was found that an N1 potential was present before postural corrections and the peak amplitude of N1 was dependent on stance difficulty. The researchers theorized

this was because the demand for quicker and stronger postural reactions increased (Varghese et al., 2015). Cortical involvement in balance and postural control has been largely studied beginning in the 1990's, but interest in neural imaging and the cortex has sparked a wide network of research regarding the role of the cortex separately from the role of the brainstem and spinal circuits. This interest has led to the use of EEG (electroencephalography) as an electrophysiological monitor during dual-task trials, resulting in the conclusion that the cortex is more involved in balance maintenance than previously indicated. The effect is seen not only at the electrical level of the cortex, but in the change of reactive behaviours in the face of changes in cortical contributions to control. In 1998, Andersson, Yardley, and Luxton conducted a study to determine if dual-task paradigms influence the performance of the cognitive task as well as performance of the balance task.

This study found that when examining the mental task, the mean number of correct answers, as well as the percentage of correct answers, significantly decreased with the removal of sight during the sway conditions. Additionally, it was found that sway increased when implementing the mental task compared to no additional mental task in both patients and control subjects. Due to these findings, this study concluded that there is a complex interface between cognitive and physical domains in the context of balance task, and that balance tasks do require cognitive activity to be performed (Anderson et al., 1998). This cognitive activity indicates high levels of cortical activity during balance task paradigms, which can be seen on EEG during balance task trials.

Although the previously mentioned studies indicate that the addition of cognitive tasks negatively impacts postural stability, it has also been indicated through frequency analysis of EEG during static stance conditions that manipulation of sensory input can not only impact global cortical activity, but the recruitment of specific areas of the cortex. For example, removing visual input through complete visual occlusion during static stance has been shown to affect cortical frequencies not only in the visual cortex but the somatosensory cortex as well; specifically, there was a frequency shift from theta to beta

or gamma frequencies, indicating increased cortical excitation in these specific structures (Tse at al., 2013).

1.5.2 Role of Sensory Information

Sensory information is crucial for the maintenance of upright stance in both a feedforward and feedback manner. In the context of reactive balance control during static stance, sensory information can detect minute internally produced perturbation through detection of head movement via vestibular input, feedback of muscular stretch from muscle spindle fibres, somatosensory information received through the soles of the feet, and retinal slip information from the eyes. The central nervous system can then scale muscular contraction to the detected postural sway to compensate for perturbation and reposition the centre of mass accordingly. The sensory systems then detect this internally provoked perturbation, relay this information to the CNS, and the cycle of sensory relay and CNS reaction continues (Bolton, 2015; Varghese et al., 2017; Payne et al., 2019).

1.6 Sensory Contributions

1.6.1 Vestibular

Vestibular contributions to balance control are considered to have two main functions; detect head orientation and acceleration. Vestibular sensation is detected through organs within the inner ear. The otoliths detect linear acceleration of the head while the semicircular canals detect rotational acceleration; together they determine if the head remains upright and assists in determining if and by how much the head is moving. The cortex can use this information to determine what muscles need to contract to retain upright posture and scale the muscular contractions to the amplitude of perturbation (Agrawal et al., 2009).

1.6.2 Proprioceptive/Somatosensory

Proprioception is defined as the knowledge of where body sections are in space; proprioceptive input is crucial during both static and dynamic balance. Proprioceptive information is detected by golgi tendon organs within the interface of muscle and tendon, joint receptors within the joint capsule, and muscle spindles embedded within the muscle fibres. Golgi tendon organs detect force exerted over the tissues while joint receptors relay joint position information to the CNS. Finally, muscle spindle fibres determine muscle stretch and can activate reflex activity to contract the muscle when stretch is determined to be past threshold. Together, these receptors determine where limbs and segments are in space compared to other segments as well as avoid injury due to forces on the limb, either external or internal (Wingert, 2014).

Proprioception is crucial for balance preservation in static stance, specifically the muscle spindles. When the body sways during static stance, the muscles in the lower leg and foot experience stretch which is detected by the muscle spindles. This stretch is relayed to the cortex for processing regarding limb position. The muscle that has been stretched contracts to counteract the stretch without descending information from the cortex. However, the cortex does integrate this information along with vestibular, somatosensory, and visual information to determine where the lower limb is for the purposes of a possible change in support balance reaction (Schoultz et al., 1972; Wingert et al., 2014).

Somatosensory information for the purposes of static stance is also detected by somatosensory mechanoreceptors on the sole of the foot. Past studies have indicated that manipulation of incoming sensory information to the bottom of the foot, such as adding foam to the bottom of the foot, results in increased postural sway amplitude as well as a lower threshold for stepping reactions post-perturbation (Kennedy & Inglis, 2002). Researchers postulate that glabrous mechanoreceptors in the sole of the foot send information regarding pressure distribution to the cortex, which is then integrated into the somatotopic model of the human body on the somatosensory cortex (Maurer et al., 2001). Finally,

sensory information due to haptic touch can be used to reduce postural sway, which will be further explained in section **1.9.2**.

1.6.3 Visual

Vision is specifically crucial for balance control because vision detects motion and orientation of the body in reference to the external environment. Motion detection occurs when the eye experiences retinal slip; the motion of a visual scene across the retina. Additionally, the vestibular system and visual system work together to detect postural sway during static stance (Patla et al., 1996; Patla, 1997; Hammami et al., 2014). The vestibulo-ocular reflex works to stabilize visual images on the retina by moving the eyes in response to motion as detected by the vestibular system; as the head moves and the vestibular system in the inner ear detects acceleration, the muscles around the eye respond in reflex in order to foveate on the target (Somisetty & Das, 2020).

Additionally, vision works with the vestibular system in order to determine orientation of the head and body in association with the external environment. The cortex uses incoming visual information in comparison with expected orientation of objects (ie. lights appear on the roof, chairs appear on the floor) to determine if static posture is being maintained or is at risk (Patla et al., 1996; Patla, 1997; Hammami et al., 2014). Together, vestibular, proprioceptive, somatosensory, and visual information inform the cortex about postural sway and body orientation, however when one method of incoming information is compromised the cortex can rely on an adaptable hierarchy in order to ensure upright posture and therefore physically safety is maintained.

1.6.4 Adaptable Hierarchy Model

The adaptable hierarchy model of balance, otherwise known as sensory reorganization, is based on the notion that weighting of sensory input is based on the availability of stimulus. This reorganization results in modulated excitation of sensory cortical areas allowing for maximum efficiency and efficacy of muscular contraction to remain stable, which is determined by the availability of incoming stimulus

(Merabet et al., 2010). For example when visual information is unavailable cortical areas primarily excited by somatosensory and vestibular input will increase in frequency while areas excited by visual input will remain in lower frequencies, all the while upright stance will still be achievable in normal healthy adults. Even in extreme cases of complete sensory loss the areas of the brain normally reserved for the loss sense are recruited by the sensory areas that remain (Merabet et al., 2010).

This effect is seen specifically in older adults with balance deficits directly related to the inability of the cortex to reweight reliance on a variety of sensory modalities based on environment and postural challenge. For example, Woollacott and colleagues (1986) produced a study comparing static posture of older adults and young healthy adults in differing sensory circumstances using the moving room paradigm. Although basic and older, this method of study illuminated glaring effects of sensory reorganization on balance specifically in children and older adults, and for this reason it is worth mentioning. It was revealed that the moving room experiment produced effect on muscular recruitment and amplitude of muscular contraction. When the amplitude of the moving room increased the amplitude of muscular contraction in older adults increased inappropriately in combination with incorrect recruitment of the muscles of the lower limbs (Woollacott et al., 1986).

Through examination of cortical frequencies as well as attributes of the motor compensation it is abundantly clear that the adaptable hierarchy model has a profound impact on balance control; as vision is a large contributor to the maintenance of upright stance when it is incompatible with other sensory input the result can be ineffective motor strategies. To understand how impactful the adaptable hierarchy of senses can be to cortical excitation and postural sway it is crucial to also understand how the whole cortex is involved in the maintenance of upright posture in static stance as well as perturbation evoked reactions.

1.7 Cortical Processing of Visual Information During Balance Control

In order for vision to be integrated into the network of postural control, the human

brain needs to detect the visual stimulus and process the orientation, colour, physical features, and texture of the external environment. Visual information enters the human brain via the optic nerve, which becomes the optic chiasm, then separates again into the optic tract (Brindley, 1960). The optic tract terminates bilaterally onto the later geniculate nucleus (LGN), which then initiates depolarization of the optic radiation, which then terminates onto the primary visual cortex (V1) (Brindley, 1960). V1 is commonly referred to as the striate cortex, as it is organized into ocular dominance columns (Hubel et al., 1977). Ocular dominance columns are collections of neurons organized into columns or "stripes", with each column being particularly sensitive to information received from the left or the right eye (Hubel et al., 1977). All visual areas of the cortex outside of V1 are known as the extrastriate cortex and are considered to be higher order areas used for fine processing of visual information (Brindley, 1960).

Feature extraction of external stimuli is the function of the striate and extrastriate cortex. The striate cortex is known to process relatively simplistic features of the external environment and then relay this information to the higher order areas of V2, V3, V4, and V5 (Brindley, 1960). Cells within the striate cortex are classified as "simple" and "complex" based on their respective receptive fields.

According to Carandini et al. (2005), simple cell receptive fields contain clear delineations between areas of excitatory response and inhibitory response. Each cell is most responsive to large amounts of light that fall within the excitatory regions and small amounts that fall in the inhibitory regions. In order initiate an optimal response from a simple cell the visual information must have the correct size, orientation, and position.

Despite their name, complex cells of the striate cortex respond to comparatively simpler stimuli than simple cells. Because complex cells do not have inhibitory and excitatory regions, these cells do not respond to the specific orientation of stimuli, but merely the position of the stimulus. Additionally, complex cells respond to the direction of motion of the stimulus. The combination of excitation from the

simple and complex cells leads to a rudimentary representation of the external environment (Carandini et al, 2005).

The striate cortex is also organized into 6 distinct cellular layers with sublayers in layer 4; 1, 2, 3, 4A, 4B, 4Ca, 4Cb, 5, and 6. Layers 1, 2, 3, and 6 are comprised of complex cells, while layers 4A and B, 4Ca, and 4Cb are comprised of simple cells. Each layer receives input from either the magnocellular or parvocellular layer of the LGN. Hubel and Weisel (1977) determined that striate cells are organized according to orientation tuning as well as ocular dominance. Rows of cells across the cortex are highly sensitive to specific orientations of the stimulus but moving deeper into the cortex reveals that cells perpendicular to the surface are sensitive to the same orientation stimulus. Additionally, through cytochrome oxidase staining, Hubel and Weisel (1977) revealed that lined up within the ocular dominance columns of the striate cortex are colour "blobs". Upon further examination, these blobs are not reactive orientation of any kind, but only respond to colour. These cells project to V2 within the extrastriate cortex, and then V4. As stated by Hubel and Weisel, this forms the "colour analysis stream" within the cortex (Hubel & Weisel, 1977). The combination of output generated by simple, complex, and colour "blobs" travels to higher order areas of the occipital lobe for the purposes of feature extraction and the early stages of interpretation for purpose driven responses (Hubel & Weisel, 1977).

Components of the extrastriate cortex include V2, V3, V4, V5, and V6. These areas, in conjunction with V1, form the appropriate visual representation of the external world based on sensory input from light on the retina. In order to fully understand the role of vision in postural control and as a consequence a piece of the puzzle that is cortical involvement in balance control, it is essential to understand the roles of each component of the extrastriate cortex, especially areas responsible for attention allocation to visual stimuli.

The first visual area outside V1 is V2. V2 is the first location within the visual association area. (Carandini et al., 2005; Petras et al., 2019). To communicate effectively with other areas of the cortex,

V2 shares feedforward and feedback connections with V1, as well as feedforward connections to V3, V4, and V5 (Carandini et al., 2005; Petras et al., 2019). Similar to V1, V2 is highly tuned to colour, object orientation, and spatial frequency, the latter of which is especially crucial for feature extraction in a visually complex world (Orban, 2020). Unlike V1, V2 is additionally responsible for subjective contours (contours around objects not delineated by physical lines), discrimination between the ground and figures, and minor attentional allocation (Orban, 2020). Additionally, recent studies have indicated that in addition to the lateral occipital complex, V2 is crucial for object recognition due to its direct communication with the hippocampus (Lopez-Aranda et al., 2009).

The next area involved in the stream of visual information within the cortex is V3. Through the use of fMRI, Braddick et al. (2001) were the first to definitively determine that area V3 is highly responsible for the detection of global motion, not just the detection of coherent motion, as described by previous studies (Braddick et al., 2001; Lui et al., 2006). V3 also has strong extensions to the posterior parietal cortex and is therefore considered a crucial component of the dorsal visual pathway; responsible for vision for action (Braddick et al., 2001; Lui et al., 2006). V3 does contain comparatively weak connection to the inferior temporal cortex (part of the visual perception pathway) but is largely considered a major contributor to the dorsal pathway (Braddick et al., 2001; Lui et al., 2006).

V4 is located adjacent to V3 and has similarities in function to V2. Like V2, it detects colour, spatial frequency, and orientation, however it is able to discriminate simple geometric shapes (Zeki, 1974). V4 receives strong input from V2, weak input from V1, and sends projections to the inferior temporal cortex. Additionally, V4 is highly tuned to attentional orientation, and for these reasons is considered a strong contribution to the ventral visual pathway (Moran & Desimone, 1985).

V5, otherwise known as the middle temporal visual area, structures and strong feedforward and feedback connections to V1, V2, and V3. Despite this complexity, stimulation studies performed on primates have revealed that V5 is responsible for perception of motion. Specifically, when

microstimulation is applied to neurons on the primate cortex the primate is most likely to report motion of objects in the direction the neuron is highly tuned to (Britten & van Wezel, 1998).

Finally, V6 has been recognized as an area specifically involved in the discrimination of self-motion from object motion. Through retinotopic mapping and voluntary discrimination of motion perception, Pitzalis and colleagues (2010) determined that V6 is highly involved in determining what motion detected by previous areas of the visual cortex (such as V1 and V2) are due to motion of the object or motion of the subject themselves. They then theorized that V6 activity is reliant on the presence of retinal slip and eye motion, however anatomical proof such as connectivity to the superior colliculus has yet to be established (Pitzalis et al., 2010).

Although visual detection of objects and environment is crucial for sensing the external world, it is only the first step in the cortical process responsible for representing the environment, it is up to additional regions of the brain such as frontal attentional networks to form a comprehensive representation of location in 3D space for the purposes of action, such as balance retention.

1.8 Postural Set

The idea that postural reactions evoked by instability are dependent on the state of the nervous system at the time of a perturbation, such as an internal representation of the surrounding environment, is linked to the general concept of postural set. Postural set (also commonly referred to as "central set") is defined as the overall physical and cognitive readiness of the body to respond to externally evoked perturbation or internally generated perturbation generated through maintenance of COP control during static stance. Postural set provides an initial state of the CNS that can impact postural responses. It includes aspects of physical being such as anxiety and emotional state, expectation of amplitude and direction of perturbation, as well as physical aspects of the external environment. In fact, these main determinants provide the framework for a working model of postural set and can greatly impact the resulting postural reactions (Horak et al., 1989).

1.8.1 Determinants of Postural Set

The main determinants of postural set are; CNS awareness of physical capabilities such as strength of skeletal muscles and velocity of neural transmission, previous perturbation experience, emotional state prior to perturbation (such as anxiety or boredom), postural anxiety due to physical positioning prior to perturbation such as lean angle, aspects of environment such as location of obstacles or handholds, anticipation of stimulus, and task challenge such as standard vs. tandem stance, (Horak et al., 1989). The physical capabilities of a subject impacts postural set by dictating the possible methods of fixed support and change in support reaction to re-stabilize the COM. For example, if an elderly individual is experiencing the effects of sarcopenia and age-related reflex suppression, the postural set of the individual will reflect this lack of postural control and will make the subject more likely to react excessively to small perturbations instead of eliciting a fixed support reaction (Horak et al., 1989). This effect is theorized to impact young, healthy adults with injuries, especially lateral ankle injuries. In a study conducted by Wikstrom and colleagues (2009), adults with lateral ankle injuries were shown to have significantly decreased abilities to respond appropriately to low amplitude perturbation, due to decreased strength in the injured area (Wikstrom et al., 2009). This decrease in ankle strength of an individual, and therefore normal postural responses, would impact the current postural set by minimizing the CNS' reliance on lateral ankle response to perturbation, and increasing the reliance on other muscle groups to re-stabilize COM (Wikstrom et al., 2009).

Previous perturbation experience impacts postural set by pre-programming postural responses based on past postural history. This can be seen in stark reality when watching people walking on known slippery surfaces. When a known slippery surface is confronted, a subject will likely make a marked decrease in locomotion velocity, take smaller steps, and land flat footed instead of heel-toe (Marigold & Patla, 2002). This is due to prior knowledge of how a slippery surface impacts postural control, and how best to mitigate these factors. Subjects will make postural adjustments prior to impacting the surface

and produce different locomotion patterns based on what strategies produced safe locomotion previously (Marigold & Patla, 2002). This adaptation based on previous experience is a result of an adaptation to postural set, and results in an increased likelihood of stability. Additionally, emotional state prior to perturbation or instability assists in dictating the consequent postural responses. This has been quantified using two emotional states: valence (pleasantness) and arousal (anxiety). Horslen & Carpenter (2011) stated that arousal produced by anxiety inducing images increases COP sway, and therefore has the same physical consequences as standing in physically arousing situations, such as on the ledge of a cliff (Horslen & Carpenter, 2011).

A similar aspect to emotional state that determines postural set is physically induced postural anxiety due to postural state prior to perturbation. Postural anxiety is known as the unconscious CNS state due to the subject being placed in a situation that may cause threat to stability, and therefore may increase the risk of falling. For example, a subject standing on a high ledge may not consciously feel anxious or aroused, but due to the threat to stability the CNS will decrease reaction thresholds, making postural reactions more likely (Carpenter et al., 2004). This differs from emotional state, as emotional state is consciously felt while postural anxiety is unconscious. Increased postural anxiety has been proven to not only increase the likelihood of postural reactions but increase amplitude of the reactions as well. In a study conducted by Carpenter and colleagues (2004), subjects placed in postural anxiety inducing situations were significantly more likely to overreact to perturbation. This effect was not only seen with unexpected perturbations but expected perturbation and stretch-reflex induction as well as well as fixed support balance reactions elicited by naturally occurring postural sway; static standing in a posturally anxious state resulted in higher RMS and centre of pressure velocity. This indicates an adaptation of the overall state of the CNS, and therefore impacts postural set (Carpenter et al., 2004).

Postural set is also influenced by anticipation of the upcoming stimulus. Influence of postural set has been observed when postural set does not match with the actual perturbation, leading to errors in

evoked compensatory reactions (Horak et al., 1989). According to Horak et al. (1989), postural set allows "descending commands to prepare sensory and motor systems for anticipated stimulus and task conditions; setting aspects of the response in advance can decrease the time it takes the CNS to transform an eliciting stimulus into an appropriate response". This is the most well-researched area of postural set and is therefore the most understood. For the purposes of this thesis, the external environment was manipulated prior to the execution of a voluntary reach-to-grasp action. This action is similar to the upper limb change-in-support balance reactions discussed in section 1.4.2, and therefore by viewing cortical excitation prior to the execution of a voluntary reach-to-grasp action it is possible to connect this isolated action of voluntarily reaching to- and grasping an object to the manipulation of postural set without other confounding determinants of postural set.

Postural set is also likely influenced by mapping of the external environment prior to perturbation, which is indicated by presenting an environment with relevant surfaces for stability, then perturbing the subject (Van Ootteghem et al, 2013; McIlroy & Maki, 1995). Through perturbing subjects and studying oxygen uptake in cortical tissues, Mihara and colleagues determined that the prefrontal cortex (PFC), which is responsible for attention allocation, emotional response, and action planning, is highly active during balance reactions. They determined that preparation for the execution of unpredictable balance reactions likely occurs pre-perturbation and is likely a result of attention allocation and environmental mapping (Mihara et al., 2008). It is likely that this mapping occurs constantly to prepare for a perturbation event, and as a result determines postural set and the resulting balance reactions. It is unknown whether this preparation occurs in everyday situations or exclusively in experimental situations. This can be discovered through manipulation of situations mimicking natural life, which will further decode neural modules associated with reactive balance control.

When standing still postural set is influenced by the task challenge and/or consequences such as when standing in tandem vs. standard stance. One can manipulate task challenge by altering sensory

inputs, such as vision or touch, and would be reflected by changes in neural weighting in the related areas as explained in section **1.6.4** on the adaptable hierarchy within the sensory areas of the cortex. Such set related changes in sensory processing would be revealed by changes in event related potential amplitude (specifically the N1) or frequency space alterations. For example, Sibley and colleagues (2010) investigated N1 morphology during static stance at low (ground level) vs. high (elevated 160cm) heights, this manipulating postural anxiety and task challenge. It was found that N1 amplitude was significantly larger in the high condition, reflecting postural set manipulation in preparation for possible perturbation (Sibley et al., 2010). Postural set is also reflected in frequency alteration during static stance, as discovered by Tse et al. (2013) as visual information was manipulated during static stance. In order to understand why these measures accurately represent changes in postural set it is crucial to understand the measures themselves.

1.9 EEG Markers of Cortical Processing

examination and cortical frequency examination. Studies performed for the purposes of upright balance examination commonly use event related potentials as markers for discrete cortical excitation due to the ease with which perturbation events can be time-locked to individual potentials. However, frequency observation has become an increasingly powerful tool in the examination of postural control during static stance.

1.9.1 Event Related Potentials

Cortical activity during balance tasks can be observed through EEG time-locked events, more specifically ERPs (event related potentials). ERPs are neural electrical events globally elicited over the cortex, which can indicate sensory or cognitive processes. They are thought to be a reflection of the summation of postsynaptic potentials when a large group of pyramidal neurons fire simultaneously (Petsche et al., 1984; Buzsáki et al., 2012). Within ERPs, there are many possible waveforms that can be

visible on EEG, but for the purposes of this paper only the waveforms that occur around 100ms from the onset of one single stimulus will be examined.

The first waveform to appear is the N1, or first negativity waveform. The N1 is always a negative deflection from the initial EEG output. N1 peak post balance perturbation occurs between 90 and 200ms after the onset of an unexpected stimulus, and its maximum amplitude can be used to determine cortical activity characteristics based on the presented stimulus (Sur & Sinha 2009; Buzsáki et al., 2012). It is thought that the N1 is associated with a "matching" process within the brain; in other words it may be associated with the attempt to match the presented stimuli with previously experienced stimuli, however this hypothesis has not yet been confirmed (Quant et al., 2004; Quant et al., 2005; Collette et al. 2007; Maki & McIlroy, 2007). By examining the characteristics of the relevant ERP waveforms, it is possible to determine how the brain is processing and interpreting sensation. For the purposes of this research design, the waveforms elicited by the brain will be examined relative to visual stimulus introduction and perturbation to determine if the brain is mapping and interpreting the external environment in preparation for perturbation.

EEG is a widely used method to determine cortical activity post-perturbation, most often in the form of N1 analysis. N1 peak amplitude is modulated by perturbation amplitude, predictability of stimulus, arousal, and stimulus features such as perceived threat (Quant et al., 2004; Quant et al., 2005; Collette et al. 2007; Maki & McIlroy, 2007). The characteristics of N1 during manipulation of these factors is consistent and predictable, therefore this waveform plays a crucial role in the probing of cortical activation during perturbation. For these reasons, manipulation of postural set also results in attenuation of N1 peak amplitude. N1 peak amplitude is directly impacted by manipulation of arousal and lean amplitude, therefore can be used as an indication of modulation of cortical activity resulting from manipulation of postural set (Quant et al., 2004; Quant et al., 2005; Collette et al., 2007; Maki & McIlroy, 2007).

1.9.2 Frequency of Cortical Activity

Frequency activity viewed through EEG is considered macroscopic in nature. This macroscopic cortical frequency is generated by large groups of neural ensembles oscillating in a pattern large enough to be detected through EEG (Stam, 2000; Sipp et al., 2013; Bruijn et al., 2015). Macroscopic cortical frequency viewed through EEG can be utilized to examine brain excitation during sleep, cognitive tasks, emotional experiences, clinical applications for seizures and brain abnormalities, and other tasks, including balance tasks (Stam, 2000). These frequencies are separated into bands; delta (1-3Hz), theta (4-7Hz), alpha (8-12Hz), beta (13-30Hz), and gamma (31-50Hz) bands (Stam, 2000; Sipp et al., 2013; Bruijn et al., 2015;). According to Pfurtscheller & da Silva (1999), an increase in frequencies is indicative of underlying neuronal processes that reflect synchronization of neuronal activity within a neuronal population. An increased synchronization of a frequency indicates a full cooperative network of neuronal excitation within that frequency band and therefore an increase in frequency power within a set frequency band. Conversely, desynchronization of neuronal populations occurs when neural networks oscillate at dissimilar frequencies in comparison with other networks, within a frequency band. When a neuronal population is in desynchronization there is a subsequent decrease in frequency power (Pfurtscheller & da Silva, 1992; Pfurtcheller and da Silva, 1999).

According to past literature, these bands represent specific functions of the cortex. Specifically, the delta frequency band most often occurs during sleep, however it is also highly apparent while forming explicit memory (Stam, 2000; Kinsey et al., 2011; Sipp et al., 2013). Researchers have postulated that the appearance of delta waves during the sleep cycle represents a loss of physical awareness or the complete absence of physical awareness, however due to the increase of delta frequency power during explicit memory task practice (such as memorizing provincial capitals) there is an increasing body of evidence indicating the delta frequency band is crucial for the gating and suppression of sensory information and memory sorting (Stam, 2000; Kinsey et al., 2011; Sipp et al., 2013). Theta frequency is

associated with daydreaming. A common example used by authors is while driving for long stretches on highways, experienced drivers will likely be in a state of theta frequency; the brain is conscious and have physical awareness but is not focusing on one specific task (Stam, 2000; Bruijn et al., 2015). When examining theta band activity and tasks such as sensory discernment, authors determined that theta band activity was present in cortical areas that would be highly excited given the sensory task. This led to the conclusion that theta activity denoted excitation in the associated cortical area based on task or sensory experience; this led authors to hypothesize that theta frequency may be responsible in part for sensory discernment while attentional areas of the brain are not highly excited (Sipp et al., 2013; Bruijn et al., 2015). Alpha waves are observed when the subject is in a state of wakefulness but not actively concentrating on a specific task. The subject is somewhere between daydreaming and concentrated thinking. Additionally, because alpha waves are most observed in the occipital lobe when the eyes are closed, researchers hypothesized that alpha waves are associated with the idle state of the occipital lobe (Stam, 2000; Kinsey et al., 2011). Conversely, other researchers believe that alpha waves play a role in inhibiting areas of the cortex not actively in use (Sipp et al., 2013; Bruijn et al., 2015). Due to the significance that the alpha band may have on visual information within the cortex it will be of specific interest in the discussion section of this paper. Beta waves are associated with active engagement of cognitive function and concentration; a person concentrating on a specific task will elicit beta waves (Stam, 2000; Kinsey et al., 2011; Bruijn et al., 2015). Finally, gamma waves are viewed when a person is at peak attention or anxiety or if a subject is actively trying to commit information to long-term memory (Stam, 2000). Although most studies including cortical frequency analysis are associated with cognitive tasks or emotion there are emerging studies that indicate cortical frequency is highly influenced by balance tasks.

1.9.2.1 Frequency of Cortical Activity and Balance Control

The characteristics of cortical excitability, specifically frequency, during static stance is thought to be indicative of the cortical involvement required for the maintenance of postural stability. Each frequency band may have specific association to the underlying cortical processing related to the control of upright stance. For example, delta frequency bands are highly modulated within the fronto-parietal lobe of the cortex during upright static stance while concurrently performing exercises requiring force matching or texture discernment (Hwang & Huang, 2016). Specifically, oscillatory patterns of delta band frequency activity were enhanced while theta frequency activity was suppressed indicating a reliance on delta frequency activity thought to provide a gating mechanism to the fronto-parietal lobe for the purposes of correctly re-weighting somatosensory information coming from the bottom of the feet and proprioceptive receptors for the purposes of maintaining upright stance with the somatosensory information required for the force-matching or texture discrimination task (Hwang & Huang, 2016).

Conversely, this same study indicated that theta suppression and desynchronization in the parietal lobe during dual-sensorimotor and balance tasking was coupled with increased theta synchronization and enhancement in the posterior frontal lobe (Hwang & Huang, 2016; Gebel et al., 2020). This increase in theta synchronization and band power around the frontal aspect of the cortex is also reflected when there is an increase in postural instability, for example when standing in tandem stance. This increase in power and synchronization is reflected centrally as well, resulting in researchers to hypothesize that cortical theta frequency during static stance is reflective of increased attentional and error monitoring processes as a result of increased task difficulty (Stam, 2000; Gebel et al., 2020). Together, delta synchronization in the fronto-parietal lobe and theta synchronization in the posterior frontal lobe indicate attentional gating between somatosensory inputs and attentional inputs for the purposes of maintaining upright stance (Stam, 2000; Hwang & Huang, 2016; Gebel et al., 2020).

Alpha frequency power increases during static stance are thought to be indicative of a reduction in neuronal firing rates, specifically observed in the occipital lobe during motor imagery. In a study conducted by Kanokwan et al. (2019) requiring adults to stand quietly while either looking at a moving scene or imagining a moving scene, it was noted that alpha frequency power increased in the occipital lobe as well as during motor imagery and when watching a moving visual scene (Kanokwan et al., 2019). In this case, alpha frequency increased in the occipital lobe when motion was imagined with no external visual input (Kanokwan et al., 2019). Thus, this study may indicate that during static stance the increase in alpha frequency power implies inhibition of the cortical area in question.

Beta frequency bands are thought to be indicative of a reduction in cortical excitation during static stance but are more apparent in the premotor cortex during static stance. For example, previous literature noted beta bursts of frequency power and synchronization in the premotor and motor cortex just after the onset of muscular activity for the purposes of correcting postural sway (Pfurtscheller et al., 1996; Müller-Putz et al., 2007; Solis-Escalante et al., 2012; Seeber et al., 2014). Each author postulated that that after movement was initiated, the cortex was able to transition to a state of reduced excitation, with a beta burst of synchronization initiating a state of decreased excitation. With this hypothesis, it is hypothesized that beta frequency synchronization indicates a maintenance of the current motor set while suppressing newly generated movements (Engel & Fries, 2010; Jenkinson and Brown, 2011; Seeber et al., 2014).

Finally, for the purposes of static stance, gamma frequency band activity is likely indicative of feature binding and the dynamic communication of several cortical regions during multiple sensory inputs (Singer, 1999; Womelsdorf et al., 2007; Uhlhaas et al., 2009; Fries, 2009). For example, during static stance, Ray and Maunsell (2010) determined that the inclusion of multiple visual inputs (several moving objects of different shapes, colours, and textures) increased gamma frequency power and synchronization in V1 in comparison to visual stimuli consisting of a screen of one colour. Additionally,

the inclusion of somatosensory input to the soles of the feet with the simple visual input increase gamma frequency power and synchronization in both the S1 and V1 and posterior frontal lobe. The authors then concluded that an increase in gamma frequency presence was indicative of inter- and intra-cortical communication based on sensory input for the purposes of the maintenance of upright stance.

Recent literature has indicated that cortical frequency during balance tasks is highly dependent on availability of visual input as well as difficulty of the balance task. For example, Tse et al. (2013) performed a study that manipulated visual information as well as participant stance (tandem and standard) as well as surface compliance. This study found that the power spectrum density of EEG increased significantly in the posterior parietal and central areas of the cortex when vision was unavailable and when surface compliance was increased. Specifically, this study determined that the power of beta and gamma bands increased the most during conditions with no visual availability, tandem stance, on a highly compliant surface. This article concluded that with the elimination of visual input and the increased reliance on somatosensory input for the maintenance of postural stability the cortex reduced excitation in the visual structures and for preference of the somatosensory and motor structures, indicating a tangible shift in the adaptable hierarchy of the cortical balance network in response to sensory availability (Tse at al., 2013).

This conclusion was confirmed by a study performed by Hülsdüncker and colleagues (2015) that focused only on the correlation of postural instability and theta frequencies produced by the cortex during varying balance tasks. Participants were subjected to varying task difficulties by increasing surface compliance as well as stance difficulties (standard to tandem). As task difficulty increased, theta bands within the central and parietal regions of the cortex increased, as did RMS variability and velocity. As sensory information was manipulated but visual information remained consistent, reliance on

somatosensory areas of the brain increased, indicating a sensory reweighting within the cortex (Hülsdüncker et al., 2015; Gebel et al, 2020).

A study performed by Anderson and colleagues (2017) came to a similar conclusion by examining frequency characteristics in participants walking; authors examined characteristics during the stance phase and transition to single support for both legs. Participants were asked to walk on a treadmill while alternating between eyes open and eyes closed every 5 minutes. Not only did this study find that there was an increase in frequency in the central and parietal regions of the cortex from theta to beta when vision was restricted in both stance and transitional phases, but they determined that there was also an increase in synchronization within frequencies as well, indicating a clear shift in sensory reliance from visual to somatosensory when vision was unavailable, even during locomotion (Anderson et al., 2017).

Finally, a study performed by Ishigaki and colleagues (2016) confirmed that the cortex reweights sensory information based on availability in accordance with the adaptable hierarchy model. This was confirmed through the inclusion of haptic touch while occluding vision with crystal occlusion goggles; eyes remained open while vision was eliminated. As defined by the article, haptic touch is defined as a light touch on a stable surface that does not provide any physical support to the subject. Haptic touch is thought to increase spatial orientation through providing an external spatial reference. This article found that by introducing haptic touch while vision was available and unavailable, there was a significant increase in frequency power to the left primary somatosensory cortex and posterior parietal cortex, as well as a reduction of frequency power to the occipital lobe when vision was occluded (Ishigaki et al., 2016). They concluded that the left somatosensory structures would be relied on more when haptic touch was introduced due to the increased physical reference to the external environment.

By examining the previously mentioned articles it is very clear that cortical excitation during balance tasks is dependent on available sensory information and follows the adaptable hierarchy model.

The cortex can adapt reliance on sensory information based on what is available for the purposes of maximizing postural stability. This author proposes that this reweighting is a component of postural set, as this adaptation is specifically for the maintenance of upright posture and is likely not only applicable to stable stance and natural postural sway, but also applicable pre-external perturbation to ensure an efficient postural response.

1.10 Study Objectives

The present study aims to understand how manipulation of sensory inputs, specifically vision and somatosensory, during stationary standing and postural correction affects cortical excitation as a potential reflection of postural set. This work will extend understanding of the potential role of cortical processing in the control of upright balance.

Recent evidence has indicated that recruitment of cortical areas during static standing is highly reliant on incoming sensory information from the environment. Manipulation of visual input has a significant impact on the recruitment of cortical areas during static stance for the purposes of postural control. The completed studies mentioned above provide evidence of increased activity in somatosensory associated areas such as S1 and the parietal lobe; this evidence is largely gathered using frequency analysis during paradigms that include complete vision occlusion compared to full vision.

With these paradigms results indicate that when vision is fully occluded through closing the eyes or utilizing crystal occlusion goggles a frequency shift from theta to beta or gamma ranges occurs within the somatosensory structures of the brain, while a less significant increase is seen in visual areas of the brain such as the occipital cortex. Conversely, when full vision is available, there is a low to high frequency shift in the visual areas of the cortex with a less significant shift in somatosensory areas

Although this evidence does exist, these studies fail to determine if this frequency effect is carried over when vision is partially occluded or when stance is tandem. Additionally, it is unknown if cortical excitation increases in somatosensory areas when haptic touch is included with full available

vision. This study aims to confirm the effect of visual availability on the recruitment of cortical areas not only when vision is completely removed from sensory contribution, but when vision is partially available, and corroborate this evidence with the inclusion of haptic touch in addition to full visual availability. In doing so, this study will increase understanding regarding cortical contributions to balance and further reveal why vision is critical for the maintenance of upright posture.

1.11 Hypothesis

It is hypothesized that in accordance with the previously examined literature, spectral values for theta and alpha frequency bands will be significantly different between tasks. The study focused on three main comparisons: 1) task challenge (examination of stance width while eyes are closed) 2) presence/absence of haptic touch when eyes are closed during tandem stance and 3) altered visual inputs (comparing eyes closed, eyes open with restricted visual field, eyes open with vision occluded, and eyes open during tandem stance conditions).

- 1) Task challenge: With respect to task challenge it is expected that spectral values for theta frequency bands will significantly increase around electrode FZ in accordance with task challenge; theta frequency bands around FZ will be higher in the tandem and narrow conditions in comparison with the standard conditions, with alpha and delta frequency bands having higher mean power in the same conditions. This will be associated with increase challenge to control of stability as reflected by increase in RMS values and centre of pressure velocity for the tandem eyes closed condition and narrow eyes closed condition in comparison to the standard eyes closed condition.
- 2) Haptic touch: It is hypothesized that the presence of haptic touch (when eyes are closed) will be characterized by an increase in mean theta spectral values around Pz when haptic touch is introduced as compared to eyes closed alone. This increase in theta power will be accompanied by a decrease in alpha and delta frequency power around the same electrode.

- It is also anticipated that an aspect of laterality will be present in examining the grand average spectral figures, specifically around PZ. This EEG data will be accompanied by an increase in RMS values and centre of pressure velocity in the non-haptic condition, representing an increase in postural stability.
- around FZ with very little activity around OZ and PZ as compared to open eyes but completely occluded vision it is likely that while the most theta activity will remain around FZ, there will be a significant increase in theta frequency around OZ. In the tandem stance eyes open with partially occluded vision, it is hypothesized that while similar to the previous conditions there will be theta frequency activity around FZ, there will also be significantly more cortical excitation in the form of theta frequency activity around OZ than in both previous conditions. RMS and velocity of centre of pressure will be dependent on visual information availability and stance challenge, with the highest RMS and velocity present in the tandem stance with eyes closed and the lowest RMS and velocity present in the normal stance with complete visual information availability condition.

Chapter 2- Methods

2.1 Participants

Twelve young healthy adults (age 19-37 years; 6 males and 6 females) participated in this study. Participants had normal or normal to corrected to normal vision and did not report any neuromuscular disorders. Each participant voluntarily gave written consent and all procedures were done in accordance with the declaration of Helsinki. This study was approved by the Research Ethics Board of the University of Waterloo.

2.2 Protocol Summary

Participants were asked to stand with equal weight on both feet in standard stance, standard Romberg stance, as well as tandem stance; participants stood with their arms crossed during all trials except for the haptic trials, where the dominant arm was outstretched to place their index fingertip lightly on a solid surface with the non-dominant arm crossed over their chest. The standard stance (feet approximately shoulder width apart) represented a comparatively easy stance, the standard Romberg stance (feet together) represented a low challenge stance, and the tandem stance (heel toe) represented higher challenge stance (Maki & McIlroy, 1995), although all participants were able to remain in a stable upright position through all stance conditions.

Participants performed seven different task conditions. In all conditions participants were instructed to stand as still as possible with arms cross in front of the chest. The seven conditions involved different foot position/base of support (BOS) and sensory information. Alterations in BOS were used to change the underlying control of balance increasing the demand on reactive control. The tandem task condition was the most challenging and was used as the primary condition on which sensory tasks were compared.

- Standard eyes closed: Stance in a standardized stance position (Maki & McIlroy, 1995); eyes closed (no vision)
- Narrows eyes closed: narrow stance (Romberg stance) with feet together but not touching,
 eyes closed (No vision)
- Tandem eyes open: tandem stance with preferred foot forward heel to touch but not touching,
 eyes open (full vision)
- 4) Tandem eyes closed: tandem stance and eyes closed (no vision)
- 5) Tandem eyes closed with haptic touch: tandem stance, eyes closed and index finger of dominant arm making light contact on stable surface located at waist height (Ishigaki et al., 2016), the non-dominant arm remained crossed across the chest
- 6) Tandem eyes open with vision occluded: tandem stance, eyes are open but a large dome is placed on top of the participants head, occluding visual field (no visual reference to body sway)
- 7) tandem eyes open with restricted visual field: tandem stance, eyes are open but the participant is wearing goggles occluding the peripheral vision of the participant, leaving approximately 45 degrees of visual angle for the left and right eye

Each condition was repeated 3 times and stance was held for at least 30 seconds; conditions as well as trials were randomized. Prior to data collection, participants practiced each stance with one foot on a single force plate. This position was monitored to ensure it remained consistent for each trial. Trials in which subjects lost their balance (e.g. took a step) were repeated and stepping trials were not included in analysis of data. Participants experienced a stepping response for a total of 24 trials (across all subjects) which represented 9.5% of all trials. Note that the occurrence of imbalance leading to stepping occurred more typically in the most challenging task conditions (altered vision during tandem stance); these trials were excluded from analysis.

2.3 Measures

2.3.1 Force Plate

Postural sway was recorded using two force plates (AMTI OR6-5) that were positioned under each foot without touching (approximately 1mm apart).

2.3.2 Electroencephalography

Participants were outfitted with a 32 channel EEG (Compumedics Neuroscan, Charlotte NC) cap with references on the bilateral mastoids; electrode placement followed the international 10-20 system and channel impedance was reduced to below 5 kOhms with a filter of 1000Hz. Data was stored offline for analysis.

2.4 Data Analysis

2.4.1 Force Plate

A custom-made program (LabVIEW, National Instruments, TX, USA) was used to collect and determine RMS as well as velocity of sway for each condition. Data was amplified by a gain of 1000 and underwent a low pass, second order Butterworth filter at 10Hz (built-in AMTI MSA-6 MiniAmp amplifier); data was sampled at a rate of 1000Hz and stored for analysis.

Alpha level was set at p=0.05 for significance. Within subject variability was determined by one-way ANOVA for sway velocity and RMS in the mediolateral and anteroposterior directions. One ANOVA compared tasks manipulating stance challenge, another compared tasks involving haptic sensory information, and the final ANOVA compared tasks involving visual information manipulation, for a total of 12 ANOVAs total. Each planned ANOVA underwent a Kruskal Wallis test to determine normality, and each dataset tested reached significance for normality (p<0.05). Post ANOVA, comparisons that reached significance underwent Tukey post-hoc testing. All statistical calculations were performed using SPSS (IBM SPSS Statistics for Windows, Version 22.0).

2.4.2 Electroencephalography

pass filtered (linear phase FIR filter, 66000 order) at 1-50 Hz defined as the edge of the passband. Data was epoched around the beginning of each trial to 30 seconds post trial initiation, then visually inspected. EOG channels (HEOL, HEOR, VEOL, VEOU) were removed and condition trials appended into one continuous trial before the data underwent Independent Component Analysis to remove noise components caused by eye blinks, eye movement, EMG and ECG contamination, and any movement artifact characterized by high voltage shift.

Data from all subjects underwent spectral analysis to determine what electrodes collected the majority of frequency shift and at what specific frequencies. 100% of the data was sampled at 1 to 50Hz and plotted at 2, 6, 10, 20, and 40Hz to represent the full spectrum of possible frequencies. The data in appendix 1.0. was developed for ease of comparison, and based on this figure the electrode sites Fz, Cz, Pz, and Oz were chosen for grand averaging and statistical data. This decision was based on visual inspection of spectral density plots, looking for electrode sites that best represent centrally located frequency activity. Data then underwent grand average analysis for each condition resulting in figures 2.0-16.0 in order to compare stance, haptic sensation, and vision inclusion. Grand average values were topographically plotted at 2Hz (delta band), 6Hz (theta band), 10Hz (alpha Band), 20Hz (beta band), and 40Hz (gamma band). Spectral values were determined using a window length of 1000msec, fft length of 1000msec, and an overlap of 10% (Pfurtscheller et al., 1999).

Spectral frequency power underwent a log10 transformation to calculate absolute value of frequency power, resulting in the creation of a unitless "frequency power ratio". Alpha level was set at p=0.05 for significance. Within subject variability was determined using three using Two-Way repeated measures ANOVAs with factors being task condition and frequency. The number of task conditions varied depending on which hypotheses was being tested (e.g. which tasks were being compared). A

separate ANOVA was run at each electrode site (Fz, Cz, Pz, Oz). For hypothesis 1 the One Way ANOVA compared tasks manipulating stance challenge (standard stance eyes open, narrow stance eyes open, tandem stance eyes open). For hypotheses 2, tasks involving haptic sensory information were compared (tandem stance eyes closed, tandem stance eyes closed with haptic touch). For hypothesis 3, tasks involving visual information manipulation were compared (tandem stance eyes closed, tandem stance eyes closed with restricted visual field, tandem stance with vision occluded, tandem stance with eyes open), for a total of 12 ANOVAs total. The main interest of this study was to determine if there was a main effect for task on frequency power ratio at each electrode site.

Each planned ANOVA underwent a Shapiro Wilk test to determine normality; 3 planned ANOVAs did pass the standard for normality while 9 failed to reach significance. Three of the planned ANOVAs that did not pass the Shapiro Wilk tests underwent a Kruskal Wallis test as well as the two way-ANOVA to determine if the abnormal distribution of data would affect the validity of the two-way ANOVA; the Kruskal Wallis tests were the same as the two-way ANOVAs. Additionally, upon further investigation, literature has determined that normality is not a critical factor when running an ANOVA on more than 30 datapoints (Cuevas et al, 2004) and in this thesis the ANOVA with the least amount of datapoints still contained 120, therefore all data normal or abnormal underwent a two-way ANOVA without standardization. Post ANOVA, comparisons that reached significance underwent Tukey post-hoc testing. All statistical calculations were performed using SPSS (IBM SPSS Statistics for Windows, Version 22.0). It is important to note that due to COVID-19 restrictions, the author did not collect the data used in this study. Data was part of a dataset previously collected within the NiMBaL lab and the author's work on this thesis was directed to the development of rationale, hypotheses and data analysis and interpretation.

Chapter 3- Results

3.1 Task Related Differences in Centre of Pressure

Across all tasks, a very clear pattern in postural stability was revealed. Lowest RMS and centre of pressure velocity in the anteroposterior and mediolateral directions occurred during the standard stance eyes closed condition. Tandem stance with eyes closed produced the highest RMS and velocity values in both directions, and upon inclusion of haptic touch RMS and velocity decreased. Trials in tandem stance with eyes open vision occluded did decrease RMS and velocity in comparison to tandem stance eyes closed trials, but as vision became increasingly available with the introduction of foveal vision in the tandem eyes open restricted vision task RMS and velocity decreased.

3.1.1 Stance Width Comparison

For RMS in the anteroposterior direction, there was a significant main effect of task on RMS (mm) (F(2,36)=35.2, p=0.01). Planned comparisons determined that mean RMS during standard eyes closed stance (mean=4.4mm) was significantly lower than mean RMS during narrow eyes closed stance (mean=6.6mm, p=0.014) and tandem eyes closed stance (mean=10.3mm, p=0.001). It was also determined that mean RMS during narrow stance (mean=6.6mm) with eyes closed was significantly lower than mean RMS during tandem stance with eyes closed (mean=10.3mm, p=0.001) (Figure 1.0).

RMS means followed a similar pattern in the mediolateral direction. There was a significant main effect of task on RMS (mm) (F(2,36)=25.882, p=0.001). Mean RMS during standard eyes closed stance (mean=1.5mm) was significantly lower than mean RMS during narrow eyes closed stance (mean=5.7mm, p=0.0001) and tandem eyes closed stance (mean=8.4mm, p=0.0001). Mean RMS during narrow eyes closed stance (mean=5.7mm) was also significantly lower than mean RMS during tandem eyes closed stance (mean=8.4mm, p=0.025) (Figure 2.0).

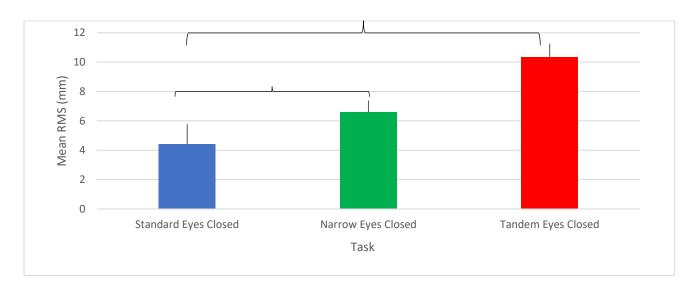


Figure 1.0: Average anteroposterior (AP) centre of pressure displacement measured as RMS across task stance width comparison. Solid bars denote in order: Standard stance eyes closed, narrow stance eyes open, tandem stance eyes closed. Error bars represent standard deviation and parenthesis represent statistical significance (p<0.05).

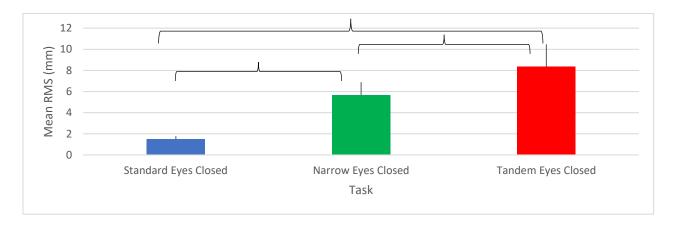


Figure 2.0: Average mediolateral (ML) centre of pressure displacement measured as RMS across task stance width comparison. Solid bars denote in order: Standard stance eyes closed, narrow stance eyes open, tandem stance eyes closed. Error bars represent standard deviation and parenthesis represent statistical significance (p<0.05).

Velocity of centre of pressure movement (mm/s) in the anteroposterior direction was significantly different depending on stance (F(2,36)=68.524, p=0.005). Mean velocity during narrow eyes closed stance (mean=11.1mm/s) was significantly lower than mean velocity during tandem eyes closed stance (mean=36.3mm/s, p=0.0001). Mean velocity during standard eyes closed stance (mean=3.8mm/s) was significantly lower than mean velocity during tandem eyes closed stance (mean=36.3mm/s, p=0.0001). However mean velocity during standard eyes closed stance (mean=3.8mm/s) was not significantly different than mean velocity during narrow eyes closed stance (mean=11.1mm/s, p=0.052) (Figure 3.0).

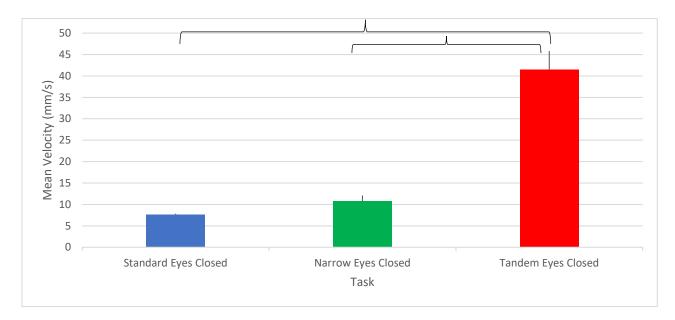


Figure 3.0: Average anteroposterior (AP) centre of pressure velocity across task stance width comparison. Solid bars denote in order: Standard stance eyes closed, narrow stance eyes open, tandem stance eyes closed. Error bars represent standard deviation and parenthesis represent statistical significance (p<0.05).

Finally, velocity of centre of pressure movement in the mediolateral direction also indicated a main effect for task (F(2,36)=184.277, p=0.02) in a similar pattern to velocity in the anteroposterior direction. Mean velocity during narrow eyes closed stance (mean=10.8mm/s) was significantly lower than mean velocity during tandem eyes closed stance (mean=41.5mm/s, p=0.0001). Additionally, mean

velocity during standard eyes closed stance (mean=7.6mm/s) was significantly lower than mean velocity during tandem eyes closed stance (mean=41.5mm/s, p=0.0001). However, there was no significant difference between mean velocity during standard eyes closed stance (mean=7.6mm/s) and narrow eyes closed stance (mean=10.8mm/s, p=0.07) (**Figure 4.0**).

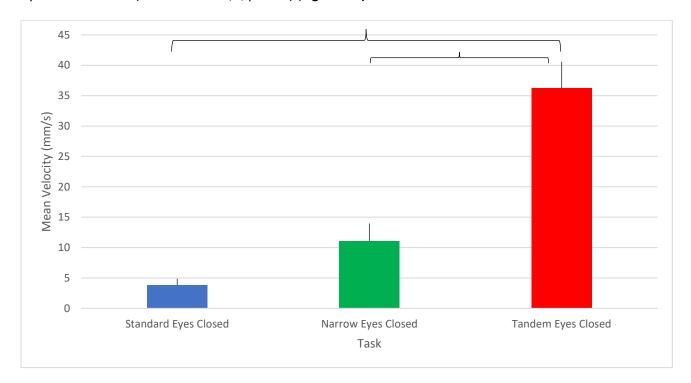


Figure 4.0: Average mediolateral (ML) centre of pressure velocity across task stance width comparison. Solid bars denote in order: Standard stance eyes closed, narrow stance eyes open, tandem stance eyes closed. Error bars represent standard deviation and parenthesis represent statistical significance (p<0.05).

3.1.2 Haptic Comparison

The inclusion of haptic touch during tandem stance with eyes closed significantly lowered RMS (mm) in the anteroposterior direction (F(2,24)=21.987, p=0.0001). Mean RMS during tandem stance with eyes closed was 10.3mm, while mean RMS during standard stance with the inclusion of haptic touch was 6.9mm (p=0.0001)(**Figure 5.0**). However, haptic touch did not statistically significantly lower the mean RMS in the mediolateral direction, where the mean RMS for tandem stance with eyes closed

was 8.4mm and mean RMS for tandem stance with eyes closed and the inclusion of haptic touch was 6.6mm (p=0.240) (**Figure 6.0**)

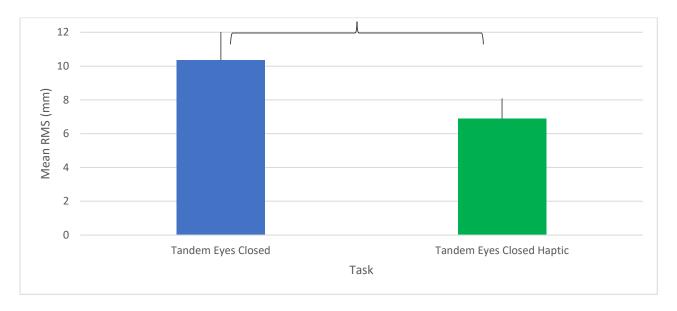


Figure 5.0: Average anteroposterior (AP) centre of pressure displacement measured as RMS across haptic touch task comparison. Solid bars denote in order: tandem stance eyes closed, tandem stance eyes closed with haptic touch. Error bars represent standard deviation and parenthesis represent statistical significance (p<0.05).

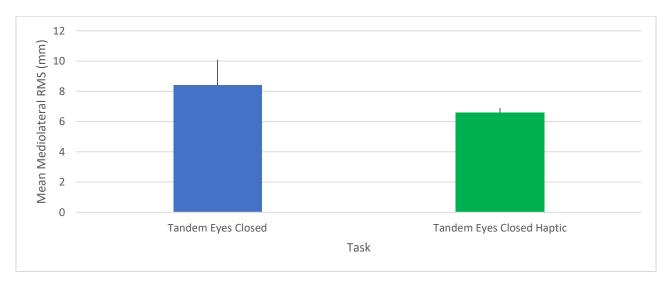


Figure 6.0: Average mediolateral (ML) centre of pressure displacement measured as RMS across haptic touch task comparison. Solid bars denote in order: tandem stance eyes closed, tandem stance eyes closed with haptic touch. Error bars represent standard deviation and parenthesis represent statistical significance (p>0.05).

Velocity of centre of pressure in the anteroposterior direction was also significantly affected by the inclusion of haptic touch during tandem stance with eyes closed (F(2,24)=17.327, p=0.01). Mean velocity during tandem stance with eyes closed was 41.5mm/s, and the inclusion of haptic touch reduced that velocity to 28.6mm/s (p=0.0001)(**Figure 7.0**). The same pattern was observed in the mediolateral direction (F(2,24)=7.202, p=0.002). The inclusion of haptic touch reduced velocity to 25.0 mm/s as compared to 36.3 mm/s during tandem stance with eyes closed (p=0.014)(**Figure 8.0**).

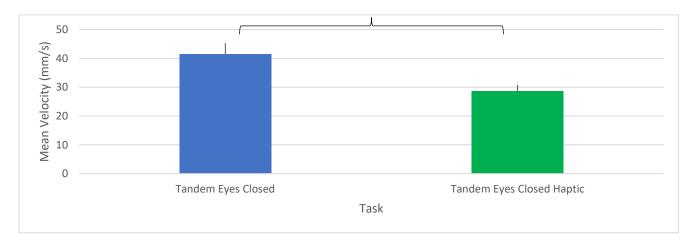


Figure 7.0: Average anteroposterior (AP) centre of pressure velocity across haptic touch task comparison. Solid bars denote in order: tandem stance eyes closed, tandem stance eyes closed with haptic touch. Error bars represent standard deviation and parenthesis represent statistical significance (p<0.05).

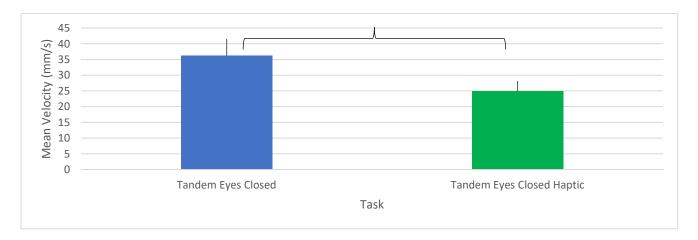


Figure 8.0: Average mediolateral (ML) centre of pressure velocity across haptic touch task comparison. Solid bars denote in order: tandem stance eyes closed, tandem stance eyes closed with haptic touch. Error bars represent standard deviation and parenthesis represent statistical significance (p<0.05).

3.1.3 Vision Availability Comparison

A main effect of task was determined when examining RMS (mm) in the anteroposterior direction (F(2,48)=19.223, p=0.003). Planned comparisons determined that mean RMS during tandem stance with eyes open (mean=5.8mm) was significantly lower than mean RMS during tandem stance with restricted vision (mean=7.9mm,p=0.018), tandem stance with eyes open but vision occluded (mean=9.6mm, p=0.0001), and tandem stance with eyes closed (mean=10.3mm, p=0.0001). Mean RMS for tandem stance with restricted vision (mean=7.9mm) was significantly lower than the mean RMS for tandem stance with eyes closed (mean=10.3mm, p=0.002) and mean RMS for tandem stance with eyes open but vision occluded (mean=9.6mm, p=0.044). However, there was no statistically significant difference between mean RMS for tandem stance with eyes closed (mean=10.3mm) and mean RMS for tandem stance with eyes open but vision occluded (mean=9.6mm, p=0.704)(Figure 9.0). There was no significant difference in RMS in the mediolateral direction between tasks (F(2,48)=1.942, p=0.35)(Figure 10.0).

A main effect of task was determined when examining velocity (mm/s) in the anteroposterior direction (F(2,48)=26.851, p=0.0001). Post-hoc comparisons determined that mean velocity during tandem stance with eyes open (mean=20.4mm/s) was significantly lower than mean velocity during tandem stance with restricted vision (mean=27.9mm/s,p=0.029), tandem stance with eyes open but vision occluded (mean=35.7mm/s, p=0.0001), and tandem stance with eyes closed (mean=41.5mm/s, p=0.0001). Mean velocity for tandem stance with restricted vision (mean=27.9mm/s) was significantly lower than the mean velocity for tandem stance with eyes closed (mean=41.5mm/s, p=0.001) and mean velocity for tandem stance with eyes open but vision occluded (mean=35.7mm/s, p=0.019). However, there was no statistically significant difference between mean velocity for tandem stance with eyes closed (mean=41.5mm/s) and mean velocity for tandem stance with eyes open but vision occluded (mean=35.7mm/s, p=0.152)(Figure 11.0).

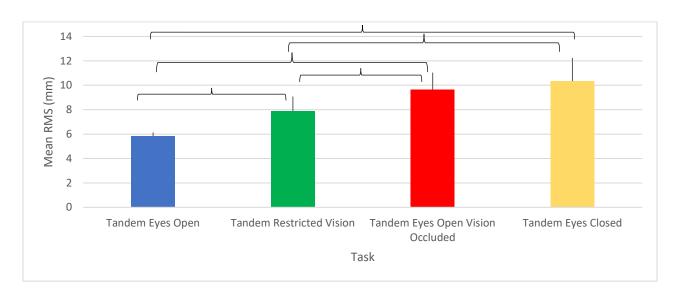


Figure 9.0: Average anteroposterior (AP) centre of pressure displacement measured as RMS across visual availability task comparison. Solid bars denote in order: Tandem stance eyes open, tandem stance restricted vision, tandem stance eyes open vision occluded, tandem stance eyes closed. Error bars represent standard deviation and parenthesis represent statistical significance (p<0.05).

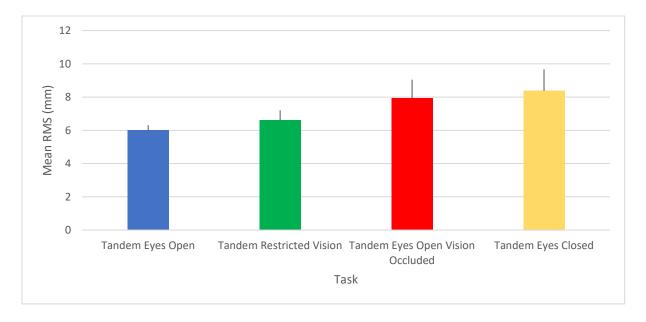


Figure 10.0: Average mediolateral (ML) centre of pressure displacement measured as RMS across visual availability task comparison. Solid bars denote in order: Tandem stance eyes open, tandem stance restricted vision, tandem stance eyes open vision occluded, tandem stance eyes closed. Error bars represent standard deviation and parenthesis represent statistical significance (p<0.05).

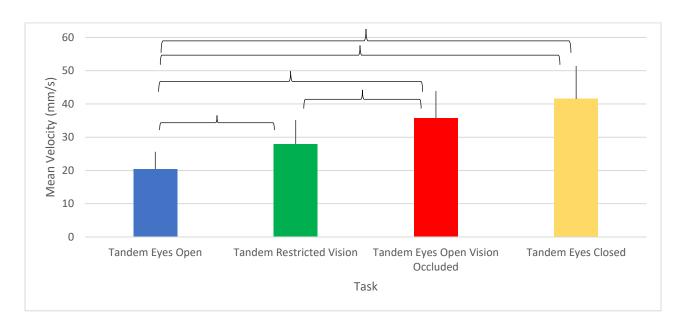


Figure 11.0: Average anteroposterior (AP) centre of pressure velocity across visual availability task comparison.

Solid bars denote in order: Tandem stance eyes open, tandem stance restricted vision, tandem stance eyes open vision occluded, tandem stance eyes closed. Error bars represent standard deviation and parenthesis represent statistical significance (p<0.05).

Finally, there was a main effect observed for task observed when comparing velocity in the mediolateral direction (F(2,48)=9.393, p=0.02). Velocity of centre of pressure during static stance with eyes open (mean=19.4mm/s) was significantly lower than the velocity of centre of pressure during static stance with eyes closed (mean=36.3mm/s, p=0.0001) and velocity of centre of pressure during static stance with eyes open but vision occluded (mean=32.5mm/s, p=0.003). However, velocity of centre of pressure during static stance with restricted vision (mean=25.4mm/s) was not significantly different than velocity during static stance with eyes open (mean=19.4mm/s, p=0.548). Mean centre of pressure velocity during tandem stance with restricted vision (mean=25.4mm/s) was not significantly different than mean velocity during tandem stance with eyes open but vision occluded (mean=32.5mm/s, p=0.187), but was significantly lower than the mean velocity during tandem stance with eyes closed

(mean=36.3mm/s, p=0.015). Mean velocity of centre of pressure during tandem stance with vision occluded (mean=32.5mm/s) was not significantly different than mean velocity during tandem stance with eyes closed (mean=36.3mm/s, p=1.000)(**Figure 12.0**).

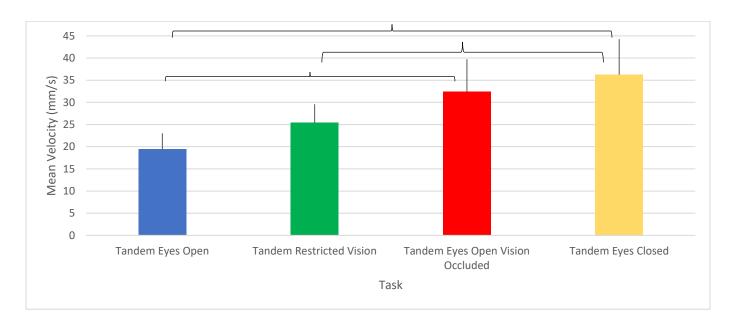


Figure 12.0: Average anteroposterior (AP) centre of pressure velocity across visual availability task comparison.

Solid bars denote in order: Tandem stance eyes open, tandem stance restricted vision, tandem stance eyes open vision occluded, tandem stance eyes closed. Error bars represent standard deviation and parenthesis represent statistical significance (p<0.05).

3.2 Task Related Differences in Cortical Activity

3.2.1 Topography

3.2.1.1 Stance Width Comparison

For electrode Fz, there was a significant main effect of frequency on spectral power density (F(5,60)= 1.775, p=0.006), an expected result as previous literature indicates at any one point in time there is likely to be significant differences in power spectral density between frequencies regardless of task (Hülsdüncker et al., 2015). However, there was no significant main effect for task(F(3,36)=0.369,

p=0.82), or interaction effect between task and frequency (F(15,65)=0.56, p=0.36), which does not support the hypothesis which states there would be a significant main effect for task. However, the pattern of means for each frequency band around the Fz electrode follow a pattern; it is likely that confounding factors and an under powered sample size resulted in insignificance, which will be discussed in further sections. Frequency power ratio patterns around Cz, Pz, and Oz did not approach significance (Figure 13.0).

Upon visual examination of the narrow stance condition, standard stance condition, and tandem stance condition it is apparent that the pattern of excitation within the delta frequency range is similar. There is a higher power of delta frequency anterior of Fz, tapering off posteriorly, which is then limited to anterior of Pz. Excitation is symmetrical with no laterality. The highest power in delta band is seen anterior of Fz in the standard stance condition which likely indicates lower level excitability (**Figure** 13.0).

Between the narrow stance, standard stance, and tandem stance conditions there is a similar pattern of activity; theta frequency is largely central. In all conditions the highest power of theta activity is around FCz. Frequency power is more posterior that delta frequency, it extends past Pz and begins to approach Oz. The highest amount of theta activity is seen around FCz in the tandem condition, and the lowest amount around FCz in the standard condition. It appears that cortical activity is rising in frequency with increased stance difficulty, which was expected. There is no laterality seen in any conditions (Figure 13.0).

There is the same pattern of alpha frequency activity across all conditions; it is largely centralized with a small degree of laterality to the left. Alpha frequency activity extends more posterior, past Pz and approaching Oz. The largest power of alpha frequency is around Cz and CPz. Both narrow and tandem stance conditions have high power of alpha frequency around Cz, CPz, and Pz, but the area

of power in the tandem stance condition extends increasingly anterior to encompass FCz as well (**Figure 13.0**).

The excitation in the beta frequency band is largely centralized with a low degree of laterality to the left in standard and tandem stance conditions. The area of beta frequency power is smaller compared to alpha frequency and is largely centralized to FCz to Pz, although tandem stance does extend anteriorly as well. The largest power of activity is around Cz and CPz and tandem stance very obviously has high beta frequency activity around FCz, Cz, and CPz. Frequency activity extends posteriorly to include O electrodes, but activity is relatively low in power in these areas (Figure 13.0).

There is a pattern difference in gamma frequency activity across conditions, specifically in the tandem stance condition. There is an increase in high frequency gamma activity in frontal regions. There is a small power of gamma activity centrally located in narrow and standard stance, but theta activity largely does not extend past CPz (Figure 13.0).

3.2.1.2 Haptic Comparison

There is a similar pattern of activity frontally with higher delta frequency contribution in the no haptic condition. Delta frequency activity largely does not extend past Pz with little Oz contribution.

There is a symmetrical laterality in the no haptic condition with excitability extending laterally (**Figure 14.0**).

The pattern of theta frequency contribution is centrally located in both conditions with higher theta frequency power around Fz and FCz. There is a slightly higher power of activity in the non-haptic condition. Additionally, there is a degree of laterality in the haptic condition; frequency power moves left as it moves posteriorly. In both conditions, activity extends past Pz and approaches Oz (**Figure 14.0**).

There is a centralized power of alpha frequency with laterality and, similar to other bands, the same observation that the overall power appeared lower in haptic versus no haptic condition although

this difference does not appears as great as theta or betas bands. The highest power of alpha frequency contribution is around FCz, Cz, and CPz in both conditions (**Figure 14.0**).

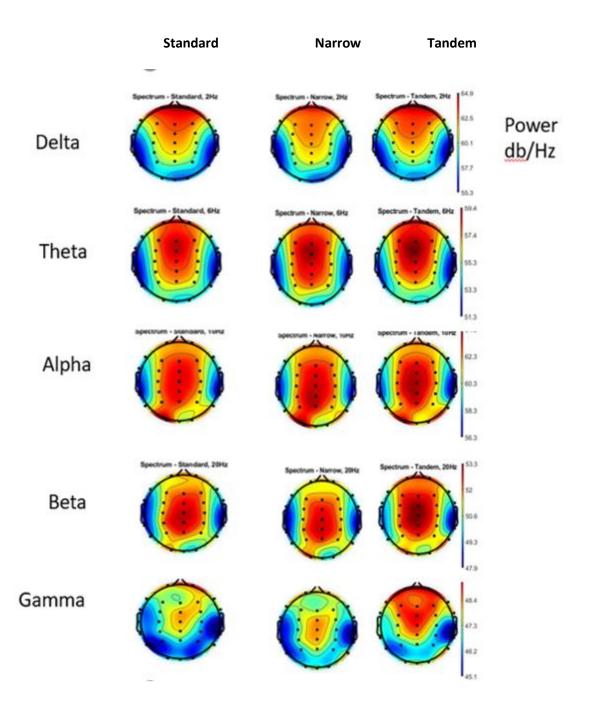


Figure 13.0: Grand average topographic representation of delta, theta, alpha, and beta frequency power (db/Hz) for stance width comparison.

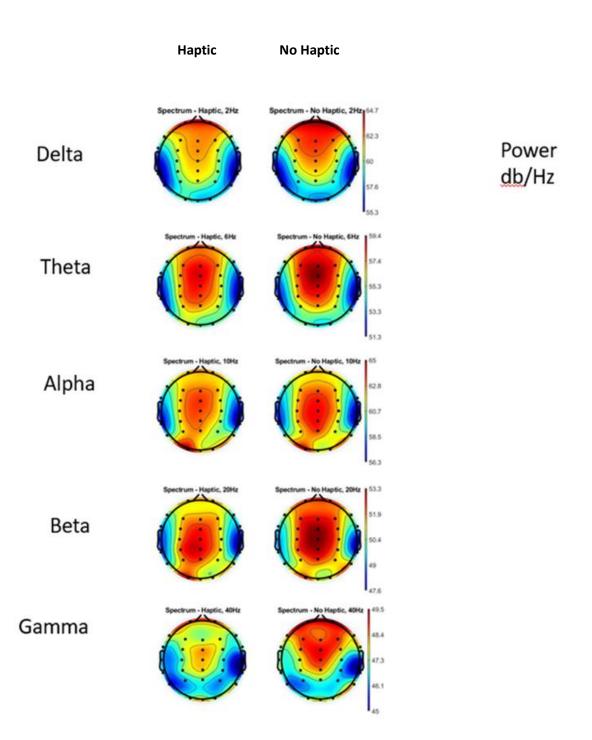


Figure 14.0: Grand average topographic representation of delta, theta, alpha, and beta frequency power (db/Hz) for haptic touch comparison.

Similar to the alpha frequency figure, there is a band of beta activity stretching laterally, frontally, and posteriorly. Laterality in haptic condition is more apparent, with highest power of activity located lateral of CPz, and activity is beginning to encompass O1, Oz, and O2. The no haptic condition exhibits high delta activity around FCz, Cz, and CPZ, as well as increased excitation frontally extending to F1 and F2 (Figure 14.0).

Gamma frequency contribution is largely frontal, with a small power of gamma excitation centrally located around FCz, Cz, and CPz in the haptic condition. Despite this, activity covers a large part of the frontally located electrodes. Activity largely does not extend past CPz in both conditions (**Figure 14.0**).

3.2.1.3 Vision Availability Comparison

The low frequency delta band is frontal; although it does extend slightly posteriorly, it is limited to Pz in the eyes closed condition; activity starts to include Oz in the eyes open, eyes closed vision occluded, and restricted visual field conditions. The eyes open vision occluded and restricted visual field figures are very similar, with a slight extension of high power areas posteriorly in the restricted visual field condition (Figure 15.0).

There is a central power of theta activity with the highest power being around FCz. The restricted visual field and eyes closed conditions have areas of high theta activity, eyes open vision occluded has very small power around FCz but does not extend posteriorly as much as the other conditions. All conditions have theta frequency in occipital areas, but the eyes open condition has increased power of theta activity around O electrodes compared to the other conditions (**Figure 15.0**).

The alpha frequency contribution is very central with a small amount of laterality to the left.

The large area of alpha activity appears as a band extending posteriorly. The restricted visual field and eyes closed condition have high degree of alpha power, but the eyes closed condition has frequency power in a largely central area (**Figure 15.0**).

Beta activity is centralized, mostly around FCz, Cz, and CPz, but extending anteriorly and posteriorly as well. All conditions have beta activity extending over occipital regions. The highest beta frequency contribution is seen in the eyes closed condition, with the least being seen in the eyes open vision occluded condition. The eyes closed condition includes high power of beta activity extending frontally (Figure 15.0).

The gamma frequency pattern of activity varies between conditions. The eyes closed condition is largely frontal with minimal posterior extension and shows the highest degree of high frequency power. Gamma contribution does not extend past Pz in any condition. The eyes open condition shows largely central activity, with the most posterior extension. The eyes open vision occluded condition shows comparatively little gamma frequency power compared to every other condition, and what gamma activity there is mostly centralized with some frontal extension. The restricted visual field condition shows some frontal and posterior inclusion, but most gamma activity is localized to around Cz (Figure 15.0).

3.2.2 Peak Amplitude

3.2.2.1 Stance Width Comparison

For electrode Fz, there was a significant main effect of frequency on spectral power density (F(5,60)=21.775, p=0.03), however, there was no significant main effect for task(F(3,36)=0.369, p=0.91) or interaction effect between task and frequency (F(15,65)=0.56, p=0.93), which does not support the hypothesis which states there would be a significant main effect for task. However, the pattern of means for each frequency band around the Fz electrode follow a distinct pattern that approaches significance; it is likely that confounding factors and an under powered sample size resulted in

insignificance, which will be discussed in further sections. Frequency power ratio patterns around Cz, Pz, and Oz did not approach significance (**Figure 16.0**).

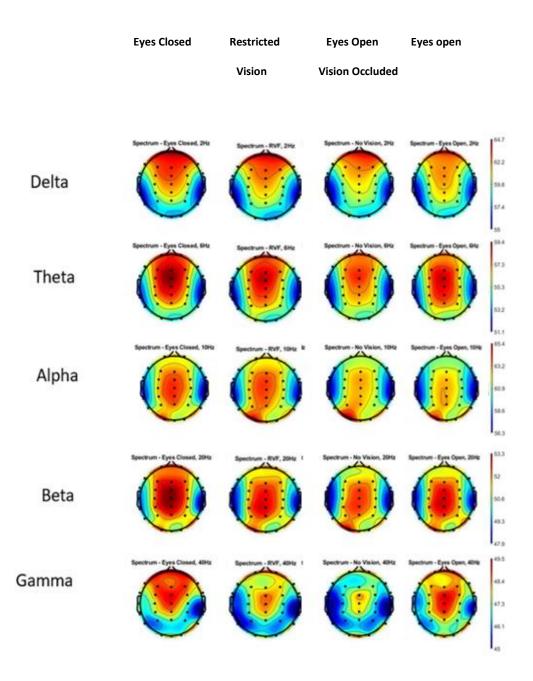


Figure 15.0: Grand average topographic representation of delta, theta, alpha, and beta frequency power (db/Hz) for visual availability comparison.

Power db/Hz

The results of delta frequency power around Fz glean no significant pattern. Mean delta frequency was highest during standard stance (mean=10.742), lower during the narrow stance (mean=10.178), and lowest during tandem stance (mean=10.120) (**Figure 16.0**).

Upon examining the theta frequency band comparison around the Fz electrode, the lowest frequency power ratio mean occurs during the narrow eyes closed stance (mean=4.460), with a higher frequency power ratio during the standard eyes closed stance (mean=4.675) and the highest mean frequency power ratio during the tandem eyes closed stance (mean=5.503)(Figure 16.0).

Upon examining the alpha frequency band comparison around the Fz electrode, it is apparent that the lowest frequency power ratio mean occurs during the narrow eyes closed stance (mean=7.113), with a higher frequency power ratio during the standard eyes closed stance (mean=7.617) and the highest mean frequency power ratio during the tandem eyes closed stance (mean=9.109)(Figure 16.0). Examination of beta frequency power ratio around Fz reveal similar patterns between tasks. Lowest mean occurred during narrow stance (mean=0.815), then standard stance (mean=0.849), and highest occurred during tandem stance (mean=1.120) (Figure 16.0).

Gamma frequency excitation also follows the same pattern as previously examined frequencies. Narrow stance provided the lowest gamma frequency mean (mean=0.361), followed by standard stance frequency power ratio (mean=0.405), with highest gamma frequency power ratio occurring during tandem stance (mean=0.582) (**Figure 16.0**).

3.2.2.2 Haptic Comparison

For electrode Pz, there was a significant main effect of frequency on spectral power density (F(5,60)=17.761, p=0.003.). However, there was no significant main effect for task(F(2,24)=11.021, p=0.53), or interaction effect between task and frequency (F(15,110)=0.060, p=0.83), which does not support the hypothesis which states there would be a significant main effect for task. Similar to the

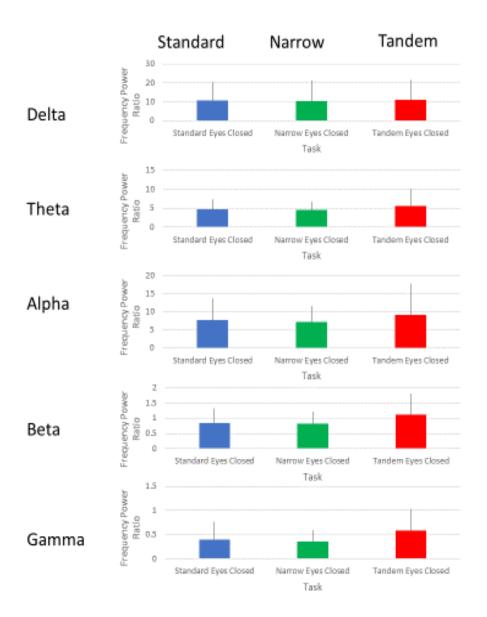


Figure 16.0: Peak amplitude representation of delta, theta, alpha, and beta frequency power ratio for stance width comparison around electrode Fz. Solid bars denote in order: Standard stance eyes closed, narrow stance eyes open, tandem stance eyes closed (p>0.05).

Comparison of frequency power ratio across stance manipulation, a main effect for task did approach significance at electrode Pz and shows clear patterns of attenuation (**Figure 17.0**). Through examination of the delta frequency band, delta frequency mean during tandem stance with haptic inclusion (mean=5.804) is modestly larger than delta frequency band frequency power ratio during tandem stance without haptic inclusion (mean=5.468)(**Figure 17.0**).

The pattern of theta frequency power ratio during tandem and eyes closed stance confirms results observed by previous authors. Mean theta frequency power ratio during tandem stance (mean=3.681) was less than the mean observed during tandem stance with haptic inclusion (mean=4.189)(Figure 17.0).

Alpha mean during tandem eyes closed stance (mean=9.786) was larger than the alpha mean during tandem eyes closed with haptic touch (mean=9.237). Mean frequency power ratio in the beta and gamma frequency bands all followed the same pattern; mean frequency power ratio during tandem eyes closed stance was larger than ratio during tandem eyes closed stance with haptic inclusion.

(Tandem eyes closed stance; beta mean=1.191, gamma mean=0.548, tandem eyes closed with haptic inclusion; beta mean= 1.045, gamma mean=0.353)(Figure 17.0).

3.2.2.3 Vision Availability Comparison

For electrode Oz, there was a significant main effect of frequency on spectral power density (F(5,60)=24.240, p=0.001). However, there was no significant main effect for task(F(4,48)=0.319, p=1.00), or interaction effect between task and frequency (F(20, 225)=0.286, p=0.80), which does not support the hypothesis which states there would be a significant main effect for task. However, similar to the comparison of frequency power ratio across stance and haptic manipulation, a main effect for task did approach significance at electrode Oz and shows clear patterns of attenuation (**Figure 18.0**).

The results of the current study show a pattern of attenuation in the delta frequency band that have not been examined by previous studies. It is apparent that the highest mean frequency power ratio in the delta band occurred during tandem eyes open vision occluded stanc (mean=3.287), slightly lower is the mean revealed during tandem restricted vision stance (mean=3.245), second lowest mean delta frequency power ratio occurred during tandem eyes open stance (mean=3.189), and the lowest mean delta frequency power ratio occurring during tandem eyes closed stance (mean=3.122)(Figure 18.0).

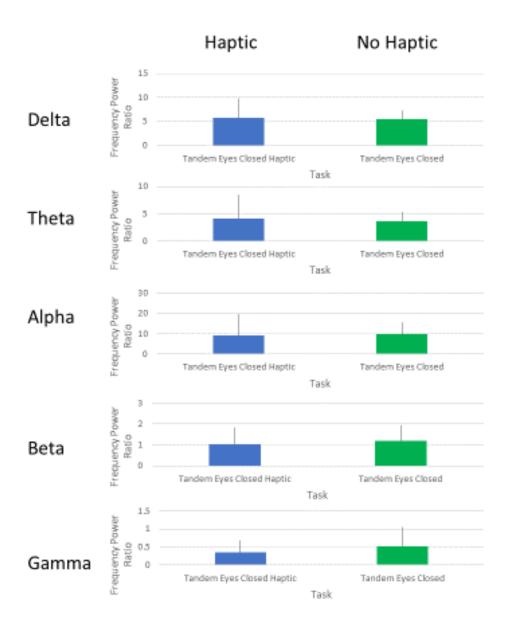


Figure 17.0: Peak amplitude representation of delta, theta, alpha, and beta frequency power ratio for haptic comparison around electrode Pz. Solid bars denote in order: tandem stance eyes closed with haptic touch, tandem stance eyes closed (p>0.05).

Mean power frequency ratio across tasks in the theta frequency bands reveals more expected findings. The highest mean frequency power ratio in the theta frequency band occurred during tandem eyes open stance (mean=3.049), with the means for tandem eyes open vision occluded (mean=2.657) and tandem restricted vision (mean=2.547) following behind. The lowest mean theta frequency power ratio occurred during tandem eyes closed stance (mean=2.218)(Figure 18.0).

The pattern of mean power frequency of the alpha band indicates the expected result; as visual information enters the nervous system, alpha frequency activity increases in the occipital regions of the cortex. Lowest alpha frequency activity was observed when no visual information was available, regardless of whether the eyes were open or not (tandem eyes closed mean=5.648, tandem eyes open vision occluded mean=5.670), indicating a heightened state of arousal around Oz even though vision is technically unavailable. When visual information was available, mean alpha frequency power ratio increased (tandem restricted vision mean= 8.012, tandem eyes open mean=6.644) (**Figure 18.0**).

Mean frequency power ratio patterns of the beta frequency band yield expected as well as surprising results. The largest frequency power ratio mean occurred during tandem eyes open stance (mean=0.951), which is contrary to expectation. However, the second largest beta frequency power mean occurred during tandem eyes closed stance (mean=0.859), which expected as the posterior areas of the cortex are reaching a state of decreased excitation state due to the lack of visual input. Lowest mean occurred during tandem restricted vision (mean=0.845) and tandem eyes open vision occluded (mean=0.850), indicating a heightened state of the regions around Oz (**Figure 18.0**).

Mean frequency power ratio of the gamma band shows very little attenuation due to task challenge (tandem eyes closed mean=0.591, tandem restricted vision mean=0.484, tandem eyes open vision occluded mean=0.515, tandem eyes open mean=0.503) (**Figure 18.0**).

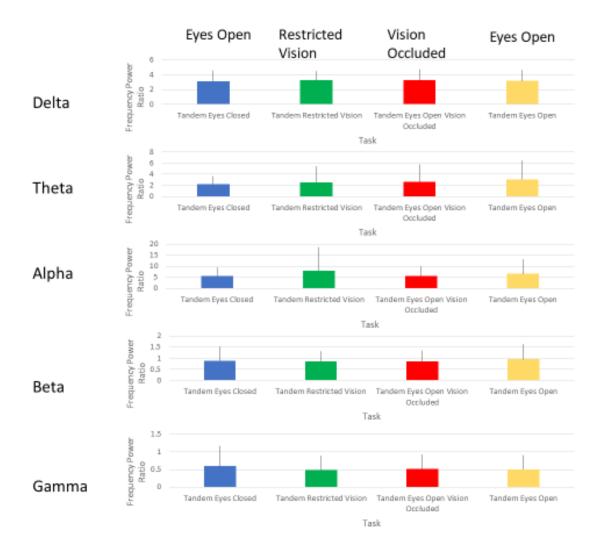


Figure 18.0: Peak amplitude representation of delta, theta, alpha, and beta frequency power ratio for visual availability comparison around electrode Oz. Solid bars denote in order: Tandem stance eyes open, tandem stance restricted vision, tandem stance eyes open vision occluded, tandem stance eyes closed (p>0.05).

Chapter 4- Discussion

4.1 Discussion

The current study set out to determine if manipulation of incoming sensory information and task during standing balance would be associated with changes in cortical activity. It has been proposed that the cortex plays a role in the control of upright balance, even the most automatic control that is characteristic of standing still (Varghese et al., 2015). This study set out to determine if changes in sensory contributions would be characterized by activity linking sensory processing at the level of the cortex. The study did explore the impact of task challenge, as reflected by changes associated with altered base of support. This was conducted to provide an indication of cortical changes related to more difficult balance tasks. This was deemed important to understand changes that may be associated with altered sensory inputs since these sensory manipulations would also impact task challenge. Overall, the manipulation of task challenge did result in significant changes in COP as a measure of task challenge, however, in contrast to the hypotheses there were no statistically significant task-related differences in cortical activity as measured by frequency.

In accordance with previous literature (Pfurtscheller et al., 1996; Stam, 2000; Müller-Putz et al., 2007; Kinsey et al., 2011; Solis-Escalante et al., 2012; Sipp et al., 2013; Seeber et al., 2014), examination of frequency was centred around fluctuations of power within frequency bands as representation of fluctuations of excitation of the cortical area of interest. An increase in theta and delta power implies an increase in excitation while an increase in alpha and beta power implies decreased excitation (Hwang & Huang, 2016; Gebel et al., 2020). Additionally, an increase in gamma power implies an increase in communication between areas of the cortex, therefore also implying increased excitation of the areas in question (Pfurtscheller et al., 1996; Müller-Putz et al., 2007). There appeared to be some modest task related differences in frequency that were characterised by higher peak power in the most challenging balance task but these did not reach statistical significance. With respect to changes in sensory

information, the availability of haptic information was used to determine evidence of unilateral parietal cortical involvement that would have been consistent with the spatial specificity of the sensory input.

Again, there were no statistically significant differences across these task comparisons. The comparison between tasks did result in mean differences that approached significance. The direction of these potential differences was in the direction of the proposed hypothesis of an increase in theta power and decrease in alpha power over the Pz electrode. With respect to changes in visual inputs there was an expectation of varying activity in occipital power of theta and alpha frequency; when vision is available it was expected that theta power would increase and alpha power would decrease in the posterior regions of the cortex to denote increased excitation in accordance with increased visual input. Regardless of data trends, the differences were not statistically significant and therefore the results did not confirm the experimental hypothesis.

The absence of statistically significant differences in EEG frequency responses in contrast to the hypotheses and the significant differences in balance control may be due to several possible reasons.

The first is that the cortex may play no role in the control of sensory processing for balance control and as a result we would not expect changes in frequency associated with the current task manipulations.

This possible explanation is less likely, largely on the evidence of other studies that have revealed a link between sensory contributions and balance control (Horak & Nashner, 1986; Patla et al., 1996; Patla, 1997; Bolton et al., 2009; Hammami et al., 2014). Instead it is possible that the lack of statistically significant differences may arise due to methodological and conceptual problems with the proposed hypotheses. One concern is statistical power. Centrally the evidence of some mean differences, particularly in the haptic task conditions, provides some support for task related changes. The lack of power could arise from several possible sources. The first is the number of participants. Calculating an estimated sample size required for the current effect size (haptic versus no haptic; and vision/no vision) reveals a need for approximately 24 and 32 subjects, respectively. Low signal to noise may have also

been a problem as the study considered the frequency changes to be constant over the 30 second trials consistent with the idea of postural set. While it was anticipated that the changes in state of the CNS would be relatively consistent during specific task challenges, it is possible that the state is far more dynamic and that time varying changes in frequency may be expected as stability challenge varies over time. In this regard event related spectral analysis (ERSP) may be an approach to better explore underlying sensory processing changes in the future. In a related challenge, the time varying influence of the continuously occurring instability and associated evoked potentials may likely underpin the main frontocentral activity that dominates most frequency bands. The challenge is that in most cases changing the sensory state also leads to increased instability and the resulting activation that may be primarily related to this dynamic stability control and unrelated to reorganization of sensory processing. In this regard, the absence of a control (non-standing condition) makes it difficult to determine if the underlying cortical activity in these sensory regions is high even when standing still with standard stance. These topics for consideration are addressed in the sections that follow. In addition, while there were few statistically significant differences, the possible trends in task-differences are also addressed in part to help guide decision for future studies.

4.2 Measure of Balance Control Across Tasks; Continuously Evoked Postural Responses

When examining cortical and centre of pressure behaviour during static stance it is crucial to note that upright postural stability is maintained as a result of repeated postural corrections elicited by muscular contractions as a result of internally produced perturbation (Varghese et al., 2015). This is evident from the time varying changes in centre of pressure that were characterized by changes in RMS amplitude and velocity across task conditions. As expected, both amplitude and velocity revealed increased challenges and stability control as the base of support was narrowed (standard – narrow – tandem) and when sensory information was removed or limited (eyes open – eyes closed – vision restricted). The observations presently made regarding the centre of pressure differences across tasks

are consistent with the many studies in the literature that have compared such task conditions (Winter et al., 1990; Wollacott et al, 1997; Horak et al., 2006). The one task condition which increased sensory contributions, haptic touch, revealed an improvement in centre of pressure sway compared to no haptic touch. This is also consistent with the literature (Bolton et al., 2009) revealing the benefits to control in the presence of sensory information that can improve the detection of instability. As will be noted later, the maintenance of upright stance requires continuous monitoring of sensory information and the transformation of these signals into motor responses in order to prevent a loss of balance. The increase in centre of pressure sway and velocity denotes an increased demand on reactive control as one shifts along the continuum from easier tasks to more difficult tasks. It should be noted that while there is the potential for contribution from feedforward control particularly in easier task conditions as noted by Carpenter and colleagues (2011) the tasks selected in this study were to force reliance on reactive control. It is the reason that the tandem stance condition was the main task used when evaluating the influence of changes in sensory information. Overall, the behavioral data captured from centre of pressure analysis, revealed that the task challenges introduced had the expected impact on the control of stability. This is used to reinforce the important point that removal or addition of sensory information impacts the reactive control of stability and therefore likely demands changes to central nervous system processing of specific sensory signals for the varying task conditions. It was on this assumption that differences in the underlying cortical activity both in terms of frequency amplitude and topography were predicted.

4.3 Frontocentral Activity

Overall, while there were no statistically significant task-related differences, there was a consistent pattern of frontocentral activity that was observed across task conditions in all frequency bands though most evident in theta range. It is proposed that this activity may be associated with the well reported N1 potential, which is evoked frontally and centrally with an amplitude in accordance with

perturbation amplitude, predictability of stimulus, arousal, and stimulus features such as perceived threat (Quant et al., 2004; Quant et al., 2005; Collette et al., 2007; Maki & McIlroy, 2007). While the N1 response has been most commonly observed in response to external perturbations, Varghese et al. (2015) revealed evidence of evoked N1 responses during stationary standing when averaging to the moments of COP displacement. Varghese et al. (2015) proposed that these observations reveal that when standing still there was continuous reactive control with repeated occurrence of N1 responses in proportion to amplitude of instability. Because N1 is comprised of mostly theta, alpha, and delta frequency bands (Quant et al., 2004; Quant et al., 2005; Collette et al., 2007; Maki & McIlroy, 2007) the occurrence of the frontally evoked N1 likely may serve to confound the ability to detect other events in such frequency ranges and may have impacted ability to detect other changes. It is proposed that the large amplitude frontocentral power seen for most frequency bands, and that appears scaled to task challenge, may be associated with these underlying N1 responses. The activity is present across all task conditions, even the simplest task (standard eyes closed condition). The origins of the N1 response and the underlying purpose/role remains unclear. Initially, Dietz et al. (1993) considered the N1 a sensory evoked response since it was scaled to the amplitude and aligned to the timing of perturbation. Staines et al. (2001) proposed the N1 may reflect cortical excitation related to sensory inputs potentially representing activity related to the vestibular cortex. However, several studies have revealed the N1 is associated with stimulus or perturbation predictability (Adkin et al., 2004; Mochizuki et al., 2010) which led to the proposal that the N1 was related to event detection. Marlin et al. (2014) proposed a potential link between the N1 and anterior cingulate activation that may be linking two attentional networks, however they localized the N1 to the supplementary motor area. Ting and colleagues (2017) have proposed a link to motor activation in more recent work. To date there is no consensus regarding the role and the underlying regions that contribute to the N1 response.

4.4 Task Challenge

It was anticipated that increasing task challenge would result in an increase of theta frequency activity and a reduction of alpha frequency activity around the Fz electrode, which would accompany an increase in stance RMS and velocity, reflecting a change in central nervous system state as a result of stance. It was found that although the frequency results were not statistically different, there was an increase in theta frequency activity around Fz while standing in tandem. However, against expectations, the lowest theta frequency activity occurred during narrow stance, which presents a higher task challenge than standard stance. The same pattern occurred when examining alpha frequency activity, which also went against expectations; it was expected that the lowest alpha frequency power around Fz would occur during tandem stance, but the opposite occurred. RMS and centre of pressure velocity behaved as expected, reaching statistical significance. RMS and centre of pressure velocity in the anteroposterior and mediolateral during tandem stance was significantly larger between tandem and narrow and also between narrow and standard stance.

While the overall differences in frequency of activity at the cortex between tasks were non-significant there appeared to some evidence of increases in power particularly in the theta range for the most difficult task conditions. There may have also been differences in gamma band activity with higher power in the more difficult task condition. There are different possible explanations for these potential differences in activation. One possible explanation, as noted previously, is the potential contribution associated with evoked N1 response which would be of larger magnitude during tandem as opposed to standard stance conditions (Varghese et al., 2015). A second possible explanation is that this potential difference in activation arises from state changes, or postural set differences, between the tasks. These possible explanations are discussed in more detail below.

Postural set is defined as the overall physical and cognitive readiness of the body to respond to externally evoked perturbation or internally generated perturbation generated through maintenance of COP control during static stance. It is possible that the increase in potential challenge leads to a state change as opposed to the explanation of increased reactive control that might be associated with reactive N1 responses. Modulation of postural set through manipulation of task challenge is well documented in previous literature (Horak et al., 1989; Schoultz et al., 1972; Wingert et al., 2014). Manipulation of stance to increase task challenge results in increased postural instability due to a decrease in base of support, which therefore increases postural anxiety and CNS reactivity to internally provoked perturbation regardless of amplitude (Horak et al., 1989).

However, in opposition to previous literature, there is also an increase in delta and alpha power frequency ratios during tandem stance; theoretically, alpha and delta frequency power ratio values should decrease frontally as a result of increased excitation due to increased stability and the postural set change as a direct result of task challenge (Hwang & Huang, 2016; Kanokwan et al., 2019).

In fact, it is likely that another aspect of postural set manipulation is resulting in the alpha and delta frequency activity seen in this study. The increased gamma frequency power around Fz during tandem stance is not surprising, as the cortex is likely relying on all aspects of its hierarchy in order to retain postural stability; an increase in instability results in an increase in all areas of the cortex (except the occipital regions in this case, as eyes are closed), which results in an increase in communication between cortices, specifically in the frontal lobe as attentional networks are increasingly excited. However, the decrease in gamma frequency power around Fz during narrow stance compared to standard stance is not an expected result. Logically, next steps in examining the meaning behind alpha and delta cortical frequencies should be examined, as there is a confounding variable in the current study resulting in these unexpected results.

4.5 Haptic Touch

The addition of haptic touch during tandem stance was expected to result in an increase in theta activity and a decrease in alpha activity around Pz. The focus on parietal activity was obviously linked to the possibility of the involved somatosensory regions or posterior parietal regions associated with processing of touch sensation from the finger. One might have predicted lateralized involvement given only the right hand, however the topographic representations did not reveal such a statistically significant lateralisation. It is noteworthy that there may have been a focal increase in beta power lateralized over the parietal cortex but the current analysis was restrict to central sites. Again, there were no statistically significant differences, but there is a potentially higher theta frequency power around Pz occurring during tandem stance with haptic touch inclusion, and a lower alpha frequency power occurring during the same task.

The potential frequency power changes viewed around Pz during the eyes closed tandem stance and eyes closed tandem stance with haptic touch, as well as the potential lateralization of power over electrode P3/4, may reflect increased reliance on the parietal areas of the cortex when haptic touch is available. This would support the work by others such as Bolton et al, (2009) who proposed cortical contribution to sensory processing for haptic touch during standing balance. This potential increase in power around Pz may reflect adaptable hierarchy reorganization as discussed in section 1.6.4, which involves reweighting of selected inputs (e.g. somatosensory input from the right hand). Theta band increase coupled with an alpha band decrease would have been indicative of increased excitation of the area and would have indicated a larger reliance on the somatosensory cortical areas as a result of haptic touch availability. These frequency characteristics were coupled with increased postural stability (a reduction in centre of pressure RMS and velocity) which confirms previous conclusions of increased stability when haptic touch is included (Ishigaki et al., 2016). Specifically, Ishigaki et al. (2016) reported higher theta activity in the parietal structures, specifically theta synchronization, during haptic touch.

The possible decrease in alpha power frequency around Pz during haptic touch conditions supports previous literature that indicates alpha frequency power increases in cortical structures that are comparatively idle as compared to when they are highly excited (Kanokwan et al., 2019). In this case, alpha frequency was higher in the parietal regions of the cortex during conditions with no haptic touch due to the somatosensory cortex's relative deexcitation. Conversely, alpha frequency power was potentially higher during haptic inclusion conditions, as the somatosensory cortex was actively using the haptic touch information for the purposes of retaining postural stability.

As previous literature does not explain delta frequency behaviour at depth during haptic stance, it is a new development that low frequency attenuation does occur during haptic inclusion; delta frequency activity increases, likely due to a dampening of excitation in the cortex due to increased stability during haptic stance, as an increase in stability leads to a decrease in frontal N1 (Quant et al., 2004; Quant et al., 2005; Collette et al., 2007; Maki & McIlroy, 2007). Due to the inherent nature of EEG, spatial resolution is relatively low, therefore it is likely that the behaviour of the fronto-central N1 extending posteriorly towards Pz.

4.6 Visual Information

Manipulation of visual availability was expected to result in an increase in theta frequency power around Oz as a direct result of an increase in visual input, with alpha frequency power decreasing in the same pattern. Theta activity differences around Oz did not reach statistical significance but did follow a recognizable pattern. The largest theta frequency power occurred when visual information was fully available during the tandem stance open condition, and the lowest theta frequency power occurred during the tandem stance eyes closed condition where no visual information was available. The second largest theta frequency power occurred when the participant had their eyes open but vision occluded, and the second lowest theta frequency power occurred when the participant was standing in tandem stance with restricted visual scene. This distinct difference in theta frequency power when

vision is not fully available presents an interesting finding, as intuitively the occipital lobe should be more active when a partial scene is presented.

Alpha frequency results did not reach statistical significance. It was expected that alpha frequency power would be lowest during tandem stance eyes open trials, and highest during tandem stance eyes closed trials, representing an idle nature of the occipital lobe when vision is not available. However, alpha frequency power was lowest during tandem eyes closed and tandem eyes open vision occluded trials, with the highest alpha frequency power occurring when participants were in tandem stance with their eyes open.

As expected, there was a statistically significant increase in postural instability as visual scene became unavailable. RMS and centre of pressure velocity in the mediolateral and anteroposterior directions was highest during tandem stance eyes closed, second highest during tandem stance eyes open vision occluded, second lowest during tandem stance with restricted visual field, and lowest during tandem stance with eyes open. This represents increased postural stability as visual scene is available, likely due to increased opportunities for postural orientation with external objects in accordance with previous literature (Patla et al., 1996; Patla, 1997; Hammami et al., 2014). These results corroborate conclusions drawn by previous authors stating that postural instability increases as visual information is removed (Yamamoto et al., 2015), but this instability is largely in the anteroposterior direction. Additionally, these results indicate that instability is largely affected by if visual availability includes the external environment is minimally affected by if vision is available or not, supporting the notion that postural stability is highly reliant on vision for the purposes of orienting the body to the external environment (Hammami et al., 2014). The results viewed when manipulating visual availability indicate an unexpected pattern in theta and alpha frequency band. As expected, theta frequency power ratio was highest when the eyes were open providing full visual availability. However, contrary to expectations, the second highest frequency power ratio occurred when the eyes were open, but a visual

scene was unavailable. These results indicate an increase in theta band activity in the occipital regions of the cortex during stance tasks with visual input. As previous literature indicates frequency attenuation in the theta band occurs when eyes are open regardless of visual input, due to the fact that the eye lids are open and the cortex expects depolarization due to visual input in the occipital lobe (Anderson et al., 2017). However, these results indicate that further attenuation occurs when visual input is fully available. Intuitively, the occipital lobe should be most active when a visual scene with complex textures, forms, and colours as this complicated sensory input would force the multiple components of the occipital lobe to communicate with each other to fully process the multi-input visual scene (Gale et al., 1971). In fact, due to this dynamic communication, gamma frequency should also be highest when a complicated visual scene with multiple features is presented (Gale et al., 1971); this result was not confirmed in this study. This result may be due to large between subject variability, as seen in appendix 1.0 or large confounding effects from the frontally evoked N1 as a result of the high degree of task difficulty.

4.7 Limitations

One explanation for these findings is an excess of between subject differences, resulting in a reduction in the appearance of within subject differences during statistical analysis. Upon examination of **appendix 1.0** it is very clear that topographical mapping of spectral density plots revealed significant between subject differences regardless of task.

Part of the challenges associate with a lack of power can be mitigated by increasing the subject and trial numbers. This likely resulted in an underpowering of the statistical analysis. In order to produce a minimal effect size of d=0.2 and a p value of 0.05, subjects should be increased to 24 for the purposes of haptic/no haptic comparison, and 32 for the purposes of vision manipulation comparison.

Another inherent limitation of this study design is a confounding of task challenge and sensory manipulation resulting in frontally evoked N1 waveform activity that appears as mid-frequency spectral

power (Varghese et al., 2015). These posturally evoked N1 potentials are a significant occurrence during postural tasks and the amplitude is related to task difficulty and magnitude of postural instability (Varghese et al., 2015). Therefore, manipulation of visual input and haptic touch during tandem stance (a stance known for its ability to reveal postural instability) will likely result in any spatial frequency modulation being hidden underneath the strong N1. A way to mitigate this effect would be to manipulate vision and haptic touch during standard stance, thus reducing postural instability due to stance and revealing postural instability and frequency modulation due to sensory input alone.

Finally, using EEG as a research method when examining spatial modulation of cortical excitation carries its own inherent limitations. EEG is known for its high temporal resolution and limited spatial resolution, making it an exceptional tool for examining cortical excitation in relation to timing of external events, but it is limited in its ability to determine frequency sources over a topographical area (Srinivasan, 1999). Minor spatial differences due to sensory manipulation during this study paradigm may not have been revealed due to the insensitive nature of EEG. In order to improve spatial and temporal resolution, a Laplacian algorithm model as well as Current Source Density estimates may be applied to reduce the effect size of individual electrodes, minimizing volume conductance issues that may arise from recording neuron potentials from increasingly large distances (Srinivasan, 1999).

Additionally, applying a 64 electrode EEG cap instead of the standard 32 electrode cap may reduce volume conductance results that reduce spatial and temporal resolution (Srinivasan, 1999).

4.8 Conclusions and Future Directions

Although manipulation of incoming sensory information, including stance, vision, and haptic sensation results in meaningful changes in the underlying control of balance as reflected by COP, there was no statistical evidence of changes measured by frequency of EEG signals. At face value, this would raise some concerns regarding the hypotheses of the potential role of the cortex in the control of sensory information during balance control. Increasing stance challenge did appear to impact in theta,

alpha, beta, and gamma activity in the frontal regions of the cortex. During conditions with increased stance challenge (ie. tandem stance), there appeared some evidence of a similar increase in theta frequency power around Fz as compared to conditions with standard or narrow stance. This result is in accordance with previous literature that states theta frequency will increase frontally as frontal structures are recruited for use during postural instability (Pfurtscheller et al., 1996; Müller-Putz et al., 2007; Stam 2000; Solis-Escalante et al., 2012; Seeber et al., 2014; Hwang & Huang, 2016; Hebel et al., 2020). If true, however, this would not speak to the processing of sensory information but rather changes in CNS activity linked to the balance control challenge independent of sensory state.

Adding haptic touch to tandem eyes closed stance did seem to lead to an increase in delta and theta frequency activity but also a reduction in alpha, beta, and gamma activity in the parietal regions of the cortex. If such changes are real then they may reflect, as suggest in the literature (Merabet et al., 2010) a relationship to reweighting of reliance on the respective cortical locations. The addition of haptic touch resulted in a modest increase in theta activity around Pz, possibly indicating an increased reliance on parietal structures when haptic touch is present vs. absent. Consequently, the alpha frequency activity was slightly reduced during haptic inclusion trials as compared to no haptic inclusion trials, possibly indicating a deexcitation of the parietal structures during conditions where haptic touch was not included; this was not confirmed statistically. Additionally, the addition of haptic touch reduced postural instability; velocity and RMS were significantly reduced in the anteroposterior direction, and velocity was reduced in the mediolateral direction.

Manipulation of incoming visual information resulted in no statistically significant changes in activity. During the tandem stance eyes open condition, there was a modest increase in theta activity around the Oz electrode as compared to theta activity during tandem stance conditions with eyes closed, restricted vision, and eyes open but vision occluded. However, the expected alpha increase during conditions where vision was available did not occur, and there was an increase in alpha

frequency power around Oz during tandem eyes open conditions. Finally, force plate data during manipulation of incoming visual sensation indicated an increase in postural stability as an external visual scene was available, confirming previous literature that states postural stability increases as external objects are available for the purposes of postural orientation (Patla et al., 1996; Patla, 1997; Hammami et al., 2014).

Due to the restrictions associated with the Covid-19 pandemic, this author was unable to complete the planned initial study based on her own research design and was required to analyze data from a previously collected dataset. One opportunity of the experience of developing hypotheses, analyzing and interpreting the results on a dataset that was prior collected, was the chance to reflect on an optimal study design that may have been better suited to address these specific questions. First, sensory manipulation tasks should be conducted across all stance conditions. For the current study, sensory manipulation was performed in tandem stance only, resulting in a pattern of cortical frequency that only reflected the challenging stance, not the sensory manipulation itself. In order to reduce this effect the following tasks should be performed in standard stance, narrow stance, and tandem stance; eyes closed, eyes closed with haptic touch, eyes open vision occluded, eyes open restricted visual field, and eyes open full visual availability. In examining frequency patterns across all tasks in all stances, it may be possible to observe effects of sensory manipulation that may have been present during tandem stance but were hidden by the effect of stance challenge itself. Additionally, non-balance tasks such as a seated eyes closed task should be conducted in order to provide a baseline comparator which may determine if frequency power patterns when standing is significantly different to the patterns observed when reactive balance control is not a crucial role of the cortex at that point in time. Also, the potential importance of exploring spatial differences with an increase in electrode density from 32 to 64 channels would afford improved ability to resolve spatial differences. The number of subjects should be increased to 32 in order to achieve a effect size of 0.2 for the current data.

There were also limitations of the analytical approaches adopted in the present study. When examining frequency power across electrodes, an approach to accommodate individual variation in spatial location of peak power (rather than rely on fixed electrode locations) may have better revealed task related differences. Such an approach would also benefit from improved electrode density as noted in the previous paragraph. One other option would be to determine peak power amplitude averaged across all subjects at each electrode for each stance during the sensory task that would intuitively produce the largest peak frequency power, then determine patterns of frequency activity around that electrode. For example, when examining visual manipulation, peak power amplitude for each electrode should be calculated for the eyes open condition across all stances. Then, frequency power should be calculated in all other conditions of interest at that specific electrode. In the current study design, it was assumed that patterns would be discernable for all tasks in midline electrodes which may not be the reality; significant fluctuations in frequency power may be lateralized and determining peak frequency amplitude across all electrodes and examining frequency behavior at a more accurate electrode may reveal patterns not viewed in the current study. In addition, the current study was limited to quantitative descriptions of the topographic characteristics of EEG activity and quantitative analysis was restricted to a limited numbers of sites. More advanced approaches such as network or connectivity analysis may be undertaken to further reveal such cortical changes as a result of manipulating postural set.

The findings from this data indicate that frequency modulation in related areas of the cortex may occur as a result of sensory manipulation, although the current study format failed to reach statistical significance. A follow-up study should be performed using similar postural tasks during all stances, specifically standard stance. Performing all tasks during standard stance may reduce confounding effects of frontally evoked N1s and reveal clearer attenuation of frequency activity. Following that study, a paradigm should be developed including manipulation of size and complication

of visual field to determine if complicating visual field results in an attenuation of frequency in the occipital regions of the cortex, further revealing cortical contributions to balance in relation to visual and somatosensory input.

References

Agrawal Y., Carey J., Della Santina C. (2009). "Disorders of Balance and Vestibular Function in US Adults". *Internal Medicine*. 169(10): 938-934.

Anderson G., Yardley L., Luxon L. (1998). "A Dual-Task Study of Interference Between Mental Activity and Control of Balance". *The American Journal of Otology*. 19(5): 632–637.

Bolton D. (2015). "The Role of the Cerebral Cortex in Postural Responses to Externally Induced Perturbations." *Neuroscience and Biobehavioral Reviews*. 57(15): 142–55.

Braddick O., O'Brien J., Wattam-Bell J., Atkinson J., Hartley T., Turner R. (2001). "Brain Areas Sensitive to Coherent Visual Motion". *Perception*. 30(1): 61-72.

Britten K., van Wezel R. (1998). "Electrical Microstimulation of Cortical Area MST Biases Heading Perception in Monkeys". *Nature Neuroscience*. 1(1): 59-63.

Brindley G. (1960). "Physiology of the Retina and the Visual Pathway". *Proceedings of the Royal Society of Medicine*. 53(10): 875-889.

Bruijn S., van Dieën J., Daffertshofer A. (2015). "Beta Activity in the Premotor Cortex Is Increased during Stabilized as Compared to Normal Walking." *Frontiers in Human Neuroscience*. 9(2): 593.

Bruijn S., van Dieën J. (2018). "Control of Human Gait Stability through Foot Placement." *Journal of The Royal Society Interface*. 15(143): 201.

Buzsáki G., Anastassiou C., Koch C. (2012). "The Origin of Extracellular Fields and Currents — EEG, ECoG, LFP and Spikes." *Nature Neuroscience Reviews*. 13(6): 407–20.

Carandini M., Demb J., Mante V., Tolhurst D., Dan Y., Olshausen B., Gallant J., Rust N. (2005). "Do We Know What the Early Visual System Does?". *The Journal of Neuroscience*. 25(46): 10577-10597.

Carpenter M. G., Frank J. S., Adkin A. L., Paton A., Allum, J. (2004). "Influence of Postural Anxiety on Postural Reactions to Multi-Directional Surface Rotations". *Journal of Neurophysiology*. 92(6): 3255–3265.

Collette C., Micaelli A., Andriot C., Lemerle P. (2007). "Dynamic Balance Control of Humanoids for Multiple Grasps and Non-Coplanar Frictional Contacts". *IEEE*. 1(1): 1-4.

Cuevas A., Febrero M., Fraiman R. (2004). "An ANOVA Test for Functional Data". *Computational Statistics and Data Analysis*. 47(1): 111-122.

Gale A., Coles M., Boyd E. (1971). "Variation in visual input and the occipital EEG: II". *Physiological Psychology*. 23(2): 99-100.

Gomez-Ramirez J., Freedman S., Mateos D., Valiante T. (2017). "Exploring the alpha desynchronization hypothesis in resting state networks with intracranial electroencephalography and wiring cost estimates". *Scientific Reports*. 7(240): 30-42).

Gurfinkel V., Lipshits M., Popov K. (1974). "Is the stretch reflex a basic mechanism in the system of regulation of human vertical posture?" *Biofizika*. 19(4): 744-748.

Hammami R., Behm D., Chtara M., Otham A., Chaouachi A. (2014). "Comparison of Static Balance and the Role of Vision in Elite Athletes". *Journal of Human Kinetics*. 41(8): 33-41.

Gebel A., Lehmann T., Granacher U. (2020), "Balance task difficulty affects postural sway and cortical activity in healthy adolescents". *Experimental Brain Research*. 238(43): 1323-1333.

Horak F. B., Diener H. C., Nashner L. M. (1989). "Influence of Central Set on Human Postural Responses". *Journal of Neurophysiology*. 62(4): 841–853.

Horak F. B., Shupert C. L., Mirka A. (1989). "Components of Postural Dyscontrol in the Elderly: A Review". *Neurobiology of Aging*. 10(6): 727–738.

Horak F., Nashner M. (1986). "Central programming of postural movements: adaptation to altered support-surface configurations". *Journal of Neurophysiology*. 55(6): 1369-1381.

Horak F. (2006). "Postural Orientation and Equilibrium: What do we Need to Know About Neural Control of Balance to Prevent Falls?". *Age and Aging*. 35(2): 103-110.

Horslen B. C., Carpenter M. G. (2011). "Arousal, Valence and their Relative Effects on Postural Control". *Experimental Brain Research*. 215(1): 27–34.

Hubel D., Wiesel T., LeVay S., Basil Barlow H., Gaze R. (1977). "Plasticity of Ocular Dominance Columns in Monkey Striate Cortex". *Philosophical Transactions of the Royal Society of London*. 278(961): 377-409.

Hubel D., Wiesel T. (1959). "Receptive Fields of Single Neurones in the Cat's Striate Cortex". *Journal of Physiology*. 148(17): 574-591.

Hülsdüncker T., Mierau A., Need C., Kleinoder H., Struder H. (2015). "Cortical Processes Associated with Continuous Balance Control as Revealed by EEG Spectral Power". *Neuroscience Letters*. 592(33): 1-5.

Hwang I., Huang C. (2010). "Neural Correlates of Task Cost for Stance Control with an Additional Motor Task: Phase-Locked Electroencephalogram Responses". *PLOS One*. 1(1): 14-20.

Ishigaki T., Ueta K., Imai R., Morioka S. (2016). "EEG Frequency Analysis of Cortical Brain Activities Induced by Effect of Light Touch". *Experimental Brain Research*. 234(6): 1429-1440.

Kanokwan S., Pramkamol W., Wipatcharee K. (2019). "Age-related differences in brain activity during physical and imagined sit-to-stand in healthy young and older adults". *Journal of Physical Therapy Science*. 31(5): 440-448.

Kennedy P., Inglis T. (2002). "Distribution and Behaviour of Glabrous Cutaneous Receptors in the Human Foot Sole". *The Journal of Physiology*. 538(3): 995-1002.

Kibushi B., Hagio S., Moritani T., Kouzaki M. (2018). "Speed-Dependent Modulation of Muscle Activity Based on Muscle Synergies during Treadmill Walking." *Frontiers in Human Neuroscience*. 12(1): 1–13.

Kuo A. (2005). "An Optimal State Estimation Model of Sensory Integration in Human Postural Balance". *Journal of Neural Engineering*. 2(3): 10-19.

Laessoe U., Voigt M. (2008) "Anticipatory Postural Control Strategies Related to Predictive Perturbations". *Gait and Posture*. 28(1): 62-68.

Lakhani B., Miyasike-daSilva V., Vette A., McIlroy W. (2013). "Priming' the brain to generate rapid upper-limb reactions". *Experimental Brain Research*. 230(1): 261-270.

Lord S., Menz H. (2000). "Visual Contributions to Postural Stability in Older Adults". *Gerontology*. 46(6): 306-310.

Lopez-Aranda M., Lopez-Tellez J., Navarro-Lobato I., Masmudi-Martin M., Gutierrez A., Khan Z. (2009). "Role of Layer 6 of V2 Visual Cortex in Object-Recognition Memory". *Science*. 325(5936): 87-89.

Lui L., Bourne J., Rosa M. (2006). "Functional Response Properties of Neurons in the Dorsomedial Visual Area of New World Monkeys" (Callithrix Jacchus)". *Cerebral Cortex*. 16(2): 162-177.

Maki B. E., McIlroy, W. E. (1997). "The Role of Limb Movements in Maintaining Upright Stance: The 'Change-in-Support' Strategy." *Physical Therapy*. 77(5): 488-507.

Maki B. E., McIlroy W. E.(2007). "Cognitive Demands and Cortical Control of Human Balance-Recovery Reactions." *Journal of Neural Transmission*. 114(10): 1279-1296.

Marigold D. S., Patla A. E. (2002). "Strategies for Dynamic Stability During Locomotion on a Slippery Surface: Effects of Prior Experience and Knowledge". *Journal of Neurophysiology*. 88(1): 339–353.

Maurer C., Mergner T., Bolha B., Hlavacka F. (2001). "Human Balance Control During Cutaneous Stimulation of the Plantar Soles". *Neuroscience Letters*. 302(1): 45-48.

McIlroy W., Maki B. (1995). "Early activation of arm muscles follows external perturbation of upright stance". *Neuroscience Letters*. 184(3): 177-180.

Merabet L., Pascual-Leone A. (2010). "Neural Reorganization Following Sensory Loss: The Opportunity of Change". *Nature Reviews Neuroscience*. 11(1): 44-52.

Meyns P., Bruijn S. M., Duysens J. (2013). "The How and Why of Arm Swing during Human Walking." *Gait and Posture*. 38(4): 555–562.

Mihara M., Miyai I., Hatakenaka M., Kubota K., Sakoda S. (2008). "Role of the Prefrontal Cortex in Human Balance Control". *NeuroImage*. 43(2): 329–336.

Moran J., Desimone R. (1985). "Selective Attention Gates Visual Processing in the Extrastriate Cortex". *Science*. 229(4715): 782-784.

Neville C., Ludlow C., Rieger B. (2015). "Measuring Postural Stability With an Inertial Sensor: Validity and Sensitivity". *Medical Devices: Evidence and Research*. 8(1): 447-455.

Orban G. (2020). "Higher Order Visual Processing in Macaque Extrastriate Cortex". *Physiological Reviews*. 88(1): 59-89.

Palmieri R. M., Ingersoll C. D., Stone M. B., and Krause B. A. (2002). "Center-of-Pressure Parameters Used in the Assessment of Postural Control". *Journal of Sport Rehabilitation*. 11(1): 51–66.

Patla A. E., Prentice S. D., Gobbi L. T. (1996). "Visual control of obstacle avoidance during locomotion: strategies in young children, young and older adults". *Advances in Psychology*. 114(1): 257-277.

Payne A. M., Ting L. H., Hajcak G. (2019). "Do Sensorimotor Perturbations to Standing Balance Elicit an Error-Related Negativity?" *Psychophysiology*. 56(7): 56-61.

Petras K., Ten Oever S., Jacobs C., Goffaux V. (2019). "Coarse-to-Fine Information Integration in Human Vision". *NeuroImage*. 186(1): 103-112.

Petsche H., Pockberger H., & Rappelsberger P. (1984). "On the Search for the Sources of the Electroencephalogram." *Neuroscience*. 11(1): 1-27.

Pfurtcheller G., Lopes da Silva F.H. (1999). "Event-Related EEG/MEG Synchronization and Desynchronization: Basic Principles". *Clinical Neurophysiology*. 110(12): 1842-1857.

Pitzalis S., Sereno M., Committeri G., Fattori P., Galati G., Patria F., Galletti C. (2010). "Human V6: The Medial Motion Area". *Cerebral Cortex*. 20(2): 411-424.

Quant S., Adkin A. L., Staines W. R., McIlroy W. E. (2004). "Cortical Activation Following a Balance Disturbance." *Experimental Brain Research.* 155(3): 393–400.

Quant S., Maki B. E., McIlroy W. E. (2005). "The Association between Later Cortical Potentials and Later Phases of Postural Reactions Evoked by Perturbations to Upright Stance." *Neuroscience Letters*. 381(3): 269–274.

Ray S., Maunsell J. (2010). "Differences in gamma frequencies across visual cortex restrict their possible use in computation". *Neuron*. 67(5): 885-896.

Schafer E. W. P., Marcus M. M. (1973). "Self-Stimulation alters human sensory brain responses". *Science*. 181(4095): 175–177.

Schoultz T., Swett J. (1972). "The Fine Structure of the Golgi Tendon Organ". *Journal of Neurocytology*. 1(1): 1-26.

Seeber M., Scherer R., Wagner J., Solis-Escalante T., Muller-Putz G. (2014). "EEG beta suppression and low gamma modulation are different elements of human upright walking". *Frontiers in Human Neuroscience*. 87(102): 1367-1399.

Sibley K., Mochizuki G., Frank J., McIlroy W. (2010). "The Relationship Between Physiological Arousal and Cortical and Autonomic Responses to Postural Instability". *Experimental Brain Research*. 203(5): 533-540.

Sipp A. R., Gwin J. T., Makeig S., Ferris D. P. (2013) "Loss of Balance during Balance Beam Walking Elicits a Multifocal Theta Band Electrocortical Response." *Journal of Neurophysiology*. 110(9): 2050–2060.

Soames R. W., Atha J. (1982). "The Spectral Characteristics of Postural Sway Behaviour." *European Journal of Applied Physiology and Occupational Physiology*. 49(2): 169-177.

Somisetty S., Das J. (2020). "Neuroanatomy, Vestibulo-ocular Reflex". Neuroanatomy. 17(3):33-42

Srinivasan R. (1999). "Methods to Improve the Spatial Resolution of EEG". *International Journal of Bioelectromagnetism*. 1(1): 107-116.

Stam C. J. (2000). "Brain Dynamics in Theta and Alpha Frequency Bands and Working Memory Performance in Humans". *Neuroscience Letters*. 286(2): 115-118.

Sur S., Sinha V. K. (2009). "Event-Related Potential: An Overview". *Industrial Psychiatry Journal*. 18(1): 70–73.

Tang P.F., Woollacott M. H., Chong R. K. Y. (1998). "Control of Reactive Balance Adjustments in Perturbed Human Walking: Roles of Proximal and Distal Postural Muscle Activity". *Experimental Brain Research*. 119(2): 141–152.

Thomas D. P., Whitney R. J. (1959). "Postural Movements during Normal Standing in Man." *Journal of Anatomy*. 93(15): 524–539.

Tse Y., Petrofsky J., Berk L., Daher N., Lohman E., Laymon M., Cavalcanti P. (2013). "Postural Sway and Rhythmic Electroencephalography Analysis of Cortical Activation During Eight Balance Training Tasks". *Medical Science Monitor*. 19(1): 175-186.

Van Ooteghem K., Lakhani B., Akram S., Miyasike Da Silva V., McIlroy W. (2013). "Time to disengage: holding an object influences the execution of rapid compensatory reach-to-grasp reactions for recovery from whole-body instability". *Experimental Brain Research*. 231(1): 191-199.

Varghese J., Beyer K., Williams L., Miyasike-daSilva, McIlroy W. (2015). "Standing Still: Is There a Role for the Cortex?". *Neuroscience Letters*. 590(14): 18-23.

Varghese J. P., McIlroy R. E., Barnett-Cowan, M. (2017). "Perturbation-Evoked Potentials: Significance and Application in Balance Control Research." *Neuroscience & Biobehavioral Reviews*. 83(7): 267–280.

Wikstrom E., Naik S., Lodha N., Cauraugh J. (2010). "Balance Capabilities After Lateral Ankle Trauma and Intervention: a Meta-Analysis". *Gait and Posture*. 31(4): 407-414.

Winter D. A., Patla A. E., Frank J. S. (1990). "Assessment of Balance Control in Humans." *Medical Progress through Technology*. 16(1–2): 31–51.

Wingert J., Welder C., Foo P. (2014). "Age-Related Hip Proprioception Declines: Effects on Postural Sway and Dynamic Balance". *Archives of Physical Medicine and Rehabilitation*". 95(2): 253-261.

Woollacott M., Shumway-Cook A., Nashner L. (1986). "Aging and Posture Control: Changes in Sensory Organization and Muscular Coordination". *International Journal of Aging and Human Development*. 23(2): 97-114.

Woollacott M., Pei-Fang T. (1997). "Balance control during walking in the older adult: Research and its implications". *Physical Therapy*. 77(6):646-660.

Yamamoto T., Smith C., Suzuki Y., Kiyono K., Tanahashi T., Sakoda S., Morasso P., Nomura T. (2015). "Universal and Individual Characteristics of Postural Sway Suring Quiet Standing in Healthy Young Adults". *Physiological Reports*. 3(3):42-47.

Appendix 1.0: Spectral density plots of all participants across all conditions. Number denotes subject identification.

