Characterizing the dynamics of vestibular reflex gain modulation using balance-relevant sensory conflict

by

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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.

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Abstract

Electrical vestibular stimulation (EVS) can be used to evoke reflexive body sways as a probe of vestibular control of balance. However, EVS introduces sensory conflict by decoupling vestibular input from actual body motion, prompting the central nervous system (CNS) to potentially perceive vestibular signals as less reliable. In contrast, light touch reduces sway by providing reliable feedback about body motion and spatial orientation. The juxtaposition of reliable and unreliable sensory cues enables exploration of multisensory integration during balance control. I hypothesized that when light touch is available, coherence and gain between EVS input and center of pressure (CoP) output would decrease as the CNS reduces the weighting of vestibular cues. Additionally, I hypothesized that the CNS would require less than 0.5 seconds to adjust weighting of sensory cues upon introduction or removal of light touch. In two experiments, participants stood as still as possible while receiving continuous stochastic EVS (with a frequency of 0-25 Hz, amplitude of ± 4 mA, and a duration of 200-300 seconds), while either: lightly touching a load cell (<2 N); holding their hand above a load cell; or intermittently switching between touching and not touching the load cell. Anterior-posterior (AP) CoP and linear accelerations from body-worn accelerometers were collected to calculate the root mean square (RMS) of AP CoP, as well as the coherence and gain between EVS input and AP CoP or acceleration outputs. Light touch led to a decrease in CoP RMS (mean 49% decrease) with and without EVS. Significant coherence between EVS and AP CoP was observed between 0.5 Hz and 24 Hz in the NO TOUCH condition, and between 0.5 Hz and 30 Hz in the TOUCH condition, with TOUCH having significantly greater coherence from 11 to 30 Hz. Opposite to coherence, EVS-AP CoP gain decreased in the TOUCH condition between 0.5-8 Hz (mean decrease 63%). Among the available acceleration data, only the head exhibited a significant increase in coherence above 10 Hz in the TOUCH condition, compared to the NO TOUCH condition. Light touch reduced CoP displacement, but increased variation in the CoP signal that can be explained by EVS input. Light touch may cause the CNS to attribute EVS signals to head movements and therefore up-weight vestibulocollic responses while downweighting vestibulospinal balance responses. Changes in coherence and gain started before the transition to the NO TOUCH condition and after the transition to the TOUCH condition. The loss of sensory information may be more destabilizing than addition, necessitating anticipatory adjustments. These findings demonstrate the ability of one sensory modality to modulate the utilization of another by the CNS, and highlight asymmetries in the timing of responses to the introduction and removal of sensory information, which may impact behavior.

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Literature Review

1.1 Introduction

Control over standing balance is needed to complete everyday activities and avoid falls, as they can lead to injuries, disabilities and even death in some cases. Gaining a better understanding of balance control in neurotypical populations will serve as a foundation for investigating balance dysfunction in those who are prone to falling. Improving balance is especially important for the elderly, as 30% of people over 65 years of age living in the community fall each year (Gillespie et al., 2012).

Balance control requires sensory information from balance relevant modalities to be integrated to detect centre of mass (CoM) movement and body posture (Gurfinkel et al., 1995; Peterka, 2002). The sensory systems that contribute to balance control include visual, vestibular and somatosensory cues (Kandel et al., 2021). The combination of sensory signals in the central nervous system (CNS) is thought to be achieved by adding each sensory input into a weighted sum (Peterka, 2002). These weights are typically not equal between modalities and are able to change depending on the task or environmental conditions (Blouin et al., 2011; Horslen et al., 2014; Jeka et al., 2008; Luu et al., 2012; Peterka, 2002). Although there are multiple sensory systems that contribute to balance control, the focus of this dissertation will be on vestibular cues and cutaneous somatosensory cues from light touch.

Light touch cues can be reliable cues in balance context because the somatosensory system provides feedback signals associated with the location and motion of body segments, contact with external objects, and postural orientation (Chen & Tsai, 2015; Jeka et al., 1996). The vestibular system organs, located in the inner ear, convey information about how the head is rotating and translating in space to various areas in the CNS (Day & Fitzpatrick, 2005). Both light touch and vestibular cues contribute to the internal representation of CoM movement and body posture relative to the environment and to the gravito-inertial plane (Gurfinkel et al., 1995; Peterka, 2002).

Sometimes, sensory modalities conflict with each other by presenting contradicting balance relevant cues (Jeka et al., 2010; Oie et al., 2002; Weech et al., 2020). This can happen when cues that are decoupled from how the body is positioned with respect to gravity contradict other balance relevant cues. Sensory conflicts can perturb postural control, sometimes causing instability and falls

(Buatois et al., 2007; Jeka et al., 2010; Teasdale et al., 1991; Wolfson et al., 1992). To help resolve this, the CNS is thought to increase the weight of reliable cues while decreasing the weight of unreliable cues (Peterka, 2002). It is not fully known if there are rules for how the CNS determines which cues are reliable.

Electrical Vestibular Stimulation (EVS) can be used to probe the vestibular system, as it is a non-invasive electrical stimulus delivered to the vestibular system that evokes vestibular balance responses, in isolation from other sensory modalities (Fitzpatrick & Day, 2004). EVS and galvanic vestibular stimulation (GVS) are terms that are sometimes used interchangeably. Galvanic vestibular stimulation is a form of EVS that has traditionally been used to study vestibulo-motor control (Fitzpatrick & Day, 2004). GVS is a direct form of current that has a level shift in the signal, such as square pulse waves (Fitzpatrick & Day, 2004). EVS also includes alternating currents, where the signal alternates around a mean (Fitzpatrick & Day, 2004). Since this dissertation will discuss both galvanic vestibular stimulation and EVS, I will be using the term EVS to encapsulate both methods.

EVS is an effective tool to probe vestibular processing, as the EVS input can be controlled so that any changes in vestibular responses reflect central reflex modulation (Blouin et al., 2011; Horslen et al., 2014; Lim et al., 2017; Tisserand et al., 2018). The EVS cues also no longer reflect body motion with respect to gravity and are disruptive to balance control (Dilda et al., 2014; Weech et al., 2020). This is because the pattern of activation by EVS is unlike any produced by natural motion, as vestibular afferents of all directional sensitivities are activated simultaneously (Dilda et al., 2014; Fitzpatrick & Day, 2004). This means that EVS cues are artificial and lead to responses decoupled from head orientation within the gravito-inertial plane, and it may be favourable to downweight these cues (Dilda et al., 2014; Weech et al., 2020).

Light touch cues provide a balance-relevant reliable source of sensory information when finger contact is made with a solid, earth-mounted surface (Chen & Tsai, 2015; Jeka et al., 1996). It is thought that if both light touch and EVS cues are given simultaneously, light touch cues may be upweighted while EVS cues may be downweighted. Conflicts between vestibular and light touch inputs present a paradigm where the dynamics of sensory conflict in balance control can be studied. While it is understood that sensorimotor re-weighting can occur, little is known about specific situations that provoke these changes, how the CNS recognizes these situations and adjusts multiple sensory weights, and how long it takes the nervous system to effect change.

Specifically, it is not known how the introduction to a novel sensory input that was not previously present affects the gain of another sensory modality that is receiving unreliable balance cues. These findings can lead to further speculation on whether increasing the weight of one sensory system influences others to be re-weighted in a compensatory manner.

Determining time latencies to resolve sensory conflict is needed because more transient modulations could be influenced by structures within the brain stem, while longer modulations may require influence from the cortex (Horslen et al., 2014; Martin, 2021; Mian & Day, 2009; Sozzi et al., 2012). Providing indirect insight into the neural structures that are involved in re-weighting sensory input may help motivate further research to identify these structures. Once these structures are identified, targeted treatments to these areas for those with impaired ability to sensory re-weight may also be researched further.

1.2 Balance Control

1.2.1 Introduction: Balance Control

Human balance is an intricate process that has been studied in detail, yet still warrants further research. There is a basic understanding of how balance is controlled through neurophysiologic and biomechanical mechanisms; however, a better understanding of how sensory information is integrated during balance control is needed. This section will describe and outline how the CNS influences the biomechanics involved in human balance control.

1.2.2 Biomechanics of Balance

Postural control is defined as the act of maintaining, achieving or restoring a state of balance during any posture or activity (Pollock et al., 2000). There is no universally accepted definition of human balance, however standing balance has been described as the regulation of the body CoM within a base of support to avoid falling (Horak, 1987; Winter, 1995).

The CoM is a point that represents the average position of the body’s total mass, while the base of support is defined as the contact point between the body and a supporting surface (Kandel et al, 2021). Although gravity pulls on all body segments, the net effect on balance maintenance acts through the body’s CoM (Kandel et al., 2021). The CoM is typically located at the height of the sacral vertebrae and is positioned in front of the ankles when standing upright (Horak, 1987). If the vertical projection continuing from the CoM falls within the base of support defined by the lateral, anterior, and posterior edges of the feet, then upright stability can be achieved (Forbes et al., 2018; D. Winter, 1995). When the line continuing from the CoM falls outside the base of support, then the body is outside the range of stability and falls can occur (Forbes et al., 2018; Winter, 1995).

To measure how the body combats these instabilities, ground-reaction forces (GRFs) can be recorded using a force plate (Kandel et al., 2021). GRFs include all the forces acting between the foot and the ground and can be summed into a single force vector (Kandel et al., 2021). The GRFs are comprised of the gravitational projection of the CoM and torques generated at the ankle joint in the anterior–posterior (AP) plane and the hip joint in the medial–lateral (ML) plane (Winter, 1995; Winter et al., 1996). The location of the GRF vector on the surface is the point at which the rotational effect of all the forces on the feet are balanced and is termed the center of pressure (CoP) (Winter, 1995; Winter et al., 1996). The CoP is considered to be constantly counteracting the estimated position of the CoM to reduce sway, and this can be achieved by passive mechanical stiffness, tonic muscular activation and reactive balance control elements (Bottaro et al., 2008; De Groote et al., 2017; Jacono et al., 2004; Lockhart & Ting, 2007; Loram et al., 2007; Winter et al., 1998). Even with this level of control, the CoP and CoM are continually in motion and are rarely perfectly aligned, leading to some level of postural sway in quiet stance (Kandel et al., 2021). Balance can be a challenge even for neurotypical populations, and there is a lot of research being conducted as to why balance challenges arise, and which environmental factors can exacerbate these challenges.

1.2.3 Challenges of Balance Control

The human body has a relatively high center of mass and a small base of support, which complicates the problem of maintaining stability (Winter, 1995). When the body begins to sway from a perfect upright position, gravity accelerates the body further away from perfect upright stance (Peterka, 2002; D. Winter, 1995). Additionally, there are continual disturbances that need to be compensated for such as breathing, heart beat and noise from sensory and motor systems (Anastasio et al., 2000; Forbes et al., 2018; Jeong, 1991; Soames & Atha, 1982). It is thought that neurons fire by assessing the conditional probability of stimulus value, meaning that neurons must attempt to determine if a target is present or not within the receptive field (Anastasio et al., 2000) This uncertainty leads to inherent noise, as sensory input is not strictly deterministic (Anastasio et al., 2000).

These complications mean that the standing body cannot be stabilized by passive tissue structures alone, even in environments which are not considered disruptive to balance (Bottaro et al., 2008; Jacono et al., 2004; Lockhart & Ting, 2007; Loram et al., 2007). Therefore, human upright stance is naturally unstable and requires the CNS to make adaptations to changing environmental conditions (Lockhart & Ting, 2007; Peterka, 2002). Tonic muscular activation and reactive balance control are both managed by the CNS, and have different mechanisms by which they contribute to balance.

1.2.4 Passive Structural Stiffness and Tonic Muscular Activation

To remain upright during quiet stance, some support is provided by passive bone-on-bone forces in joints such as the knees and in stretched ligaments such as those at the front of the hips (Jacono et al., 2004; Kandel et al., 2021; Winter et al., 1998). However, the CNS still has to set an appropriate "background" or tonic level of muscle stiffness in balance-relevant muscles to help stabilize the body (Jacono et al., 2004; Loram et al., 2007; Morasso & Schieppati, 1999). This passive structural stiffness and tonic muscle activity to create stiffness is also important because the first muscle activity is delayed by 80 ms to perturbations (Horak & Nashner, 1986), which leads to net neuromuscular delays of between 150 and 260 ms of the CoP behind the CoM (D. A. Winter et al., 1998). A degree of stiffness acts almost instantaneously as the joint angle is changed, causing the CoP to move in the same direction as the CoM to help reduce the impacts of a destabilizing stimulus (De Groote et al., 2017; Loram et al., 2007; Morasso & Schieppati, 1999; Winter et al., 1998). The stiffness helps to protect against a limited range of body sway and is effective until sensory receptors are stimulated past a certain threshold (Forbes et al., 2018; Loram et al., 2007). For example, the stiffness of muscles in the absence of tonic activity generates an extensor torque capable of sustaining unstable balance at a mean CoM-ankle angle of 1.6 degrees (Loram et al., 2007). CoM- ankle angles above this value would require input from the CNS.

1.2.5 Reactive Balance Control

Larger perturbations and more dynamic balance situations require feedback from the different sensory systems to detect how the CoM deviates from sensory reference positions (Gurfinkel et al., 1995; Peterka, 2002). These reference positions include the orientation with respect to the gravity vector for vestibular cues, visual world orientation for visual cues, and support surface orientation for proprioceptive cues (Gurfinkel et al., 1995; Peterka, 2002). Control theory argues that patterns of synergistic muscle activity that corresponds with reactive balance behaviour can be reproduced by modelling responses to kinematic CoM motion (Lockhart & Ting, 2007). When imbalances occur, muscular torque is used to adjust biomechanical parameters such as muscle stiffness and adjusting the CoP location to counteract movement of the CoM (Forbes et al., 2018; Winter, 1995). For this to happen, the CNS must construct an image of CoM motion, which then these drives balance reactions (Gurfinkel et al., 1995; Peterka, 2002). This image or representation is estimated from combined sensory feedback from the different sensory modalities that are relevant to balance control.

1.2.6 Sensory Systems Involved in Balance Control

The sensory systems that contribute to balance control include visual, vestibular, and somatosensory cues (Kandel et al., 2021). Vestibular sensors detect rotations and translations of head orientation with respect to gravity and visual sensors detect head orientation relative to the visual world (Day & Fitzpatrick, 2005; Jeka et al., 2008; Peterka, 2002). Somatosensation detects cutaneous pressure, limb orientation relative to the environment and muscle stretch or muscle tension (Chen & Tsai., 2015; Peterka 2002). When information from these senses is combined to form a representation of posture and CoM movement, the CNS can control motor responses that adapt to changing conditions in the environment to help stay balanced (Gurfinkel et al., 1995; Peterka, 2002).

1.2.7 Sensory Integration

The combination of sensory signals in the CNS is done by adding each sensory input into a weighted sum (Peterka, 2002). These weights are typically not equal between modalities and are able to change depending on the task or environmental conditions (Blouin et al., 2011; Horslen et al., 2014; Jeka et al., 2008; Luu et al., 2012; Peterka, 2002). The remainder of this section will discuss how modeling techniques of the sensorimotor control of balance can be used to better understand how sensory information is weighted and combined in the CNS.

1.2.8 Transfer Functions

Techniques from system design engineering have been used, such as control theory, to provide a framework to quantify the weights of sensory information (Forbes et al., 2018; Mergner et al., 2003; Prochazka & Gorassini, 1998). Control theory provides many different models, analogies and terms that can be applied to the human body (Prochazka & Gorassini, 1998). It uses dynamical systems to develop models that use system inputs to drive system outputs, like behavior, to a new state (Mergner et al., 2003). The dynamical system in this case would be a neural balance controller, where sensory feedback drives the maintenance of balance. This theory is used to estimate optimal or near optimal sensory feedback gains using a cost function that minimizes control signals from around the CNS such as muscle activity or torque, or state variables such as whole-body sway or energy consumption (Forbes et al., 2018).

To reach a new state, each element in the system receives an input and transmits it in modified form, to the next element in the system (Prochazka & Gorassini, 1998). The modification might be a simple amplification, but often dynamic changes are also involved (Prochazka & Gorassini, 1998). In a linear system, a transfer function describes each such modification (Prochazka & Gorassini, 1998).

A linear system means that the relationship between a system input and system output can be represented by a linear equation. In a balance context, it means that that the relationship between stimulus amplitude and motor response can be characterized by a linear equation. The calculations performed to approximate sensory weights are done by using transfer functions between a perturbing stimulus amplitude and motor responses, often postural sway (Peterka, 2002), CoP variation (Horslen et al., 2014), or muscle activity (Blouin et al., 2011). Transfer functions can be used to characterize the dynamic behavior of a system by showing how coupling and response sensitivity between a sensory input and motor response change across different stimulus frequencies (Peterka, 2002). They also indicate the temporal relationship between postural response and stimulus motion (Peterka, 2002).

Coherence calculations within the transfer function provide a bounded normative measure of association between the input signal and output motor response in the frequency domain, taking on values between 0 and 1 at each frequency (Halliday et al., 1995). Zero represents the case of independence while 1 represents the case of a perfect linear relationship. This reflects the coupling between a signal and the motor response, or how closely the balance system follows the input. The gain of the transfer function gives the ratio of the amplitude of the response to the stimulus amplitude at each frequency, often on a log scale (Halliday et al., 1995). The gain quantifies the magnitude of the transfer function by showing the response sensitivity, or how much the magnitude of the motor response changes per unit of stimulus amplitude. Gain is often used to represent sensory weighting (Peterka, 2002). Phase of the transfer function represents the magnitude of how much the sway response leads or lags the stimulus by determining the shift in degrees of the output relative to the input signal (Halliday et al., 1995). This can give insight into how long it takes for the motor response to occur after the input stimulus occurs.

Transfer functions are used in a variety of studies to reveal insights into how sensory information is used by the CNS. Peterka (2002) used transfer functions in their study which allowed them to build a model of the sensorimotor control of balance. Figure 1 represents an example transfer function from Peterka (2002), which shows gain, phase, and coherence.

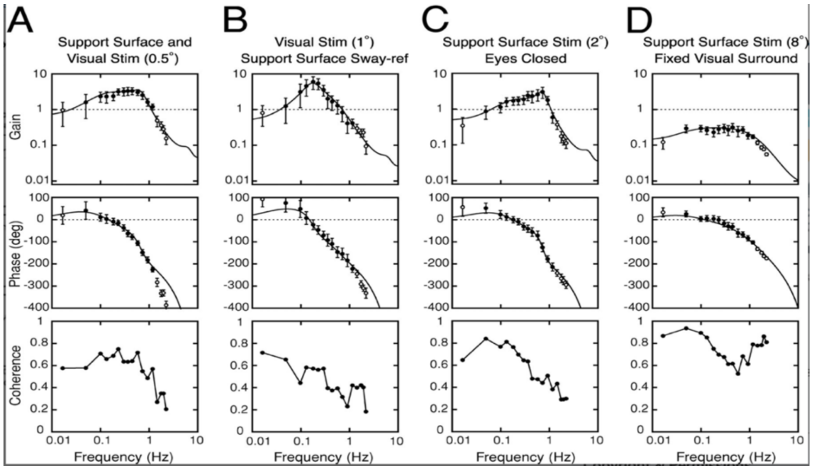

Figure 1: Example Transfer Function Adapted from Peterka (2002).

Example transfer functions from 4 different stimulus conditions in 4 different neurotypical participants. Gain data on a log scale and phase data on a linear scale are plotted against stimulus frequency. Coherence function estimates as a function of stimulus frequency are shown for each test condition. Error bars indicate 95% confidence intervals around the gain and phase estimates (● and ○). Unity gain (1) and 0 phase responses signify the result expected if participants were able to maintain perfect body alignment to the moving visual surround and/or support surface stimulus.

1.2.9 Conclusion: Transfer Functions Require Techniques to Probe Sensory Modalities

To use transfer functions, experimenters need to understand how each sensory system encodes information to accurately probe it. Then, different outcomes can be measured to reveal insights into how this sensory information is used within the CNS. Although visual, vestibular, and somatosensory systems contribute to balance control, the focus of this dissertation will be on vestibular input and cutaneous somatosensory cues from light touch.

1.3 Light Touch Sensory Information

1.3.1 Introduction: Light Touch and Contributions to Balance

Lightly touching a solid, earth-mounted surface with the fingertip gives somatosensory feedback about body movement and its relationship to the external space and can reliably contribute to balance control, even when contact forces are too small to provide mechanical stabilization (Jeka et al., 1996). Modeling studies on the amount of mechanical force required to attenuate postural sway confirm that loads less than 2 Newtons could not account for the observed reduction in sway that are seen with light touch studies (Holden et al., 1994). Light touch, haptic cues and cutaneous inputs are terms that are used interchangeably; however, I will be using light touch for this dissertation.

When lightly touching a surface with the finger, novel sensory information about body sway is made available that otherwise does not contribute to balance control. Light touch cues can be reliable cues in balance context because the somatosensory system provides additional feedback signals associated with the location and motion of body segments, contact with external objects, and postural orientation (Chen & Tsai., 2015). This information contributes to a more holistic internal representation of CoM movement and body posture within the environment and with respect to the gravito-inertial plane.

When lightly touching a surface, the mechanoreceptors of the fingertip are stimulated due to the fingertip shearing across the stationary surface corresponding with body sway (Silva et al., 2019). Position and velocity dependent motion information are conveyed simultaneously through the somatosensory system to create a spatial reference frame of orientation (Jeka et al., 1998).

Light touch is very effective at attenuating sway, such that the postural sway that is seen when vision is removed is fully attenuated by light finger touch applied to a stable surface (Jeka & Lackner, 1995). The magnitude of how much light touch can influence postural sway can also be measured through reductions in GRF variability and reduced degrees of body sway (Holden et al., 1994; Jeka et al., 1996). Holden et al (1994) measured mean sway amplitude in the ML direction when participants were standing on one leg and compared sway when touching a load cell with forces kept under 1 N versus not touching a load cell. When the eyes were open, mean sway amplitude decreased from 0.63 cm to 0.52 cm when touching the load cell, representing a 17% reduction in sway. When the eyes were closed, mean sway amplitude was reduced from 1.86 cm to 0.72 cm when touching the load cell, representing a 68% sway reduction. These reductions in sway demonstrate that light touch cues can be used to help improve balance in various conditions with differing levels of sensory availability.

1.3.2 Sensory Encoding of Light Touch Cues

Effects of light touch can originate from touch mechanoreceptors found within the fingers, hands or feet, depending on which parts of the body are in contact with a surface (Morasso & Schieppati, 1999). This dissertation will focus on light touch information originating from the fingertips, as this information can be discreetly introduced and removed experimentally.

It is suggested that non-spindle fingertip afferents provide the bulk of the sensory feedback associated with the fingertip that is touching a stable object during quiet standing (Silva et al., 2019). The study by Silva et al (2019) indicated that there was no statistical worsening of ML and AP postural sway parameters (such as CoP RMS) when the muscle spindles associated with the fingertip flexors and extensors were disengaged. They compared conditions of when the middle finger was held flexed 90° at the proximal interphalangeal joint to withdraw the sensory information from both flexor and extensor muscles of the middle finger, to when the middle finger was kept free. In both conditions, the middle finger was in contact with a load cell, with contact force under 1 N. Silva et al (2019) concluded that sway was primarily reduced by cutaneous somatosensory cues, since ML and AP postural sway parameters were similar between conditions.

However, when the arm is flexed to lightly touch a surface, cutaneous signals from the fingertip are suggested to still be related to proprioceptive information about arm and hand configuration (Rabin et al., 1999). Even though cutaneous somatosensory cues provide the bulk of sway attenuation, this proprioception information helps to reduce sway in conjunction with cutaneous somatosensory cues (Rabin et al., 1999).

1.3.3 Sensory Receptors: Cutaneous Somatosensory Information

Light touch information is transmitted by somatosensory afferents where tactile end organs filter mechanical stimuli (Nakatani et al., 2015). These cells contain mechanotransduction channels, which convert physical stimuli into membrane potential changes (Nakatani et al., 2015). These are called receptor potentials, and they trigger neuronal action potentials (Nakatani et al., 2015). These action potentials are transmitted by sensory afferents to the brain, where perception of these sensory afferents is achieved (Nakatani et al., 2015).

The vertical forces of the fingertip are likely to activate Pacinian corpuscles and Meissner corpuscles which are known to encode vibration (Rabin et al., 1999). The encoding of magnitude of sway toward and away from the stable surface may be amplified by these fast-adapting receptors (Rabin et al., 1999). This sway can be encoded from 1-300 Hz; optimally around 50 Hz (Kandel et al., 2021). Other mechanoreceptors would be involved, such as Merkel's discs, which are the receptors known to be slowly adapting and detect maintained deformation or sustained touch on the skin (Nakatani et al., 2015). This dissertation will not differentiate between these types of receptors in the experimental protocol.

1.3.4 Sensory Receptors: Proprioceptive Information

Receptors found in muscles and joints also provide sensation of limb position and movement to supplement cutaneous somatosensory cues from light touch (Forbes et al., 2018). Muscle spindles are fusiform-shaped organs consisting of several intrafusal fibers embedded within muscles that encode muscle length and velocity, which help detect changes in limb position and posture (Forbes et al., 2018). Golgi tendon organs are capsular mechanoreceptors at the muscle tendon junction that encode active muscle force production (Forbes et al., 2018). They may encode muscle tension exerted to maintain arm positioning and upright balance (Forbes et al., 2018).

1.3.5 Light Touch Information Processing in the Cortex

Touch signals from the fingertip and proprioceptive signals from the hand and arm enter the spinal cord and ascend through the dorsal columns where they eventually project to the brainstem, cerebellum, and the cerebral cortex via the thalamus (Martin, 2021). Within the cerebral cortex, the sensory information is relayed to the primary somatosensory cortex, then secondary somatosensory cortex, and higher cortical association areas including pre-motor frontal regions for further processing (Martin, 2021).

1.3.6 Latencies to Attenuate Sway with Light Touch

Sozzi et al (2012) calculated the mean AP position and ML oscillation of the CoP during transitions between touching a load cell under 2 N and not touching a load cell. They fit the time to baseline of the steady state pertaining to the new sensory condition (i.e., touching or not touching conditions) with an exponential model. Adding touch cues was found to reduce body sway and electromyography (EMG) within 0.5- 2s. Specifically, the increase in the tibialis anterior EMG started 500 ms after light touch information was introduced and CoP followed the tibialis by 0.2 s. Subsequently, the time taken to reach the steady-state was 1–3 s. The time from withdrawal of light touch information to destabilizing sway was shorter, around 1s. Sozzi et al (2012) suggested that the CNS rapidly detects the loss of the stabilizing input, and oscillating sway increases which engages proprioceptors in the leg muscles to gain more sensory information.

When touching a load cell, it takes time to stabilize the position of the finger on the load cell and reach an appropriate force level. In a study by Rabin et al (2006), it took about 4 seconds after participants were instructed to touch the load cell for participants to apply about 0.4 N steadily. Mean sway amplitude of the body upon finger contact decreased by 50% with a time constant of 1.6 s (Rabin et al., 2006). After 500 ms of initial finger contact, correlated changes in the center of pressure were delayed from fingertip force fluctuations by 275–300 ms, which was before stabilization of the finger. Overall, sway is attenuated quickly by introducing light touch information from the fingertip. This is also similar across different locations of the support surface.

1.3.7 Location of Support Surface

Finger contact is most effective when it is in the unstable plane of body sway, as it leads to larger reductions in joint angles due to the ability to better code direction of body motion (Rabin et al., 1999). With fingertip contact under 1 N in the unstable plane, the mean sway amplitude of ML CoP sway was 0.35 cm; with touch perpendicular to the unstable plane, 0.6 cm; and with no touch, 0.9 cm (Rabin et al., 1999). Although the effectiveness of finger contact is changed based on different positions of the arm and body (such as switching the plane of stability or changing the whole-body orientation to the Romberg stance), the pattern of results shows that the same overall strategy is used with light touch. The latencies for correlated changes in CoP from light touch force fluctuations were similar by about 250 ms across all conditions, so Rabin et al (1999) suggested that there is a similar strategy that is used regardless of arm orientation. However, these latencies are subject to minor change depending on if touch is active or passive.

1.3.8 Active Versus Passive Touch

Active touch refers to situations where the participant intentionally touches a surface, while passive touch refers to when contact with the surface is caused by external action without movement or intention by the participant (Sozzi et al., 2012). Sciutti et al (1972) thought that an efference copy, which is the information derived from a copy of the motor commands that generate the exploratory hand movements that would occur dung active touch, may improve sway attenuation. However, it was found that sway attenuation amplitude is relatively similar during active and passive touch (Sozzi et al., 2012). There was only a minimal sway attenuation latency advantage of 160 ms, on average, which was found in favor of active touch (tibialis anterior EMG and ML CoP oscillation collapsed). Additionally, reductions in sway amplitude never occurred ahead of introduction to light touch cues. Due to the minimal change in latency and no effect on amplitude of sway, Sciutti et al (2010) and Sozzi et al (2012) concluded that the efference copy does not improve the effectiveness of light touch for attenuating sway. However, it is not known how active versus passive light touch cues differentially modulate reflexes from other sensory modalities.

1.3.9 Light Touch Modulation of Reflexes

Light touch cues are known to modulate balance relevant reflexes since they modify the excitability of the spinal proprioceptive reflexes (Lackner et al., 2000; Schieppati & Nardone, 1991). Vibrating the Achilles tendon leads to intramuscular stretch reflexes which cause backward or medial-lateral sway, depending on orientation of the vibrator and postural stance (Eklund, 1972). In the study by Lackner et al (2000), a vibrator caused a ML CoP displacement peaking at 2.5 cm, without light touch cues. The addition of light touch cues modulates these reflexes so that if participants are lightly touching a surface, there are no differences in CoP displacement between when there is vibration versus no vibration (Lackner et al., 2000). Furthermore, when participants had light touch cues, their CoP displacement was significantly reduced more than when there was no touch with and without vibration.

1.3.10 Conclusion: Light Touch Cues as a Source of Sensory Information for Balance Control

Light touch has been shown to effectively attenuate sway due to the cues about body motion. Therefore, introduction of light touch information can be used in a paradigm to study how sensory information is integrated for balance control, as it makes other congruent sensory inputs richer. Vestibular information can also provide balance relevant cues and will be discussed in the next section.

1.4 The Vestibular System

1.4.1 Introduction: Vestibular System Function

The vestibular system organs, located in the inner ear, convey information about how the head is rotating and translating in space to various areas in the CNS (Day & Fitzpatrick, 2005). The domains of vestibular function can be divided into 3 groups: (1) reflexive sensorimotor control of gaze and balance by the brain stem and cerebellum (2) perception of active and passive self-motion and balance by cortical and subcortical structures and (3) higher vestibular functions for cognition (Dieterich & Brandt, 2015). Functions of the vestibular system include perception of self and non-self-motion, movement, oculomotor control, spatial orientation, balance reflexes and so forth (Day & Fitzpatrick, 2005). These functions do not operate independently of each other. For example, reflexive control of gaze and balance must be integrated with voluntary movement and locomotion so that balance is maintained (Dieterich & Brandt, 2005). This section will describe how the vestibular system encodes and processes sensory information, with particular focus on contributions to balance control.

The vestibular system is comprised of the vestibular organs located in the inner ear, vestibular nuclei in the brainstem, several vestibular processing locations in the cortex and the associated pathways connecting these areas (Day & Fitzpatrick, 2005). There are ascending pathways from the vestibular organs to the vestibular nuclei and then to other areas of the brainstem, the thalamus, the cerebellum, and the cortex to manage perception of self-motion and orientation with respect to gravity (Dieterich & Brandt, 2005). The vestibular organs also provide sensory input that evokes brainstem mediated descending reflexive motor responses to adjust eye, head, and body to maintain balance (Dieterich & Brandt, 2005). To understand how the vestibular system contributes to balance control, vestibular deficits can reveal some of the role that it plays to maintain balance.

1.4.2 Vestibular Deficits

Patients with peripheral vestibular deficits often show instability during stance tasks, particularly following the acute stages of the deficit (Allum et al., 2001). The sway of patients with a vestibular deficit is side to side (in the roll plane), and they fall to the side of the deficit if it is unilateral (Allum et al., 2001). It was argued that patients with profound bilateral vestibular loss underestimate sway velocity, resulting in failure to control the amplitude of sway rather than in the selection of the appropriate response strategy (Allum et al., 2008).

Postural and gait ataxia after vestibular loss also occurs due to increased amplitudes of both reactive and anticipatory postural responses, which is called hypermetria (Horak, 2010). This can occur because proprioceptively triggered postural responses are too large without the influence of the vestibular system (Horak, 2010). These effects can be seen with the large size of muscle and center of pressure responses to surface translations, and consequent movement of the CoM (Horak, 2010).

These deficits reveal how vestibular information is needed in upright balance and that it is used in a multimodal manner; being that the size of proprioceptive postural responses is dependent on vestibular information. Location specific lesions will also be discussed which reveal how vestibular information is relayed and processed at different levels.

1.4.3 Vestibular Organs

Located in the inner ear are the vestibular organs; more specifically, the otolith organs and semicircular canals (Day & Fitzpatrick, 2005). The otolith organs consist of the saccule and utricle, which both encode linear acceleration and the gravity vector (Day & Fitzpatrick, 2005). The semicircular canals consist of the horizontal, anterior, and posterior semicircular canals which encode angular acceleration (Day & Fitzpatrick, 2005).

The membranous labyrinth within the inner ear is comprised of a fluid called endolymph and the vestibular organs (Martin, 2021). The otolith organs and semicircular canals contain hair cells which are in specialized regions called the maculae for the otolith organs and the ampullae for the semicircular canals (Martin, 2021). Linear or angular acceleration causes mechanical deflection of the stereocilia which are extensions of the hair cells, so that there is depolarization or hyperpolarization of the hair cell receptors depending on the direction of the movement (Martin, 2021). Acceleration magnitude is encoded by the firing rate of these hair cells (Martin, 2021).

Primary afferents extending from these receptors can be classified as regular or irregular according to the pattern of their resting discharge (Goldberg, 2000). The response of regular units is tonic and irregular units tend to be more phasic in nature (Goldberg, 2000). This means that regular units respond more preferentially to constant acceleration such as gravity while irregular neurons respond more preferentially to changes in acceleration stimuli (Goldberg, 2000).

The utricle and saccule have a gelatinous covering over hair cells in their maculae. Within the gelatin, there are calcium carbonate crystals embedded so that they rest on the stereocilia (Martin, 2021). The saccule and utricle are collectively referred to as the otolith organs because otolith is the term for the calcium carbonate crystals (Martin, 2021). Linear acceleration causes the crystals to deform the gelatinous mass and displace the stereocilia so that the linear acceleration is detected by the firing rate of the hair cells (Martin, 2021). The saccule and utricle both encode orientation in 2 dimensions based on their hair cell orientation (Day & Fitzpatrick, 2005). However, they are positioned at right angles to each other so that linear direction is encoded in 3 dimensions and acceleration is encoded by firing rate of the hair cells (Day & Fitzpatrick, 2005).

The hair cells of the semicircular canals are also covered by a gelatinous mass called the cupula where the stereocilia are embedded (Martin, 2021). Angular head movement causes the endolymph within the canals to move which displaces the gelatinous mass and the stereocilia of the hair cells so that the angular acceleration is detected by the firing rate of the hair cells (Day & Fitzpatrick, 2005). The three semicircular canals are also aligned at right angles to each other so that rotation in any direction can be resolved. (Day & Fitzpatrick, 2005).

The hair cells are innervated by afferent bipolar neurons whose cell bodies are in the vestibular ganglion (Martin, 2021). The axons of these bipolar neurons travel to the brain stem in vestibulocochlear nerve to the vestibular division of cranial nerve VIII and terminate in the vestibular nuclei (Highstein & Holstein, 2006; Martin, 2021).

There are also vestibular efferents which originate in the brainstem and terminate on hair cells (Mathews et al., 2017). The function of these efferents in vestibular and motor coordination remains under debate. One proposed function is their role in mediating corollary discharge. This is where vestibular efferents reduce the sensitivity of stimulus encoding during self-motion. (Mathews et al., 2017). During active head movement, a copy of the expected sensory results of a motor command (called reafference) is subtracted from the actual sensory signal to create a perception of the outside world (called exafference) (Angelaki & Cullen, 2008). This process is used by the nervous system to distinguish sensory inputs that arise from external sources from those that result from self-generated movements (Angelaki & Cullen, 2008).

Overall, the vestibular organs allow detection of how the head is rotating and translating in space, and this information converges onto the vestibular nuclei (Angelaki & Cullen, 2008). The vestibular system is unique in that central vestibular processing is highly convergent and multimodal (Angelaki & Cullen, 2008). The vestibular nuclei play a role in this convergence and multimodal integration, while relaying vestibular information to other areas of the CNS.

1.4.4 Vestibular Nuclei

The vestibular nuclei are the cranial nuclei for the vestibular nerve located in the medulla and pons of the brainstem (Martin, 2021). They are a location of initial vestibular processing and sensory integration (Martin, 2021). There are 4 vestibular nuclei: the superior, medial, lateral, and inferior vestibular nuclei (Martin, 2021). The vestibular nuclei integrate sensory information from the ipsilateral primary vestibular afferents with information from the contralateral vestibular nuclei, somatosensory organs via the dorsal column medial lemniscus pathway, and the cerebellum (Highstein & Holstein, 2006).

The vestibular nuclei collectively project fibers to the spinal cord, back to the cerebellum, thalamus, and the motor nuclei of the extraocular muscles (Highstein & Holstein, 2006). The superior, medial, and inferior vestibular nuclei project bilaterally to several sites within and around the ventral posterior nucleus of the thalamus and to the cortex (Martin, 2021). The lateral vestibular nuclei also contribute to thalamic projections, but to a lesser extent (Martin et al., 2021). These pathways can lead to further vestibular processing in the cortex, such as integration of vestibular and proprioceptive input to determine directional self-movement (Lobel et al., 1999). The superior nuclei are involved in reflexive eye gaze control pathways, with a projection to the oculomotor nucleus via the medial longitudinal fasciculus (Martin, 2021). The vestibulocochlear reflex is mediated by this pathway, where head movement is compensated by an eye rotation to keep retinal images stable (Martin, 2021). The lateral and medial nuclei also have projections to motor nuclei of the extraocular muscles (Martin, 2021). However, the lateral and medial vestibular nuclei most notably give rise to descending vestibulospinal pathways to the spinal cord which reflexively help maintain balance (Martin, 2021).

Lesions throughout the brainstem can give insight into how the vestibular nuclei and their associated projections contribute to balance. Lesions in the medulla, which is the lower part of the brain stem, cause falling to the lesioned side (Dieterich & Brandt, 2005). This is because the descending influences via vestibular reflexes are affected. Lesions of the vestibular nuclei themselves cause ocular tilting during the vestibular ocular reflex so that it is difficult to maintain stable gaze during head movement (Dieterich & Brandt, 2005). Lesions between the vestibular nuclei and the midbrain cause tilts corresponding to the false perceived verticality and ocular skew torsion (Dieterich & Brandt, 2005). The lesions of the brain stem and vestibular nuclei provide insight into how they function and are needed for balance control. There are still unknowns about the vestibular nuclei's role in sensory integration.

Since the vestibular nuclei are a location of converging vestibular and somatosensory input, it is thought that this could be a location of where sensory integration can be influenced (Naranjo et al., 2016). Potentially, modulation of vestibular or somatosensory input could be partially mediated by the vestibular nuclei. The vestibular nuclei also have connections to the parabrachial nucleus network, which has been hypothesized to maintain a context representation of converging balance relevant sensory information, such as somatosensory, visual and vestibular information inputs (Balaban & Thayer, 2001). The reticular formation also receives input from the vestibular nuclei along with the cerebellum (McCall et al., 2017). Since the vestibular nuclei, parabrachial nucleus, and reticular formation all receive converging multi-modality sensory information that includes vestibular input, they all could be candidates where integration of vestibular input could be influenced. However, the reflexes themselves are mediated by the lateral and medial vestibulospinal pathways, which originate in the lateral and medial vestibular nuclei.

1.4.5 Vestibulospinal Tracts and Reflexes

The vestibular nuclei have two functionally distinct descending projections; the lateral and medial vestibulospinal tracts (Martin, 2021). The lateral vestibulospinal tract descends ipsilaterally from the lateral vestibular nuclei to the spinal ventral column in the white matter of all spinal levels and forms disynaptic and polysynaptic connections with upper and lower limb motor neurons (Forbes et al., 2013; Shinoda et al., 2006). The lateral vestibulospinal tract helps to maintain an upright and balanced posture by stimulating extensor motor neurons in the legs, trunk and arms (Martin, 2021). The medial vestibulospinal tract descends from the medial vestibular nuclei bilaterally in the ventral column white matter to the cervical and upper thoracic spinal cord to form disynaptic connections via commissural neurons at neck or axial motoneurons (Forbes et al., 2013; Shinoda et al., 2006). This tract may also receive input from the superior and inferior nuclei and plays a role in controlling head position in relation to eye position and maintaining balance (Khan & Chang, 2013; Kheradmand & Zee, 2012; Martin, 2021). These vestibulospinal tracts are required to mediate vestibular reflexes which help to maintain balance and coordinate eye movements (Martin, 2021). The primary neurotransmitters for excitatory vestibular nuclear projections include glutamate, whereas the inhibitory projections are either glycine or γ-aminobutyric acid (GABA) (Kandel et al., 2021).

The vestibulocollic reflex involves both lateral and medial vestibulospinal tract neurons (Highstein et al., 2004). It is a compensatory response that stabilizes the head in space. During everyday activities, this stabilizing response is evoked by head movements that typically span frequencies from 0 to 30 Hz (Forbes et al., 2020). The reflex is meant to oppose unwanted oscillations or motions induced by external perturbations. Simultaneously, these circuits are designed to suppress reflex responses to active and intended head motions (Highstein et al., 2004).

The vestibular evoked reflexes controlled by the lateral and medial vestibulospinal tracts lead to predictable responses that can be measured, through methods such as muscle activity (EMG) (Blouin et al., 2011; Lim et al., 2017), GRFs or sway kinematics. The cerebellum is also known to modulate these vestibular reflexes.

1.4.6 Cerebellar Contributions

The vestibulocerebellum is the portion of the cerebellum that is involved in modulating vestibular information (Martin, 2021). It receives information from primary vestibular afferents and secondary vestibular neurons originating from the vestibular nuclei (Martin, 2021). The vestibulocerebellum functions in coordinating neck muscle function with eye control via the medial vestibulospinal tract and maintaining balance via the lateral vestibulospinal tract (Martin, 2021). The cerebellum also receives information from other sensory modalities, such as the somatosensory system (Martin, 2021). The integrative nature of the cerebellum allows it to be used in making sensorimotor adaptations during error correction tasks (Thach et al., 1992). This could make the cerebellum another prime location where sensory integration could be influenced.

1.4.7 Vestibular Processing Locations in the Cortex

All the vestibular nuclei project, via the thalamus, to several cortical regions. Imaging studies reveal these regions when they are activated with vestibular information (Lobel et al., 1999). The functions of these areas were determined by measuring neuronal responses in these areas from animals, such as monkeys, in response to sensory modality specific stimuli (Schwarz & Fredrickson, 1971). These areas include the temporoparietal junction, central sulcus, intraparietal sulcus, parietoinsular cortex, and Brodmann areas 3a and 2v (Lobel et al., 1999). Area 3A receives converging vestibular and proprioceptive input and is involved in integration of these senses to determine directional self-movement (Lobel et al., 1999). More specifically, this area receives head positioning cues along with proprioceptive afferents from the neck muscles (Martin, 2021). Area 2V receives deep somatic afferents and responds to optokinetic stimulation (Schwarz & Fredrickson, 1971). The intraparietal sulcus involves vestibular - visual integration, allowing processing of spatial information, such as how the body moves through the environment (Lobel et al., 1999). Cortical lesions of these areas cause perceptual tilts and the pusher syndrome, which is when there is a push away from the damaged side due to the inability to perceive vestibular information (Dieterich & Brandt, 2005).

Vestibular information can also be relayed to additional association areas or cognitive centers for further processing. This includes the hippocampus/parahippocampus, where vestibular information can help in cognitive contributions such as spatial memory, orientation, and navigation (Dieterich & Brandt, 2005). Furthermore, the posterior parietal cortex also receives vestibular input and is referred to as an ‘associative’ cortical region because it is neither strictly sensory nor motor (Lobel et al., 1999). It is known to combine inputs from a number of areas including somatosensory, auditory, visual, motor, vestibular and prefrontal cortices (Whitlock, 2017). Due to its various inputs and function in visual-vestibular integration, it plays a role in spatial attention, spatial navigation, decision making, working memory and early motor planning (Clower et al., 1996; Whitlock, 2017). Lesions to the posterior parietal cortex result in lack of awareness of bodily posture or the position of limbs, showing that this could also be a likely location where sensory integration can be influenced (Whitlock, 2017).

There are also projections from cortex to the vestibular nuclei, shown by stimulating cortical areas in cats and measuring neuronal responses in the vestibular nuclei (Wilson et al., 1999). This provides routes for higher level processing centers in the cortex to influence vestibulospinal pathways. The cortex could play a role in modulating vestibular responses by influencing these descending pathways.

1.4.8 Conclusion: Vestibular Input and Integration with Other Modalities

The vestibular system is unique and plays many different roles; mediating from the most automatic reflexes to spatial perception and motor coordination (Angelaki & Cullen, 2008). All natural stimuli that provoke the vestibular system also provoke other sensory modalities, meaning that vestibular information is used in combination with other sensory information to perform complicated tasks such as maintaining balance.

1.5 Electrical Vestibular Stimulation as a Probe for Sensory Conflict

1.5.1 Introduction: Electrical Vestibular Stimulation Function

Electrical vestibular stimulation (EVS) can be used to probe the vestibular system, as it is a non-invasive electrical stimulation delivered to the vestibular system that evokes vestibular balance responses in isolation from other sensory modalities (Fitzpatrick & Day, 2004). EVS is a useful tool to probe vestibular processing, as the EVS input can remain constant so any changes in vestibular responses reflect central reflex modulation (Blouin et al., 2011; Horslen et al., 2014; Lim et al., 2017; Tisserand et al., 2018). For example, decreased weighting of vestibular information can be expressed by reductions in amplitude of vestibular evoked reflexes shown through reduction in EMG amplitude (Blouin et al., 2011), sway amplitude or in variation of CoP (Horslen et al., 2014). This means that EVS can be used to characterize changes in vestibular weight. This section will discuss how EVS functions and specifically why EVS can be used as a tool to measure changes in vestibular weight.

EVS electrodes are placed on the mastoid process and an electrical current is produced, most commonly around 1 mA so that responses are evoked with minimal discomfort (Fitzpatrick & Day, 2004). EVS is thought to cause hyperpolarization at the neuroepithelial level where the hair cells are embedded, bypassing the mechanical transduction of hair cells (Goldberg et al., 1984). Bilateral EVS can be achieved when there is an anodal electrode placed on one mastoid process and a cathode electrode placed on the opposite mastoid process (Fitzpatrick & Day, 2004). When the current is delivered, the perception of a ‘roll’ head movement is felt towards the cathode side (Fitzpatrick & Day, 2004). This causes postural responses, such as whole-body tilt, to be towards the anodal electrode (Fitzpatrick & Day, 2004). Vectorially summing the responses to EVS from the entire semicircular canal neuron population reveals a whole-body rotation about an antero-posterior axis, which is seen through the tilting motion (Day & Fitzpatrick, 2005). The otolith organs do not contribute much to the response, but the vectorial sum may suggest a small lateral acceleration (Day & Fitzpatrick, 2004). Since the vestibular organs are positioned slightly below the horizontal plane, participants’ heads are often positioned 18 degrees above Reid’s plane (inferior margin of the orbit to the auricular point), to get a pure roll response (Fitzpatrick & Day 2004).

Galvanic vestibular stimulation is a form of EVS that has traditionally been used to study vestibulo-motor control (Fitzpatrick & Day, 2004). It is a direct form of current that has a level shift in the signal, such as square pulse waves (Fitzpatrick & Day, 2004). EVS also includes alternating currents, where the signal alternates around a mean (Fitzpatrick & Day, 2004). Examples of this include sinusoidal and noisy stochastic signals (Fitzpatrick & Day, 2004). These types of signals have been used in more recent years because they are more comfortable, less nauseating and they don't require long stimulation times to see responses needed for analyses (Dakin et al., 2007).

Square wave pulse currents are discrete stimulations of bipolar galvanic current, which produce a tonic vestibular asymmetry (Coats & Stoltz, 1969; Day et al., 1997). This means that a participant will only lean towards the anodal stimulus. Static tilt responses that include all body segments can be seen while using galvanic stimuli, where the tilt is in opposition to the illusory perception of head tilt caused by the stimulus (Fitzpatrick & Day, 2004). Greater stimulation current amplitudes lead to greater whole-body tilts while longer stimulations lead to longer sway responses (Fitzpatrick & Day, 2004). Sinusoidal varying bipolar galvanic currents can lead to sinusoidally varying postural sway, where the leaning response occurs in different directions depending on the polarity of the current (Pavlik et al., 1999). Stochastic stimuli differ from sinusoidal stimuli in that the signal fluctuates randomly with multiple frequencies and amplitudes (Dakin et al., 2007). This dissertation will discuss all forms of EVS, and so will use the term EVS for the remainder of this paper.

1.5.2 Sensorimotor Responses to Electrical Vestibular Stimulation

Short-latency EMG responses are seen in response to direct or alternating current at about 40 ms in the arm and at about 55–65 ms in the leg, whereas the medium latency responses appear in the lower limbs at 110-120 ms and in opposite polarity to the short latencies (Britton et al., 1993; Fitzpatrick et al., 1994; Watson & Colebatch, 1997). These events in the GRFs from a force plate can yield longer latencies, due to neuromuscular delays (Horslen et al., 2014; Mian & Day, 2009). Short latency responses can be detected at around 150 ms and medium latencies can be detected around 300- 350ms (Horslen et al., 2014; Mian & Day, 2009). Both short and medium latency response amplitude increase by increasing stimulus amplitude. Prolonging stimulus duration also prolongs the medium latency response and thus the whole-body sway response but has little effect on the short latency response (Britton et al., 1993).

Previously, there was disagreement as to where the short and medium latency peaks originated from. Britton et al (1993) suggested that the short latency peaks originate from the reticulospinal pathway while the medium latency peaks are of vestibulospinal origin. The reticulospinal pathway mediates responses such as the startle response, which is a cluster of bilateral defensive responses to a sudden, intense stimulus (Rothwell, 2006). In comparison, vestibular responses are direction specific (Mian & Day, 2009). Since the direction of short and medium latency peaks is dependent on head orientation, it is suggested that there is a vestibular influence of both peaks (Mian & Day, 2009).

The medium latency peaks of the balance response is characteristic of the whole corrective response to EVS in comparison to the shorter latency responses (Britton et al., 1993; Fitzpatrick et al., 1994; Mian & Day, 2009; Pastor et al., 1993). Potentially, the shorter latency response may be involved in the muscle activity required to displace the CoP and propel the CoM towards the leg that the body is swaying towards while the medium latency response is involved in that leg taking on most of the vertical load. This could be similar to stepping, where there is an initial increase in vertical loading on the swing leg with a ML CoP displacement toward this leg to propel the CoM toward the stance limb (McIlroy & Maki, 1999). The stance leg then takes on the vertical loading and CoP.

Measuring how short and medium latency responses change can be used to identify how trial conditions influence vestibular responses. Traditionally, direct current signals are used to measure these short and medium latency responses, with trial averaging approaches (Britton et al., 1993; Fitzpatrick et al., 1994; Pastor et al., 1993). However, stochastic EVS signals and linear system approaches can be used as an alternative, since correlational analyses draw out these responses that may not be easily observed (Dakin et al., 2007, 2010). Figure 2 demonstrates how a pooled cumulant density estimate can be used to reveal short and medium latency responses while using a stochastic signal.

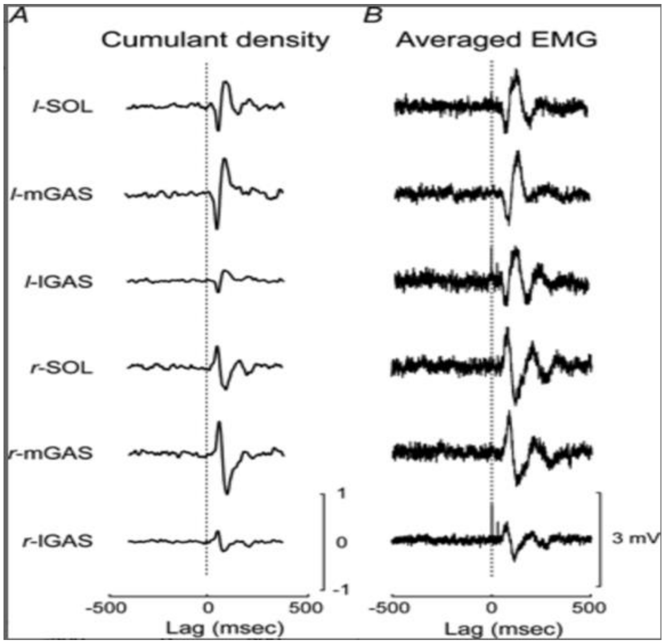

Figure 2: Short and Medium Latency Peaks in Both Averaged EMG and Cumulant Density Plots from Dakin et al (2007).

A: Represents a pooled cumulant density estimate between stochastic EVS and EMG responses. This is a time-dependent correlational analysis. The vertical dashed line indicates zero lag mark between the SVS and muscle activity. B: Represents spike trigger averaged EMG corresponding to the square-wave pulse trials. The vertical dashed line indicates the square wave EVS pulse. Both methods reveal the short and medium latency responses.

1.5.3 Modifications to Electrical Vestibular Stimulation Responses

The response to EVS is modifiable by many different factors. These include head and trunk position (Hlavacka & Njiokiktjien, 1985; Lund & Broberg, 1983; Pastor et al., 1993), standing posture (Day et al., 1997; Marsden et al., 2003), support surface properties (Fitzpatrick et al., 1994), and the availability of other sensory modality information (Baldissera et al., 1990; Britton et al., 1993). However, EVS responses cannot be modified over short periods of time (Guerraz & Day, 2005).

It is known that when the head is facing forward, there are sway responses in the ML plane. Having the head turned 90 deg to the right or left results in an AP sway response (Lund & Broberg, 1983; Mian & Day, 2009; Pavlik et al., 1999). This is because the direction of the evoked sway is approximately in the direction of the inter-mastoid line (Hlavacka & Njiokiktjien, 1985).Additionally, it has been revealed that the CNS only responds to the EVS when it is engaged in a task that balances the unsupported head and body (Britton et al., 1993). Responses may also vary depending on the muscles that are being used to maintain balance. For example, when the arm is used to stabilize the body by touching a handrail, vestibular evoked responses can be visible in the triceps brachii, which would otherwise not respond to EVS (Baldissera et al., 1990; Britton et al., 1993).

Information from other sensory modalities can be used to modulate responses. Vestibular responses to stimuli of 1, 2 and 4mA are smaller in amplitude when vision is made available, compared to when it is not (Fitzpatrick et al., 1994). However, the mean pre-stimulus EMG levels are significantly greater (around 70 %) with the eyes shut (Fitzpatrick et al., 1994). This is primarily what leads to larger responses, not the change in short or medium latency responses. Fitzpatrick et al (1996) conducted another study which indicated that vestibulo-muscular coherence does not increase with eye closure, proving that the EMG background levels were what accounted for larger short or medium latency response amplitudes.

When proprioceptive input is nulled by participants standing on foam, responses are larger (Fitzpatrick et al., 1994; Wardman et al., 2003). With an unstable surface, pre-stimulus EMG levels were 157% larger (Fitzpatrick et al., 1994). The short and medium latency response are also significantly larger when standing on an unstable support, and this remains larger when scaled relative to the pre-stimulus level. In the follow-up study by Fitzpatrick et al (1996) vestibulo-muscular gain was shown to be increased by 102% when standing on foam.

As shown, reducing the availability or reliability of other sensory cues enlarges EVS responses. The opposite may also be expected; where introducing reliable balance cues from other sensory modalities that conflict with EVS may reduce responses (Weech et al., 2020). The dynamics of introducing or withdrawing these modifications over time remain unknown. For example, it is not known how long it takes once proprioceptive input is nulled by a compliant surface to reach that 102% reduction in vestibulo-muscular gain (Fitzpatrick et al., 1996). However, without conflicting sensory cues, EVS responses are not attenuated with short periods of time.

The response to EVS is not different for unexpected or self-triggered stimuli and this effect does not appear to change with time (Guerrez & Day, 2005). It is not known for sure why this is, but there have been several suggestions made.

The vestibular system detects unambiguous signals of the acceleration of the head in space and therefore always signals motion of self (Guerrez & Day, 2005). In contrast, the visual system carries information regarding both self-motion and object motion (Guerrez & Day, 2005). A displacement of either the body or the visual scene can show similar retinal visual scenes (Guerrez & Day, 2005). Postural responses to external object motion are usually inappropriate, so it can be suppressed (Guerrez & Day, 2005). Postural responses to self-motion are required to maintain balance, which is why they might always occur when the vestibular system is activated through EVS (Guerrez & Day, 2005).

Additionally, the reflexive responses to EVS may not be cognitively modulated since EVS responses are considered a 'first line of defense' during this perturbation to balance (Guerrez & Day, 2005). EVS signals are also large and robust sensory perturbations that may be difficult to filter out without completely suppressing the vestibular system. Similarly, sudden displacements of the support surface are considered robust perturbations and evoke fast reflexive muscle responses prior to voluntary muscle activations (Horak et al., 1989). These automatic muscle responses driven in part by somatosensory inputs are also not cognitively modulated (Guerrez & Day, 2005). The segmental reflexes and vestibular reflexes are meant to resist sudden perturbations before voluntary muscle action since they take more time for the CNS to execute.

Fitzpatrick and Day (2004) also postulated that there could be a different entry level of vestibular input to the balance control system, so that these signals are not attenuated with time while most other sensory cues are attenuated with time, such as visual or somatosensory input. They also suggested that there could be decoupling of the efferent signal from the reafference that comes from the sway response. This would mean that the motor commands are not matching the copy of expected sensory results, so the proper ex-afference signal would not be accurate. It would be difficult to attenuate vestibular responses without being able to properly perceive how the vestibular responses are interacting with the environment.

1.5.4 Conclusion: Electrical Vestibular Stimulation as a Probe for Sensorimotor Integration

EVS is an effective tool to probe the vestibular system in isolation and can help reveal how the vestibular system contributes to balance control. This can be done by measuring modifications to sensorimotor responses to EVS under different conditions. One way this tool can be used to reveal insights into the vestibular system and sensorimotor integration is by modifying sensory input from other sensory modalities while using EVS.

1.6 Sensorimotor Control of Balance

1.6.1 Introduction: Sensory Weighting

As mentioned, the combination of sensory signals in the CNS is done by adding each sensory input into a weighted sum, and these weights are typically not equal and may change (Blouin et al., 2011; Horslen et al., 2014; Luu et al., 2012; Peterka, 2002; Tisserand et al., 2018). While there is an understanding that sensory feedback is typically not equal between the modalities, the research focusing on what causes changes in these relative weights is still being investigated. This section will describe the models of sensorimotor integration that have been developed along with key studies that demonstrate how the weighting of a particular sensory modality can change and why.

1.6.2 Model of Sensorimotor Integration from Peterka 2002

Peterka (2002) conducted a study to model sensorimotor control of balance, which describes how sensory information is weighted when being summed together. This is shown through the characterization of relationships between sensory input and motor outputs with a linear equation. The more heavily weighted sensory contributions result in greater sensitivity to the sensory input, exemplified by larger motor responses. This study also demonstrates that the weights of sensory information can change so that sensory information either contributes more or less to balance control, depending on context of the environmental situation. When sensory cues become disruptive to balance control, they tend to be downweighted by the CNS. Although this study was conducted in 2002, it has set balance control framework that current studies can expand on. Peterka (2002) developed a computational model that fits the behavior observed in this study and can be applied to other studies focusing on balance control, shown in figure 3.

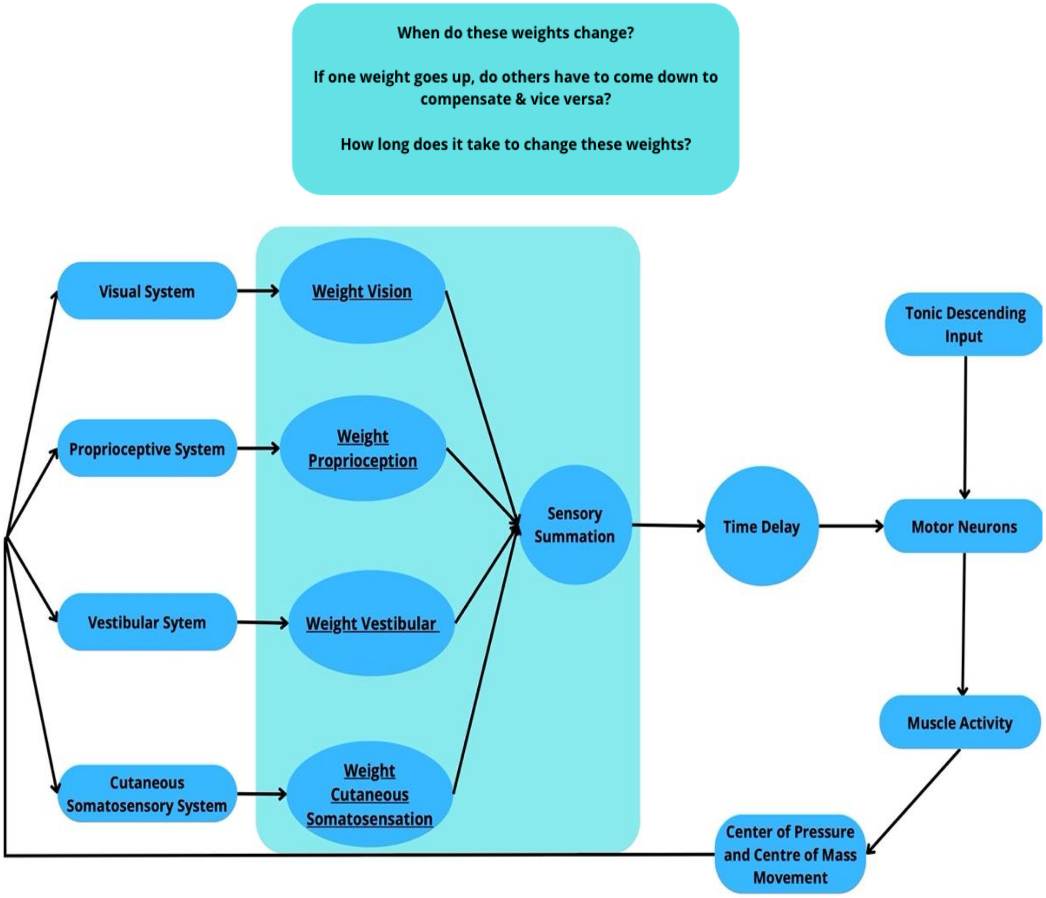

Figure 3: Model of Sensorimotor Integration for Balance Control Adapted from Peterka (2002).

This is an adapted model of the sensorimotor control of balance from Peterka 2002. Sensory feedback is achieved from visual, proprioceptive, vestibular, and cutaneous somatosensory information. This simple model predicts that all the senses detect the stimulus and pass this on for sensory summation. Feedback from each modality is then multiplied by a weight that determines the magnitude of how much each modality contributes to the weighted sum. There are time delays through this process which involve latencies to sensory transmission, processing, and muscle activation. The sensory feedback is integrated by the CNS to generate a motor response through the upper or lower motor neurons and balance-relevant muscles. There are also descending commands that influence tonic muscle activation to maintain a degree of stiffness. Muscle activity works to control center of pressure so that it can counteract movement of the center of mass and minimize destabilizing sway. The movement of the CoM and CoP is also monitored by the sensory feedback modalities, which completes the loop of this model. Questions that remain unanswered include: 1) when do these weights change? 2) If one weight goes up, does there have to come down to compensate and vice versa? 3) How long does it take to change these weights?

Peterka (2002) used continuous support surface tilts, visual surround rotational perturbations, or combinations of both at different rotation amplitudes to evoke sway in the AP direction. These kinds of continuous perturbations are appropriate to study balance for quiet stance since it is also a continuously active process. The continuous support surface tilts are thought to primarily perturb the proprioceptive system while the visual surround rotational perturbations are thought to perturb the visual systems. The vestibular system was not targeted by any perturbations. A technique called sway referencing was also used while the opposite sensory system was stimulated, which is where the support surface or visual surround systems continuously tracks and matches the participants' AP body-sway angle (for example, visual system is perturbed while proprioceptive system is sway referenced). Sway-referencing alters the normal relationship between body sway and proprioceptive cues (during support surface sway-referencing) or visual cues (during visual surround sway-referencing) and is thought to reduce the contribution of these sensory orientation cues.

Peterka (2002) found that there was a linear relationship between stimulus amplitude and the AP sway response. However, once the stimulus amplitude increased past a certain level, there was a plateau in the sway response. Body sway was larger than stimulus amplitudes at 0.5, 1 and 2 degrees but it was clearly smaller than the stimulus at 4 and 8 degrees. This means that the stimulus response relationship became non-linear and there was a response saturation. Peterka (2002) concluded that this was because the increasingly large stimuli became more disruptive in maintaining balance, and so the sensory cues were downweighted (or gain was decreased) in their contribution to the summation by the CNS.

Neither visual nor proprioceptive stimuli could probe or remove vestibular contributions, so Peterka (2002) also included a sample of participants with vestibular loss to understand the role of vestibular inputs on re-weighting effects. This also helps to reveal differences in sensory re-weighing between neurotypical populations and those with a sensory deficit. While participants with normal vestibular functioning exhibited the response saturation and nonlinear stimulus response behavior, participants with vestibular loss had linear stimulus response behavior across all stimulus amplitudes. At the highest stimulus amplitudes, those with vestibular loss showed significantly larger sway than those with normal vestibular functioning and tended to fall over. Peterka (2002) interpreted this by suggesting that those with normal vestibular functioning were able to downweight proprioceptive and visual information because the participants were able to increase weighting of vestibular information in a compensatory manner. Those with vestibular loss were not able to do this, which is why they did not downweight proprioceptive or visual cues significantly.

Peterka (2002) has demonstrated that studying changes in sensory weighting can reveal insights into the sensorimotor control of balance. However, the perturbations to visual and proprioceptive systems were not purely targeting those systems alone. For example, support surface tilts also influence the vestibular and visual systems as the body begins to tilt. The visual field changes associated with that tilt and the vestibular organs will detect the movement of the head. Sway referencing also doesn’t completely null the input from the targeted sensory system. It is not clear from this study if these changes in gain would be seen if perturbing an isolated sensory system.

Peterka (2002) also approximated what the sensory weights would be if they summed to 1. It is often assumed that sensory information sums to 1 or some set value, but it is not clear that this must happen. Potentially, this value could be surpassed, meaning that gains of other sensory modalities do not have to be perfectly adjusted to reach this value when another changes. This uncertainty is magnified in a situation such as when new sensory information is introduced that was not previously available. It is possible that the gains of all sensory modalities must be adjusted in to accommodate the incoming sensory information, or they could remain unchanged. It is not fully understood how gain changes of a single sensory modality influence gain changes of the remaining balance relevant sensory modalities.

1.6.3 Optimal Sensory Weights

It is difficult to predict if there is an optimal set of sensory weights for neurotypical individuals quietly standing in a well-lit environment with a firm base of support, but several other studies along with the estimates of sensory weights from Peterka (2002) can provide insight into what conditions yield heavier reliance on certain modalities than others.

A study by Fitzpatrick and McCloskey (1994) measured perceptual thresholds for sway of the proprioceptive, visual and vestibular system. To examine vestibular inputs alone, vision was excluded and the whole body was moved with the ankles in a fixed position. To examine visual inputs alone, the body was kept stationary, and a 'room' was moved around the participants to simulate the relative visual-field movement that occurs during standing. To examine proprioception from the legs alone, participants were held stationary, and they balanced a load that was equivalent to their own body using their ankles. In this situation, perturbations were applied to the 'equivalent body,' and these could only be perceived from the resulting ankle movements. The thresholds for the perception of sway during standing with all sensory information available were very small, typically 0.003 rad at a velocity of 0.001 rad/s. When sensory input was limited to proprioception from the legs, the thresholds for the perception of passive ankle movements were equivalent to the thresholds for the perception of sway during standing with all sensory inputs available. The visual thresholds for perceiving movement were higher than the proprioceptive thresholds at slower velocities of movement, but there was no difference at higher velocities. The vestibular thresholds were an order of magnitude greater than the visual or proprioceptive thresholds and above the largest sway movements that were recorded during normal standing. These findings indicate that, during normal standing, proprioceptive inputs from the legs provide the most sensitive means of perceiving postural sway. At higher velocities within the range of velocities of normal sway, visual inputs provided similarly sensitive means of perceiving sway. Fitzpatrick and McCloskey (1994) would argue large disturbances of posture would be required before vestibular mechanisms could provide perceptual information about body sway, based on these results. Although this study does not directly measure gains of sensory input, it can show how proprioceptive input contributes heavily to balance control based on its sensitivity. This study suggested that vestibular sensitivity increases as there are increasing perturbations to balance control, such as in the study conducted by Peterka (2002).

In Peterka's (2002) model, the weight of vision was shown to be 0.77 at lowest visual stimulation amplitudes while proprioceptive input was sway referenced so that it had a gain of approximately 0. This also led to the assumption that vestibular inputs were weighted at 0.23, by subtracting 0.77 from 1. At the highest visual stimulation amplitudes, weight of vision was shown to be 0.13 while vestibular weight increased to 0.87. At lowest proprioceptive stimulation amplitudes with vision sway referenced to have a gain of about 0, proprioceptive input was weighted at 0.7 and vestibular input was weighted at 0.3. At the highest proprioceptive stimulus amplitudes, proprioceptive input was weighed at 0.24 while vestibular input increased to 0.76. This demonstrates that with increasing stimulus amplitudes, the contribution of both visual and proprioceptive input decreases while the vestibular input is thought to increase. Although these estimated weights give some insight into how sensory information is weighted, sway referencing is an extreme situation that would rarely occur in natural environments. Peterka (2002) also assumes that sensory gains sum to 1, which may not be true. Therefore, this study does not demonstrate how sensory information is typically weighted during quiet standing conditions.

Overall, these studies suggest that proprioceptive and visual input contribute heavily to standing balance, while vestibular weighting increases in balance compromising situations. It also demonstrates that it is difficult to determine the exact contributions from each of the modalities, especially as these contributions can change. There are many other studies that measure changes in sensory weighting that build off this understanding to learn more about how the senses are integrated during balance control.

1.6.4 Studies Looking at Changes in Sensory Weighting

The study by Peterka (2002) used perturbations that did not isolate a specific sensory system. However, previous studies have looked at changes in weight isolating a specific sensory system to understand their sensory dynamics. There is research focusing on the gain of visual (Jeka et al., 2008), somatosensory (Jeka et al., 1998; Mildren et al., 2019) and vestibular input (Horslen et al., 2014).

The somatosensory system can be targeted by either looking at sway caused by cutaneous somatosensory cues or proprioceptive cues (Jeka et al., 1998; Mildren et al., 2019). Cutaneous somatosensory cues stimulate mechanoreceptors through touch pressure while proprioceptive cues stimulate stretch or tension receptors. The relationships between the frequencies of these stimuli and the sway response can be measured to calculate gains of these sensory systems via linear system analysis.

Jeka et al (1998) conducted a study that identified the relationship between oscillating motion of a contact surface to the fingertip and the resulting velocity and position dependent head and body sway. Head, center of mass, and center of pressure displacement were measured as the contact surface moved rhythmically at 0.1, 0.2, 0.4, 0.6, and 0.8 Hz. Head and body sway were highly coherent with contact surface motion at all frequencies except 0.8 Hz (above 0.95). This shows that light touch cues can drive sway in a linear relationship.

Similarly, Mildren et al (2017, 2019) looked at gain of proprioceptive input and specific muscle activity demonstrating that it is possible to calculate transfer functions at the single muscle level, non-invasively. They used noisy Achilles tendon vibration to evoke muscle activity in the soleus and medial gastrocnemius. When a person stands freely with their eyes closed, vibrating the Achilles tendon generates intramuscular stretch reflexes like those that would be observed if the body were swaying forward. In response, the person sways backward by activating the triceps surae to compensate for the illusory sway forward. They found that the soleus units demonstrated higher gain across all amplitudes of the noisy stimuli across a frequency band of 10-100 Hz, determining that soleus plays a larger role in responding to tendon vibration compared to the other muscles of the triceps surae. These studies demonstrated that proprioceptive gain can be estimated for individual muscles.

Studying the somatosensory system with linear systems analysis techniques has allowed researchers to understand more about how this information is encoded within the CNS and used for balance control. Measuring the gain of the vestibular system is also well studied and has also allowed insights into how this information contributes to balance control.

Gain of the vestibular system has often been examined using EVS, and I will review several papers that use this technique. Vestibular gain has been measured during walking to show how it is modulated through the gait cycle and when stopping or starting walking (Blouin et al, 2011; Dakin et al., 2013; Forbes et al., 2016; Tisserand et al., 2018). Vestibular gain has also been measured in static situations, focusing on how it changes due to increases in threatening conditions (Horslen et al., 2014; Lim et al., 2017; Naranjo et al., 2016). Furthermore, vestibular gain has been measured when afferent signals of body motion are decoupled from motor commands to maintain balance (Luu et al., 2012; Rasman et al., 2021). Lastly, I will discuss how vestibular gain changes after 12 weeks of weekly exposure to EVS (Dilda et al., 2014).

Blouin et al (201l), Dakin et al (2013), and Forbes et al (2017) found that vestibulo-muscular coupling is phasically modulated during locomotion. Blouin et al (2011) found that muscle activity (EMG) from the medial gastrocnemius is coherent with EVS over a 2-20 Hz bandwidth during the stance phase of locomotion (21-23% of gait cycle). However, during other phases of the gait cycle, including phases with more muscle activity such as the push off phase (38% of gait cycle), coherence is non-significant. These findings are depicted in Figure 4, showing time-dependent coherence and gain. This study demonstrates that modulation of vestibulo-muscular coupling is not dependent on modulation of muscle activity. Dakin et al (2013) expanded on these findings to other muscles of the hip, knee, and ankle to see how they were modulated through the cycle. Furthermore, Forbes et al (2017) found that that vestibular influence on locomotor activity is modulated independently in each limb. They used a split belt paradigm (2 speeds of 0.4 and 0.8 m/s) to assess vestibular-motor coupling within the different limbs. It was found that peak coherence decreased by about 15–45% and occurred at about 13–28% (200–429 ms) earlier in the stride cycle when the limb was moving at 0.8 compared with 0.4. m/s. These study results suggest that the phase- and muscle-specific influence of vestibular signals on locomotor activity is organized according to each muscle's functional role in body stabilization during locomotion. These studies also demonstrate how vestibular gain can be modulated in a cyclic fashion.

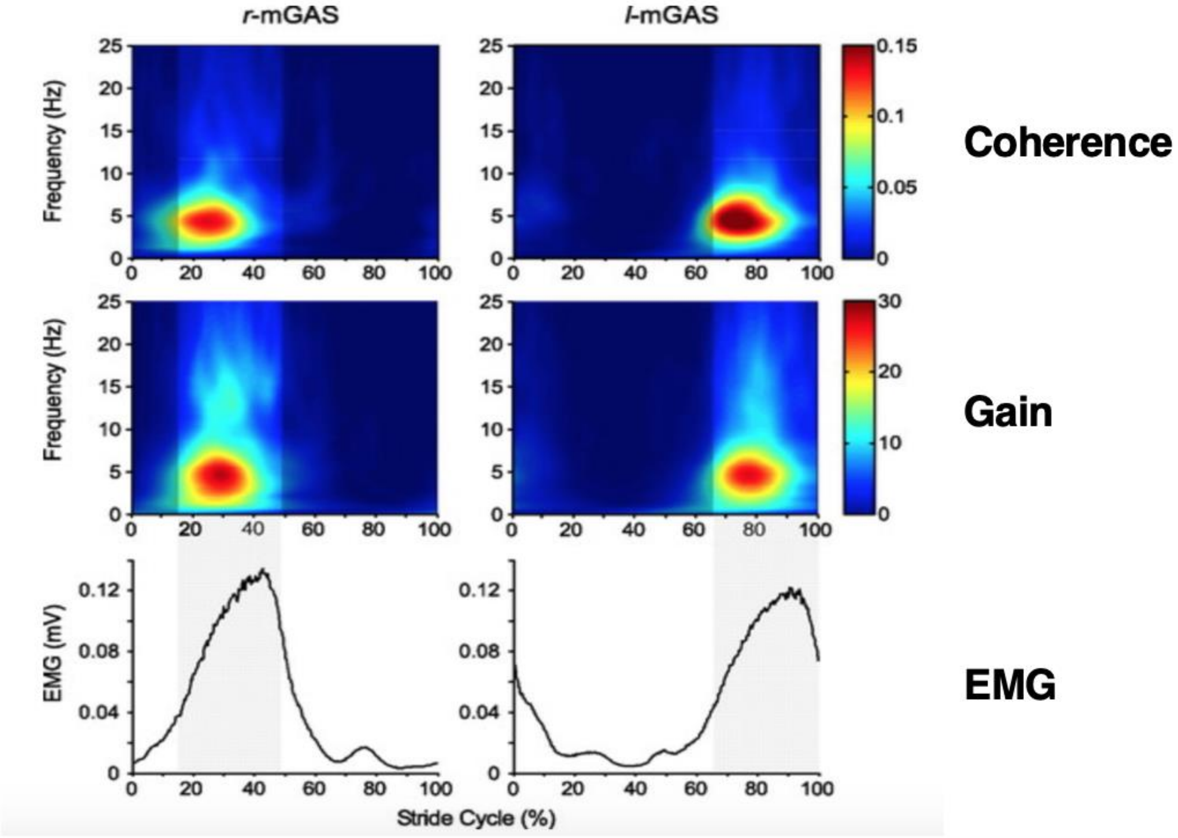

Figure 4: Time-Dependent EVS-EMG Coherence and Gain from Blouin et al (2011).

The top graphs show averaged time-dependent coherence between EVS and left and right medial gastrocnemius EMG. The middle graph shows the average time-dependent gain between EVS and muscle signals. The bottom graphs show the modulation of the corresponding muscle during the stride cycle. All figures are represented with time 0 showing right heel strike. The color bar represents the amplitude of the coherence and gain, and the shaded area, the period of single-limb support for the right and left leg. Significant coherence and gain were observed during the period of stance phase of the stride cycle (i.e., while the corresponding ankle extensor was active), both of which reached maximal amplitude before background EMG reached its peak amplitude.

Tisserand et al (2018) showed that humans unconsciously reduce the influence of the vestibular system in balance to transition between motor states. This follows optimal feedback theory, which states that transitions require the disengagement of one motor control policy before the implementation of another (Scott, 2004; Todorov & Jordan, 2002). In simpler terms, humans subconsciously ‘stop balancing’ before they start moving and ‘stop moving’ before they start balancing again. Tisserand et al (2018) looked at vestibulo-motor gain changes during transition periods such as gait initiation and termination. Participants were asked to stand still, then walk along a pathway at a preferred speed for 3.5 minutes and stop at the end of the path. Vestibular gain decreased immediately before participants started walking and before coming to a stop. Before walking, the EVS-GRF coherence decreased in all participants below the 99% confidence limit about 0.435 s prior to the onset of the transition, for a duration of about 0.860 s. The maximum coherence during the first step was about 0.15 at 3.9 Hz. This shows how vestibular gain can be decreased to sustain optimal control in a task such as walking.

Lim et al (2017), Horslen et al (2014), and Naranjo et al (2016) found vestibular gain increases in threatening situations. Lim et al (2017) used a threat of perturbation paradigm, where participants’ balance was threatened with unpredictable ML support surface tilts. Horslen et al (2014) and Naranjo et al (2016) used height induced postural threat to induce feelings of fear due to participants’ location on a raised platform. In all studies, the gain of vestibulo-motor coupling increased. In the study by Horslen et al (2014), significant increases in vestibulo-GRF coherence at height were localized to between 4.3 Hz and 6.7 Hz. On average, the gain was 81% larger at height than when compared to when on the ground. Naranjo et al (2016) expanded on these findings by investigating how vestibulospinal reflexes and vestibulo-ocular reflexes measured through vestibular evoked myogenic potentials and video head impulse test outcomes are modulated during standing increased postural threat. Vestibular evoked myogenic potentials involve delivery of brief, loud, auditory sounds, or bone-conducted stimuli, to activate the otoliths and thus test the entire vestibular reflex pathways from receptor to the muscle. The video head impulse test involves recording and comparing head and eye velocities by using cameras and gyroscopes during horizontal and vertical head thrusts to calculate the vestibulo-occular reflex gain. Vestibular evoked myogenic potential amplitudes in the lower limbs significantly increased (ranges of 17%-30%) and vestibulo-ocular reflex gains increased with high surface height conditions. These studies used to better understand the relationship between balance threats or challenges and balance control, showing that gain of vestibular information is increased during threatening situations.

Luu et al (2012) investigated whether the muscle response evoked by EVS during standing is related to congruent sensory and motor signals. They strapped participants to a robot-controlled backboard that tilted in response to AP ground reaction moments under participants feet, thereby simulating normal balance control. They then switched the feedback control off and had the robot balance the participant without using ground reaction input, which decouples the participant's motor commands from sensory feedback. In this condition, the sensory signals of whole-body motion do not match the expected sensory consequences from the motor command to generate torque at the ankle joint to control balance. During these whole trials, the participants were also being stimulated by EVS to probe vestibulo-motor coupling and gain. When the sensory feedback was decoupled from the motor command, the gain between the EVS and muscular activity was decreased. Total coherence decreased by a mean total coherence of 40.1% in the left and 42.4% in the right soleus. This study highlights the task-dependent nature of the vestibular-evoked muscle response and that it is related to congruent sensory feedback and motor signals during standing.

Rasman et al (2021) further expanded on the study by Luu et al (2012) by imposing sensorimotor time delays into the control of balance. They used a similar robotic system as used by Luu et al (2012) to simulate human standing about the ankles in the AP direction with congruent sensory and motor signaling. However, they manipulated the latency between ground reaction moment and robot movement by 200 ms. These latencies lead to uncertainty regarding self-generated motion or robot-controlled motion. During these whole trials, the participants were also being stimulated by EVS simultaneously. As sensorimotor delays increased, vestibular gain decreased by 70-90% and below significant thresholds. This study showed that sensorimotor delays also attenuate vestibular control of balance.

A study by Dilda et al (2014) demonstrated that participants can adapt balance responses to EVS cues over a period of 12 weeks of repeated exposure. Healthy participants were exposed to 10-minute EVS on a weekly basis for 12 weeks while performing dynamic posturography and eye movement tasks. Follow up tests showed that posture was significantly impaired during EVS at first exposures, however, posturography scores recovered to baseline levels at 12 weeks. These effects were also retained at 6 months when exposed to EVS. However, the vestibulo-ocular reflex response to EVS was not modulated by habituation to the EVS signal.

These studies show how vestibular gain can be used to reveal how vestibular information is used to control gait, how anxiety inducing situations may influence balance control, how vestibular cues require accurate pairing between motor commands and resulting sensory feedback and that significant training can be used to adapt to EVS cues. Furthermore, these studies demonstrate that gain can change in a cyclic fashion (Blouin et al., 2011; Dakin et al., 2013; Forbes et al., 2017), decrease (Dilda et al 2014; Luu et al., 2012; Rasman et al., 2021; Tisserand et al., 2018) and increase (Horslen et al., 2014; Lim et al., 2017; Naranjo et al., 2016).

1.6.5 Conclusion: Why Sensory Re-Weighting Occurs

Sensory feedback is needed for balance control and this sensory feedback is weighted when being combined by the CNS. There is a lot of evidence which shows that gain or sensory weighting can change due to context or environmental situations. Looking at these key studies and sensorimotor balance model can demonstrate why looking at changes in gain can reveal insights about how sensorimotor integration occurs. While it is understood that individual sensorimotor weights can change, little is known about specific situations that provoke these changes and how the CNS recognizes these situations and adjusts multiple sensory gain levels.

1.7 Sensory Conflict

1.7.1 Introduction: Definition of Sensory Conflict

Sometimes, sensory modalities conflict with each other by presenting contradicting balance relevant cues (Jeka et al., 2010; Oie et al., 2002; Peterka, 2002; Peterka & Loughlin, 2004; Weech et al., 2020). To optimize balance, it is thought that the CNS will decrease weight of unreliable cues while increasing the weight of reliable cues (Peterka, 2002). Therefore, sensory conflict situations can help to better understand how changing the weight of one sensory system affects the weight of others. However, it is not fully known how the CNS determines which cues are reliable.

A hypothetical example of conflicts between sensory systems can be used to illustrate how sensory conflict occurs. If system A indicates that the body has tilted 10 degrees to the left, system B would conflict with A if it indicates: 1) no movement has occurred; 2) the body tilted to the right; or, 3) the body tilted more (or less) than 10 degrees to the left. These discrepancies could happen between any of the sensory systems that contribute to balance control.

At low stimulation amplitudes, the resulting sway is not disruptive to balance and the typical weighted summation during quiet standing of the sensory systems help to account for these discrepancies. For example, in Peterka's (2002) study where they used rotations of the visual surround and/or support surface to measure gain of visual and proprioceptive systems, they found a stimulus response saturation for both modalities at higher stimulation amplitudes. Body sway was larger than stimulus amplitudes at 0.5, 1 and 2 degrees. However, body sway was clearly smaller than the stimulus at 4 and 8 degrees. As stimulation amplitudes increase, these discrepancies need to be resolved primarily by sensory re-weighting. The downweighting of visual or proprioceptive input (depending on the perturbation type) creates a non-linearity in coupling between the perturbations and sway responses, where the participants no longer respond as strongly. This section will describe situations that provoke sensory conflicts, why they need to be resolved, how they are thought to be resolved and how these situations can be researched in a lab setting.

1.7.2 Situations that Provoke Sensory Conflicts

Sensory conflicts can perturb postural control, causing instability and sometimes falls (Buatois et al., 2007; Jeka et al., 2010; Peterka, 2002; Teasdale et al., 1991; Wolfson et al., 1992). Cues that are decoupled from how the body is positioned with respect to gravity contradict other balance relevant cues, sometimes causing instability. For example, compliant or uneven floors give poor proprioceptive cues because they deform under the feet, leading to postural sway without or with diminished change in ankle angle (Buatois et al., 2007; Jeka et al., 2010; Peterka, 2002; Teasdale et al., 1991; Wolfson et al., 1992). This means that the proprioceptive sensors within the calf, such as muscle spindles, are not stretched in proportion to the sway that is occurring. These signals conflict with other sensory systems, such as vision, which reliably reveal the amount of sway in the visual field. This sensory conflict may lead to uncertainty in the CNS about how the body is positioned relative to the gravitational field.

Similarly, large moving objects in the visual field can be poor visual cues for orientation as they may falsely indicate that the body is moving relative to the environment (Buatois et al., 2007; Jeka et al., 2010; Peterka, 2002; Teasdale et al., 1991; Wolfson et al., 1992). For example, movie screens or virtual reality headsets can leave to vision cues being decoupled from head motion (Cha et al., 2021; Weech et al., 2020). This would conflict with other balance relevant cues such as proprioception which detects quiet standing, leading to a potential instability or increased sway.

Another situation that causes sensory conflict is standing on a rocking boat (Kandel et al., 2021). The vestibular system detects large amounts of sway from the boat against the waves of the water, while proprioceptive sensors in the legs detect little sway from the surface of the deck. Visual cues can help to resolve this conflict by showing that sway of the boat against the water is occurring. This may help proprioceptive cues to be downweighted, while vestibular and visual cues are upweighted. The sensory conflict can be exacerbated if standing within the cabin of the boat, where the vestibular system still detects sway while the visual cues display the inside of the boat that does not appear to be swaying. This is a classic example of sensory conflict, and can lead to instabilities as well as motion sickness.

1.7.3 Necessity to Resolve Sensory Conflict

Sensory conflict often needs to be resolved by the CNS to maintain balance. As shown in the study by Peterka (2002), individuals with vestibular loss were not able to withstand the visual or proprioceptive perturbations at high stimulation amplitudes and they fell over. Peterka (2002) suggested this because they were not able to effectively downweight visual or proprioceptive modalities as they could not rely on vestibular cues to compensate for decreasing visual and proprioceptive input.

Additionally, elderly people are thought to have a reduced ability to re-weight sensory cues (Buatois et al., 2007; Jeka et al., 2010; Teasdale et al., 1991; Wolfson et al., 1992). Consequently, they exhibit excessive reliance on visual information which can contribute to impaired balance control and the high percentage of falls in the elderly (Buatois et al., 2007; Jeka et al., 2010). Younger populations can weight cues more effectively, and this contributes to a fewer rate of falls. However, all populations experience sensory conflicts that are disruptive to balance, so the CNS must resolve these to reduce instabilities. These examples demonstrate that those with impaired ability to re-weight sensory cues are at risk for falls and injuries related to falls.

1.7.4 Resolving Sensory Conflict with Sensory Re-weighting

Changing environmental conditions leads to changes in sensory feedback, so the CNS has to continually re-evaluate each level of contribution from the sensory modalities to optimize balance control and prevent falls (Oie et al., 2002; Peterka & Loughlin, 2004). It is thought that weights of each sensory system are determined by the availability and reliability of the afferent orientation feedback, on the time-period required to process each modality input, and possibly on the plasticity of the sensory processing pathways (Honeine & Schieppati, 2014). The weights that are applied to each cue are mostly proportional to the relative reliability of the cues, such that a less reliable cue is given less weight in perception (Angelaki et al., 2009). Sensory re-weighting occurs so that the CNS is able to receive enough sensory feedback to reliably determine body orientation with reference to the gravito-inertial plane and to regulate posture cues (Jeka et al., 2010; Oie et al., 2002; Peterka, 2002; Peterka & Loughlin, 2004; Weech et al., 2020). For the sensory re-weighting process to occur, the CNS must determine which sensory input is reliable and which sensory input is unreliable. It is not known if there are rules for this selection.

Perhaps temporal order of sensory processing may bias re-weighting towards vestibular cues over light touch cues, since they are faster to process (Honeine & Schieppati, 2014). It takes about 65 ms for short latency responses to EVS to be detected by EMG in the lower limbs (Britton et al., 1993; Fitzpatrick et al., 1994; Watson & Colebatch, 1997), whereas it takes the first increase in tibialis anterior muscle activity in response to introducing light touch cues around 500 ms (Sozzi et al., 2012).

In terms of determining the reliability of sensory cues, the CNS could use a consensus method. If some sensory modalities match each other with body orientation information while only one modality is different, the CNS may decide that the sensory modality that gives different information is unreliable and should be downweighted.

Individual differences may influence reweighing, such that weighting may be biased towards a certain modality to strengthen associated responses. Neuroplasticity, which are permanent changes to neural structures and functions in the brain, may arise due to an individual’s previous experience and training (Honeine & Schieppati, 2014). Plasticity of pathways are thought to influence the speed at which light touch sensory cues are processed, such that blind people are able to attenuate sway by significantly shorter latencies than those with normal vision (by about 0.5 s), when light touch information is available (Schieppati et al., 2014). In general, the latencies of the changes in ML CoP sway and in activity of muscles in the rear leg in response to the introduction of light touch information varied across participants from about 0.5 s to about 1.5 s, so blind individuals were towards the 0.5s of that range. The short delays were the consequence of a rapid learning process at the beginning of a series of trials, which show that fast processing of the light touch cues may be favored by neural plasticity in the blind to rely more on light touch cues. This effect may also be due to increased functional connectivity between the sensory and visual cortex and new capacities of visual areas (Dormal et al., 2012; Ioannides et al., 2013; Ricciardi et al., 2014). Additionally, light touch input could be prioritized and utilized more than vestibular cues in those experiencing unilateral vestibular loss, as there is a lack of vestibular afferent availability on one side (Bernard-Demanze et al., 2015). People with unilateral vestibular loss showed a larger percentage decrease of the root mean square of CoP displacements in the AP and ML directions with present light touch cues than neurotypical controls. For example, RMS percentage decrease in the AP direction for participants with unilateral vestibular loss when light touch input became available was about 18% whereas it was 13% for neurotypical, healthy controls. This could also mean that plasticity also leads to biases toward a re-weighting of light touch cues in those experiencing unilateral vestibular loss.

These suggestions of methods for determining how sensory cues are weighted are speculative but can provide some insight into how the CNS determines reliability of sensory cues. Looking at studies that use sensory conflict paradigms to probe sensory reweighing can also reveal insights into how the CNS re-weights cues.

1.7.5 Examples of Sensory Re-Weighting

There are examples of sensory re-weighing in response to sensory conflict in neurotypical individuals that have been studied. These include downweighting of proprioceptive input during platform tilts while holding onto a still frame and downweighting of vestibular input while using virtual reality.

Proprioceptive input from the legs is thought to decrease while on a tilted platform and holding onto a still frame with the arm (Nardone et al., 1990; Schieppati & Nardone, 1991). When participants were holding onto a still frame, 40% suppression of reflexive tibialis anterior EMG responses to toe-down rotation occurred compared to when participants were not holding on to the still frame. This is due to the conflict from proprioceptive and cutaneous somatosensory cues from the arm with the disruptive proprioceptive feedback from the legs.

EVS cues can be considered unreliable cues for balance, and it may be advantageous for the CNS to suppress these cues. This is because the pattern of activation by electrical stimulation is unlike any produced by natural motion (Dilda et al., 2014). Canal and otolith afferents of all directional sensitivities are activated by cathodal stimulation simultaneously (Dilda et al., 2014;

Fitzpatrick & Day, 2004). This means that EVS cues are artificial and lead to responses decoupled from head orientation within the gravito-inertial plane. As such, it may be favorable to decrease the weight of this unreliable vestibular information to maintain balance (Dilda et al., 2014; Weech et al., 2020).

A study by Weech et al (2020) used EVS cues in a sensory conflict paradigm. They hypothesized that vestibular cues due to EVS would be downweighted to reduce cybersickness symptoms. Cybersickness occurs because there is a conflict between expected versus actual interactions among visual, vestibular, and somatosensory inputs while using visually stimulating systems (Cha et al., 2021). In this experiment, participants were exposed to virtual reality games that were classified as either moderately or intensely nauseogenic and then self-reported their experiences of motion sickness on a quantitative scale of 20. Participants reported lower cybersickness scores during and directly after exposure to EVS while playing the nauseogenic game, compared to a group who did not receive EVS. Pre-game minus post-game sickness scores were significantly lower for the EVS group compared to the sham group while playing the nauseating game, showing differences of 1 to 2.5 versus differences of 4 to 5, respectively. These differences were not found in the moderately nauseating game. While this study showed a practical application of reducing vestibular weighting, this study only focused on the perceptual outcomes, and did not prove that vestibular re-weighting was the mechanism by which cybersickness was reduced.

There are many natural and artificial scenarios which cause sensory conflict and consequent sensory re-weighting. The process by which sensory re-weighing occurs is complex: more research about how the CNS can perform sensory re-weighing is needed. There is also debate on where sensory re-weighting occurs in the CNS.

1.7.6 Central Nervous System Locations Where Sensory Re-Weighting Can Occur.

It is difficult to predict where the CNS makes sensory-re-weighting adaptations, especially as the process of sensory re-weighting is not entirely understood. The locations involved may also vary depending on which modality specific sensory information is being re-weighted. This section will primarily focus on re-weighting of vestibular input.

As discussed, the multimodal nature of the vestibular nuclei, parabrachial nucleus and reticular formation all allow them to be candidates where sensory re-weighting and vestibular modulation can occur (Balaban & Thayer, 2001; McCall et al., 2017; Naranjo et al., 2016). The cerebellum is also where sensory information can be integrated, and it is known to make sensorimotor adaptations when motor errors are made (Thach et al., 1992). In terms of cortex possibilities for sensory re-weighting, the posterior parietal cortex has been suggested as a potential location since it is a major associative region. (Clower et al., 1996; Whitlock, 2017).

It has also been suggested that spinal interneurons may play a role in vestibular re-weighting. The studies by Iles & Pisini (1992) and Kennedy & Inglis (2002) used methods of H-reflex conditioning to reveal that forward sway evoked by EVS was found to be preceded by vestibular evoked inhibition of soleus motor neurones for about 100 to 500 ms after onset of EVS stimulation. The H-reflex is measured by exciting the Ia fibers from muscle spindles in the soleus with an electrode placed above the tibial nerve behind the knee (Kandel et al., 2021). The sensory fibers excite interneurons and associated alpha motor neurons, which in turn activate the muscle (Kandel et al., 2021). This testing revealed that vestibular input interacts with the transmission of muscle afferent spinal pathways to suppress the H-reflex response (Iles & Pisini, 1992; Kennedy & Inglis, 2002). This suggests convergence of vestibular and peripheral signals on interneurons and shows potential evidence of spinal afferent signals that could be capable of modulating descending vestibulospinal pathways. Perhaps, spinal afferent signals could be involved in re-weighting of vestibular and somatosensory inputs.

Dilda et al (2014) suggested that re-weighting did not occur within the brainstem since brainstem mediated vestibulo-ocular reflexes were unaffected in their study while participants were able to regain postural control over 12 weeks of EVS exposure. Instead, they argued the cerebellum re-weighted sensory input to prioritize somatosensory and visual information over unreliable vestibular cues to regain postural stability. However, Naranjo et al (2016) found that vestibulospinal reflexes and vestibulo-ocular reflexes were modulated in a single testing session using a height induced postural threat paradigm. This suggests a central modulation of vestibular input, by the brainstem, since both vestibulo-ocular reflexes and vestibulospinal tracts were influenced. Therefore, vestibular modulation over extended periods of time, such as the time of 12 weeks in the study by Dilda et al (2014), could involve the cerebellum. More transient modulations could be influenced by the vestibular nuclei, parabrachial nucleus, reticular formation, or spinal interneurons. This makes sense, as adaptations that take longer amounts of time typically involve structures beyond the brainstem such as the cerebellum or cortex, while more transient adaptations can be brainstem mediated. Differences in speed of processing between these CNS areas can be seen as it takes about

275-300 ms for light touch cues to cause correlated change in CoP, which needs to be processed in the primary somatosensory cortex, along with other association areas (Martin, 2021; Rabin et al., 2006). It only takes about 150 ms for reflexive brainstem mediated short latency responses to EVS to be detected in GRFs. (Horslen et al., 2014; Mian & Day, 2009). More research focusing on the speed of sensory re-weighting is needed to supplement the findings from Dilda et al (2014) and Naranjo et al (2016), since the CNS locations suggested for sensory re-weighting are just speculations. The study being proposed is not set up to reveal which CNS locations are involved in modulated vestibular input, however, it can be used to determine how long modulating vestibular input in sensory conflict situations takes.

1.7.7 Conclusion: Sensory Conflict as a Paradigm to Study Sensory Re-weighting

Balance-relevant sensory conflict presents a novel paradigm to study sensorimotor re-weighting. This is achieved by giving divergent, incongruent, or unequal information about body movement or orientation to the different sensory modalities. By discretely manipulating the availability and veracity of different balance-relevant sensory cues, it is possible to investigate how the nervous system adapts to, and resolves, sensory conflict with sensory re-weighting. This document will focus on vestibular-somatosensory sensory conflicts, as changes in weight of both modalities have been well studied and it is possible to discreetly introduce sensory cues for both modalities. Discreetly introducing sensory cues in a conflict paradigm allows for the time-dependent changes in sensory re-weighting to be measured, which is unknown. The next section will describe the few studies which can reveal insights into the timing of sensorimotor re-weighting.

1.8 Timing of Sensorimotor Reweighing

1.8.1 Introduction: Sensory Conflict and Processing Latencies

The exposure to EVS or light touch sensory inputs have predictable sway responses and latencies. It takes about 275-300 ms to for light touch cues to lead to correlated changes in CoP (Rabin et al., 2006) while it takes 150 ms for short latency responses and 300- 350 ms for medium latencies to be detected in GRFs (Horslen et al., 2014; Mian & Day, 2009). Measures of sway responses and associated latencies have also been measured for visual (Jeka et al., 2008; Oie et al., 2002) and proprioceptive perturbations (Mildren et al 2019; Schieppati & Nardone, 1991). Latencies for introductions and withdrawals of sensory inputs can be characterized with reductions in sway that are measured with EMG responses and reductions in GRF or CoP variation. However, delays associated with altering sensory weights of a modality are lesser known. This dissertation will focus specifically on delays associated with how the weight of vestibular information is modulated during the introduction of light touch information.

If vestibular-evoked balance response gain is affected by sensory conflict, the delay of the nervous system to effect these changes are not known. The CNS must determine which cues provide reliable veridical orientation information and which ones do not (Oie et al., 2002; Peterka, 2002; Peterka & Loughlin, 2004; Weech et al., 2020). This may be done by continuously evaluating the quality and quantity of sensory information and attempting to re-weight contributions from each sensory modality to see which combination of sensory weights allows the greatest control of CoM (Honeine & Schieppati, 2014; van Emmerik & van Wegen, 2002). Honeine. & Schieppati (2014) have suggested that the CNS recurrently checks the new sensory input and their magnitudes to adjust appropriate sensory weights based on estimates of cue reliability, thereby causing long time constants to attenuate sway.

There have been a few studies that have looked at time delays associated with using sensory information when the CNS is deprived of enough sensory information or receives incongruent sensory information. Carpenter et al (2010) looked at the time to increase exploratory sway in response to artificial stabilization and lack of sensory feedback, Luu et al (2012) looked at the delay to re-weight sensory cues when sensory feedback was artificially decoupled from motor commands, Rasman et al (2021) looked at delays to re-weight sensory cues when imposing artificial sensorimotor delays and Jeka et al (2008) looked at the delays to re-weight modality specific cues when they were disruptive to balance control. These studies all provide examples of delays in sensorimotor processing due to a lack of sufficient or reliable sensory information. The study being proposed differs from these in that it determines the delays associated with direct conflict between vestibular and light touch sensory information during balance control. However, these studies can be used to guide time-dependent analyses of changes in gain of sensory feedback. These studies can also be used to guide evidence-based predictions on the potential delays of adjusting sensory gains during conflict between vestibular and light touch cues. This section will describe the studies mentioned above in detail.

1.8.2 Time Delays Associated with Lack of Sufficient Sensory Information

Studies exploring the role of postural sway have hypothesized that sway variability may reflect the characteristics of an exploratory behavior (Mochizuki et al., 2006; van Emmerik & van Wegen, 2002; van Wegen et al., 2002). This implies that postural sway is not only erroneous or systematic noise, but that also allows individuals to gain more sensory information about their relationship with the environment (Carpenter et al., 2010). This movement variability allows capitalization on converging information from multiple sensory systems to allow for reliable integration and control of balance and posture (Carpenter et al., 2010).

The work by Carpenter et al (2010) demonstrates that CoP displacement can be purposefully altered by the CNS to ensure some desired quality or quantity of sensory information is received by the CNS. Carpenter et al (2010) used a method to minimize movements of the CoM in the AP direction and thus postural sway during upright stance, without participant awareness. During this 'locked' condition, GRFs are generated which is shown through increased CoP variability and fluctuations in the AP direction. These responses would normally drive sway responses and movement of the CoM, which would stimulate receptors of different sensory systems.

It takes approximately 10 seconds for the AP CoP to increase in variability once the AP center of mass is locked (Carpenter et al., 2010). This could mean that it takes the CNS 10 seconds to determine that there is a lack of sensory information by evaluating the quality and quantity of sensory information its receiving from the sensory modalities, attempt to re-weight contributions from each sensory modality to gain more sensory information, realize the re-weighting strategy did not work, and then implement motor action (Oie et al., 2002; Peterka & Loughlin, 2004). This is speculation; however, this could be a reason as to why CoP variability and fluctuation increases via exploratory sway.

The study by Sozzi et al (2012) can be used to supplement the findings by Carpenter et al (2010). It takes a longer time to reach a steady state from the addition of light touch or visual input compared to withdrawal of light touch and visual input, with a difference of 1-3 s compared with 1 s (Sozzi et al., 2012). Sozzi et al (2012) suggested that the CNS rapidly realizes the loss of the stabilizing input, and oscillating sway increases which engages proprioceptors in the leg muscles. This suggestion also falls under the exploratory hypothesis, as they interpret the increase postural sway as a method to gain more sensory information.

The study by Carpenter et al (2010) and suggestions made by Sozzi et al (2012) demonstrate that the CNS uses strategies to gain more sensory cues when there is insufficient sensory information. The CNS must undergo a process to realize this and make proper motor adjustments. The time delay for this to occur may be as slow as 10 seconds. Sensory conflict is also a situation in which sensory cues are insufficient to accurately control balance and may also lead to longer time constants to resolve sensory conflict.

1.8.3 Time Delays Associated with Decoupling Motor Commands from Sensory Feedback

Luu et al (2012) investigated how long it took to modulate vestibular input once sensory and motor commands were decoupled. When the sensory feedback was decoupled from the motor command, the coherence and gain between the EVS and muscular activity was decreased. On average, total coherence decreased (around 40%) below the pre-transition mean after 150 ms for the left and 200 ms for the right soleus (175 ms for both legs combined). Once the control of the robotic platform's motion reverted to human control, total coherence returned towards the pre-transition mean, recovering to the mean after 850 ms for the left and 900 ms for the right soleus (875 ms for both legs combined). These results are depicted in Figure 5 below.

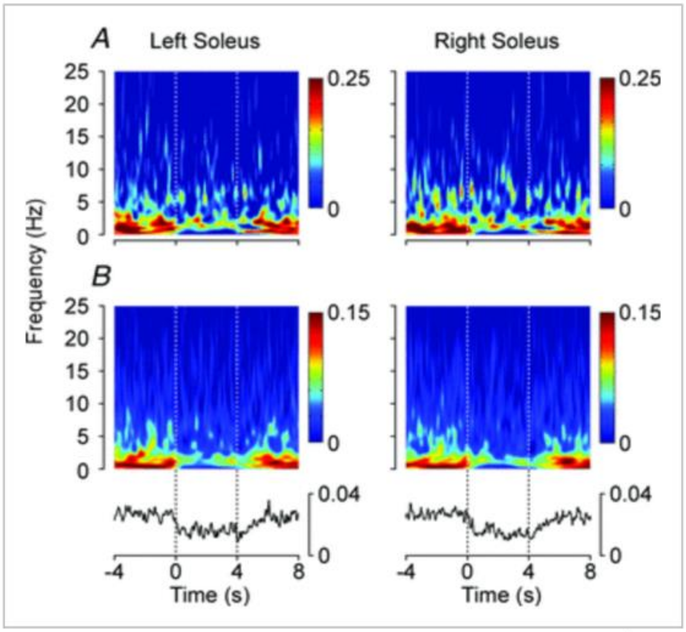

Figure 5: Time-varying Changes in Coherence Between the Vestibular Stimulus and Soleus EMG Activity During Transitions from Human- to Computer-Controlled Motion of the Robotic Platform from Luu et al (2012).

> Data are shown over 100 transitions for a single subject (*A*) and the group mean (*B*) for five participants. The 4 s period prior to time zero shows frequency-specific coherence as participants were braced on top of the platform and balanced its body-like load with their feet. Time zero represents the transition point from human-controlled balancing of the platform to a computer-controlled rotation of the platform along a predetermined path, which lasted for 4 s (between the vertical lines), before participants regained control of the platform. The mean of the coherence from 0 to 25 Hz at each time point is shown across the bottom panel. Non-significant data points have been removed so that zero coherence represents the values below the threshold of the 99% confidence limit; 0.046 for the single subject and 0.0093 for the group mean data.

These results suggest that the CNS can almost immediately recognize that the motor command to balance the body is decoupled from the actual movement of the body (Luu et al., 2012). However, it takes longer to re-associate the balancing task with human controlled postural activity than identifying a discrepancy between the expected sensory consequences from the motor command, as evidenced by re-levelling of gain. Luu et al (2012) suggested this is most likely because the participant must regain control of the platform which takes more time. The reduction in vestibular-motor gain also occurred much faster than consciously detecting a loss of control of the platform which occurred at around 2247 ms. Therefore, it is thought that the neural processes that create associations between congruent sensory and motor signals of body motion during balance operate separately from conscious awareness of balance. These latencies to decrease vestibular coherence could reflect the time it takes the CNS to determine that there is unreliable sensory information, attempt to re-weight contributions from each sensory modality to gain more reliable sensory information, realize which modalities are unreliable, and downweight them.

This study is important in that it demonstrates that reductions in vestibular gain are fast acting when whole body movement and resulting sensory feedback from multiple sensory modalities are decoupled from motor commands in balance control (Luu et al., 2012). It also demonstrates that increases in gain once sensory and motor cues are re-coupled can have different time latencies to affect sensory gain. Potentially, the addition and withdrawal of light touch to modulate vestibular information could have different time latencies, although this is not immediately clear.

Rasman et al (2021) further expanded on the study by Luu et al (2012), by using EVS and imposed sensorimotor time delays into the control of balance. This means that the latencies from ankle-produced torques and the resulting sensory feedback from whole-body motion were coupled, but the sensory feedback took longer normal. They imposed delays of 200 ms in addition to inherent sensorimotor delays of 100-160 ms. Modelling studies show that balance is impossible with delays of 300-340 ms (van der Kooij & Peterka, 2011). Vestibulo-muscular coherence and gain decreased with imposed delays of 200 ms. To characterize the time course of the gradual decrease in this vestibular contribution to balance, they fit an exponential decay function to the mean coherence over the 8 s period during which the 200 ms delay was present (coherence averaged over 0.5–25 Hz at each time point) from each participant. For vestibular responses, they reported the time when the coherence of vestibular evoked muscle responses was attenuated by 63.2 % and 95 % (extracted from exponential decay functions) during the delay period. The 63.2% attenuation (i.e., the time constant selected) for coherence occurred at about 1.5 s following delay onset while the 95% attenuation (i.e., 3× time constant selected) occurred at about 4.4 s following delay onset. The 63.2% attenuation from this mean gain estimate occurred at 2.3 s while the 95% attenuation occurred at 6.8 s. Overall, these results indicate that increased sway variability arising from an imposed delay are accompanied by an approximate 70–90% attenuation of vestibular contributions to balance.

This study also looked at training effects with these sensorimotor delays. After training with the delays over five consecutive days (two 10 min trials per day), gain returned to baseline. Even with imposed 400 ms delay and high sway variability, all participants learned to balance with the delay and this ability was partially retained 3 months later.

Rasman et al (2021) demonstrated that the time for coherence to decrease by around 63 % took longer than the time for coherence to decrease as in the study by Luu et al (2012) by 40% (1.5 seconds compared with about 150ms). It may be more challenging for the CNS to recognize that sensory feedback is not reliable when there are delays rather than when sensory feedback is completely decoupled from motor commands, reflecting this longer time delay. This study also demonstrates that gain can increase again with training effects over time. Potentially, this means that changes of gain during sensory conflict situations may also be changed with time and training effects.

1.8.4 Time Delays Associated with Decreasing Weighting of an Unreliable Sensory Modality

Previous studies showed decreases in gain when all sensory modality cues were either not present, decoupled or delayed from motor responses, and therefore the sensory feedback was unreliable from multiple modalities. Jeka et al (2008) isolated vision and made the cues unreliable by varying the projected size and the distance between triangles on a surround projection to simulate translation in an AP direction of the entire visual scene relative to the participant. They measured resulting postural sway with an OptoTrak camera position tracking system. Gain of visual information ranged from 0.50 mm to 1.04 mm during the sinusoidal motion. They conducted a phase analysis which indicates the temporal relationship between postural response and stimulus motion. When visual motion increased, gain decreased within 5 s to a value near its asymptotic value. In contrast, when visual motion decreased, it took an additional 5 s for gain to increase by a similar absolute amount. Suddenly increasing visual motion amplitude threatens balance if gain remains high, and rapid downweighting of the sensory signal is required to avoid falling. Jeka et al (2008) suggested that slow up-weighting of visual information shows a conservative CNS strategy. It may not be functional to rapidly up-weight with transient changes in the sensory environment. This study shows that it is possible to measure time-dependent changes in gain of one sensory modality by using a continuous perturbation.

The study by Tisserand et al (2018) also discusses the time-dependent changes in attenuating sensory cues from one modality but focusing on the vestibular system. The maximum coherence during quiet standing was 0.29 on average. However, the gain of vestibular input decreased 0.435 s before starting the walking sequence below significance thresholds. This may have implications for looking at the time-dependent changes of any task. Prior to a self-generated motor action, vestibular gain may be altered due to the anticipation of engaging in the task. Introducing or withdrawing light touch sensory information while looking at changes in vestibular gain may show similar effects, such that decreases in vestibular gain may precede introducing light touch information.

These two studies are important to consider when looking at gain changes of a particular sensory system. The CNS must determine that there is an unreliable sensory information source before downweighing it, which may increase time. Not only should the time delays associated with decreasing visual gain be considered when looking at changes in vestibular gain, but anticipatory effects of introducing light touch information must be considered as well.

1.8.5 Conclusion: Time Delays to Resolve Sensory Conflict

These studies leave unknowns for the time course of resolving sensory conflicts. The study by Carpenter et al (2010) shows that lack of sufficient sensory information to maintain balance control leads to time delays of 10 seconds to resolve this issue by increasing exploratory sway. However, latencies to decrease vestibular gain when motor commands are decoupled from whole body sway feedback mechanisms are much shorter and can be as fast as 150ms (Luu et al., 2012). Latencies to decrease gain of visual input and thus resolve sensory conflict takes 5 seconds, which is between the latencies mentioned above (Jeka et al., 2008). The reason that decoupling sensory and motor cues may lead to much faster changes in sensory re-weighting than increasing sway to gain more sensory information is because the sensorimotor discrepancies caused by this decoupling are more salient and disruptive to balance control. It may take the CNS longer to recognize that there is a lack of sensory information (Carpenter et al., 2010) as opposed to recognizing that the sensory feedback clearly does not match the motor commands (Luu et al., 2012). Decreasing the gain of a single modality may take more time for the CNS to decide which cues are reliable as opposed to when all the sensory feedback is decoupled from motor commands, which is why it took 5 seconds compared with 150 ms (Jeka et al., 2008; Luu et al., 2012). It still takes less time than when there is no sensory feedback due to sway (Carpenter et al., 2010), which is an unusual situation that the CNS takes longer to resolve. Overall, the differences in latencies between these studies may arise during the period of evaluating quality and quantity of sensory information being received from the sensory modalities and attempting to re-weight contributions from each sensory modality to gain optimal sensory information. Each situation is different and may be more or less challenging for the CNS to resolve.

Vestibular-light touch conflict presents a paradigm where the dynamics of sensory conflict in balance control can be studied. EVS signals are unreliable and disruptive to balance control, so it is thought that vestibular contributions would be downweighted by the CNS during sensory conflict situations (Dilda et al., 2014; Weech et al., 2020). Light touch cues provide a balance relevant reliable source of sensory information, so it is thought that these cues would be up-weighted (Chen & Tsai, 2015; Jeka et al., 1996). Similar to the study by Jeka et al (2008), the proposed study will look at the time it takes to decrease the gain of a single modality; the vestibular system. While it is understood that sensorimotor re-weighting can occur, little is known about how long it takes the nervous system to effect change.

Chapter 2

Research Questions and Hypotheses

Research Question 1. Are vestibular contributions to the representation of body posture and orientation altered when new sensory information becomes available for sensorimotor control of balance? Specifically, is vestibular-evoked standing balance response coherence affected by balance-relevant sensory conflict due to light touch, and, if so, by how much and in which direction?

Mechanistic hypothesis: I hypothesized that vestibular contributions to the representation of body posture and orientation would decrease when light touch sensory feedback was available to participants. It was expected that conflicting feedback between balance-relevant sensory modalities would cause the coupling between EVS and CoP sway responses to be decreased.

H_a: Coherence between EVS input and evoked CoP balance response output would have a statistically significant decrease when light touch feedback was available, compared to when not available.

H_o: Coherence between EVS input and evoked CoP balance response output would not be statistically different when light touch feedback is available, compared to when not available.

Research Question 2: Is vestibular-evoked response amplitude altered when new sensory information becomes available for sensorimotor control of balance? Specifically, is vestibular-evoked standing balance CoP response gain affected by balance-relevant sensory conflict due to light touch, and, if so, by how much and in which direction?

Mechanistic hypothesis: I hypothesized that the magnitude of vestibular-evoked CoP balance responses would be decreased when light touch sensory feedback was available to participants. Participants would downweight vestibular feedback and upweight light touch feedback when constructing motor responses to vestibular perturbations.

H_a: Gain between EVS input and evoked CoP balance response output would have a statistically significant decrease when light touch feedback was available, compared to when not available.

H_o: Gain between EVS input and evoked CoP balance response output would not be statistically different when light touch feedback was available, compared to when not available.

Research Question 3: Are segmental and whole-body vestibular reflex responses differentially affected by balance-relevant sensory conflict?

Mechanistic hypothesis: I hypothesized that balance-relevant sensory conflict would reduce coherence and gain between EVS and whole-body balance sways but would not change coherence and gain between EVS and head-on-trunk sways. It was hypothesized that a balance-relevant sensory input such as light touch would not affect a non-balance vestibular response such as head-on-trunk motion.

H_a: Coherence and gain between EVS input and head acceleration would not change while sternum and arm coherence and gain changes would be statistically significant with light touch.

H_0: Coherence and gain between EVS input and head, sternum and arm acceleration would not be statistically different with light touch.

Research Question 4: If vestibular-evoked balance responses are affected by sensory conflict, how long does it take the nervous system to effect the change? What does the transition look like?

Mechanistic hypothesis: I hypothesized that the CNS would require less than 0.5 s after introduction or removal of light touch to reach a new steady state. It was hypothesized that the nervous system continuously compares and re-weights different balance relevant sensory modalities to determine the optimal weights for the sensorimotor control of standing balance.

H_a: Coherence and gain between EVS input and evoked CoP balance response output would take under 0.5 s to reach a new steady state coherence and gain after introduction or removal of light touch.

H_0: Coherence and gain between EVS input and evoked CoP balance response output would not be statistically different when light touch feedback was available, compared to when not available. As such, coherence, and gain between EVS input and evoked CoP balance response output would be constant throughout the trial. Alternatively, it would take over 0.5 s for coherence and gain to reach a new steady state after introduction or removal of light touch.

Chapter 3
Methods

3.1 General Scope of Methods

To address RQ1 and RQ2, which focuses on changes in vestibulo-balance coupling and gain during balance-relevant sensory conflict conditions, balance was measured by changes in CoP from the force plate. The changes in CoP from the force plates were used to determine how big the vestibular evoked movements were; and how they differed when touching the load cell versus when not touching it. This was done by using linear systems analyses. To address RQ3 which focuses on segmental vestibular reflexes, accelerometers were worn at the head, sternum, trunk, and arm. Changes in accelerometry were measured between conditions using the same linear analysis. To address RQ4, which focuses on the time course of sensory re-weighting in response to balance-relevant light touch input, changes in CoP were analyzed throughout transitions between touching and not touching the load cell.

The first version of the study (experiment 1) was an active paradigm, where participants self-initiated lifting or lowering their finger to a load cell that was always in the same fixed position. This experiment aimed to answer research questions 1, 2 and 4. The second version of the study (experiment 2) was a passive paradigm, where the experimenter controlled a lever system that raised the load cell to a fixed position touching the index finger or withdrew the load cell. The comparison of time-dependent results of both experiments allowed differentiation between changes in coherence and gain attributed to anticipatory effects or the motor control component of the task versus independent addition or removal of light touch sensory information. Shimmer accelerometers were only worn during experiment 2. This experiment aimed to answer research question 3 and further answer research question 4. This study has been reviewed and received ethics clearance through the University of Waterloo Research Ethics Board (REB #44217).

3.2 Participants

3.2.1 Sample Size

A sample of 16 participants was chosen for experiment 1 and a sample of 10 participants was chosen for experiment 2.

3.2.2 Exclusion Criteria

For both experiments, neurotypical young adults (18-35 yrs. old) with no known neurological or orthopedic issues that affect standing balance control were recruited. Participants were recruited from the on-campus population at the University of Waterloo. Participants excluded from the study included those: 1) younger than 18 years of age or older than 35 years of age, 2) with any history of significant lower limb injuries, such as fractures or sprains, 3) with significant balance issues, 4) with any history of neurological impairments that may affect standing balance (e.g., previous brain injury, epilepsy, multiple sclerosis, vestibular impairment, etc.), or 5) taking antianxiety, antidepressants or antipsychotic drugs (whether prescribed or not). I did not exclude any participant based on sex, gender (assigned or self-identified), sexual orientation, culture, and/or religion.

3.3 Materials and Protocol

3.3.1 Preparation for Data Collection

For both experiments, the participants were asked to stand barefoot as still as possible on 2 force plates force (AMTI OR6-5, Advanced Mechanical Technology, Inc., Watertown, MA, USA), with feet placed foot length apart. Participants' foot positions were measured and marked on the force plates with tape to guide positioning between trials such that the lateral edges of their 5th metatarsals were spaced equal to their foot length.

For experiment 2, accelerometers (Shimmer3 IMU, Shimmer, Dublin, Ireland) were worn at the head, sternum, trunk, dominant arm, and ankle. They were secured the same way every time, using appropriate landmarks on the body and accelerometer itself. The accelerometer was always placed on the center of the frontal region of the head, sternum, and wrist joint line. The accelerometers were aligned and secured such that the unit positive Z and Y axes was aligned in the anterior and superior directions, respectively. The shimmers were fastened with bands that had holders for the shimmers, except for the head. The head shimmer was secured with a headband.

For both experiments, disposable electrodes with conduction gel (electrodes: EL503; Gel: GEL100, Biopac Systems, Inc., Goleta, CA, USA) were placed behind the ears on the mastoid processes which were used to mildly stimulate the vestibular system. The electrodes were also secured in place with the head band. Head position was fixed at approximately 18 degrees above Reid's plane (inferior margin of the orbit to the auricular point approximately 18 degrees above horizontal), as this head orientation aligns responses to the frontal sagittal plane (Fitzpatrick & Day, 2004). Head posture was set at the beginning of the experiment using a level and goniometer and checked before each trial. Responses were aligned in the ML direction when the head was forwards and responses were aligned in the AP direction when head was to the side. For experiment 1, the head was facing forwards for half of the trials and towards the left shoulder for the other half of the trials; each trial was completed for the ML direction and AP direction. For experiment 2, only AP trials were conducted due to the small effect sizes found from experiment 1 in the ML trials (refer to Appendix A).

After adjusting and positioning equipment, but before data collection began, participants sat in a chair for a familiarization trial and received a short exposure to the EVS delivered from a stimulator (STMISOLA Linear Isolated Stimulator, Biopac Systems, Inc., Goleta, CA, USA) for 10 seconds. This was so participants could understand how stimulation feels and were not startled during data collection. Participants could also report discomfort and allow the experimenter to make adjustments before the recorded trials. Participants were permitted multiple exposures before starting data collection if they wished.

Once the participant adopted their stance on the force plate, they were asked to slightly flex their dominant arm, so their finger rested around hip height in a comfortable position to the side of their body in ML trials and slightly in front of the body in AP trials. For experiment 1, the load cell (load cell: compression load button with 445N range, unknown manufacturer; amplifier: Model 3270 strain gage bridge conditioner, Daytronic dba Dranetz Technologies, Edison, NJ, USA) was permanently fixed in position so that the participants could touch or not touch; when not touching participants held their finger above where they assumed the load cell to be. For experiment 2, the load cell (burster 8523-5020-N000S000 tension-compression load cell with 20 N range: A-TECH Instruments LTD, Scarborough, ON, Canada; amplifier: Model 3270 strain gage bridge conditioner, Daytronic dba Dranetz Technologies, Edison, NJ, USA) was positioned so that the load cell could be raised by the experimenter to a locked position for participants to touch. There were two light touch conditions in this study. In the TOUCH condition, the participant pressed the loadcell with the index finger of their dominant hand to a maximum vertical load of 2 N (see section 3.4.2 below). In the NO TOUCH condition, the participants either held the finger above where they expected the load cell to be (experiment 1), or the experimenter removed the load cell and participants held their finger where the load cell would be if in the fixed TOUCH position (experiment 2). Arm posture remained the same for NO TOUCH and TOUCH conditions for both experiments so that this posture didn't contribute to changes in coherence and gain. Once any trial began, participants were asked to close their eyes and stand as still as possible.

Signals from the force plates, load cell and EVS were sampled at 1024 Hz with a data acquisition board (National Instruments Data Acquisition Board: National Instruments Corp., Austin, Tx, USA) and a custom LabVIEW script (National Instruments Corp., Austin, Tx, USA).

3.3.2 Trial Types and Durations

For both experiments, there were 3 types of trials. The baseline trials were shorter duration (60 s), and participants were instructed to either not touch or touch the load cell for the whole duration. There was no EVS during these trials, as these data were used to characterize participants' responsivity to the light touch independent from EVS. Steady state trials were 200 s and participants were also instructed to either not touch (NO TOUCH) or touch (TOUCH) the load cell for the whole duration. Participants were exposed to EVS for the duration of the trial, and these data were used to address research questions 1 and 2.

Switching trials had participants regularly switch between TOUCH and NO TOUCH conditions while EVS was present for the duration of the trial. These trials were used to address research question 4 and differed between experiment 1 and 2.

For experiment 1, there were 2 switching trials of 200 s with transitions every 20 seconds. For experiment 2, each participant performed 4 300-second switching trials, with transitions between TOUCH and NO TOUCH every 6-15 seconds. The intervals between transitions were randomized in experiment 2 to prevent prediction of the switching events. The flow charts below illustrate the differences between trial setup between experiment 1 and 2.

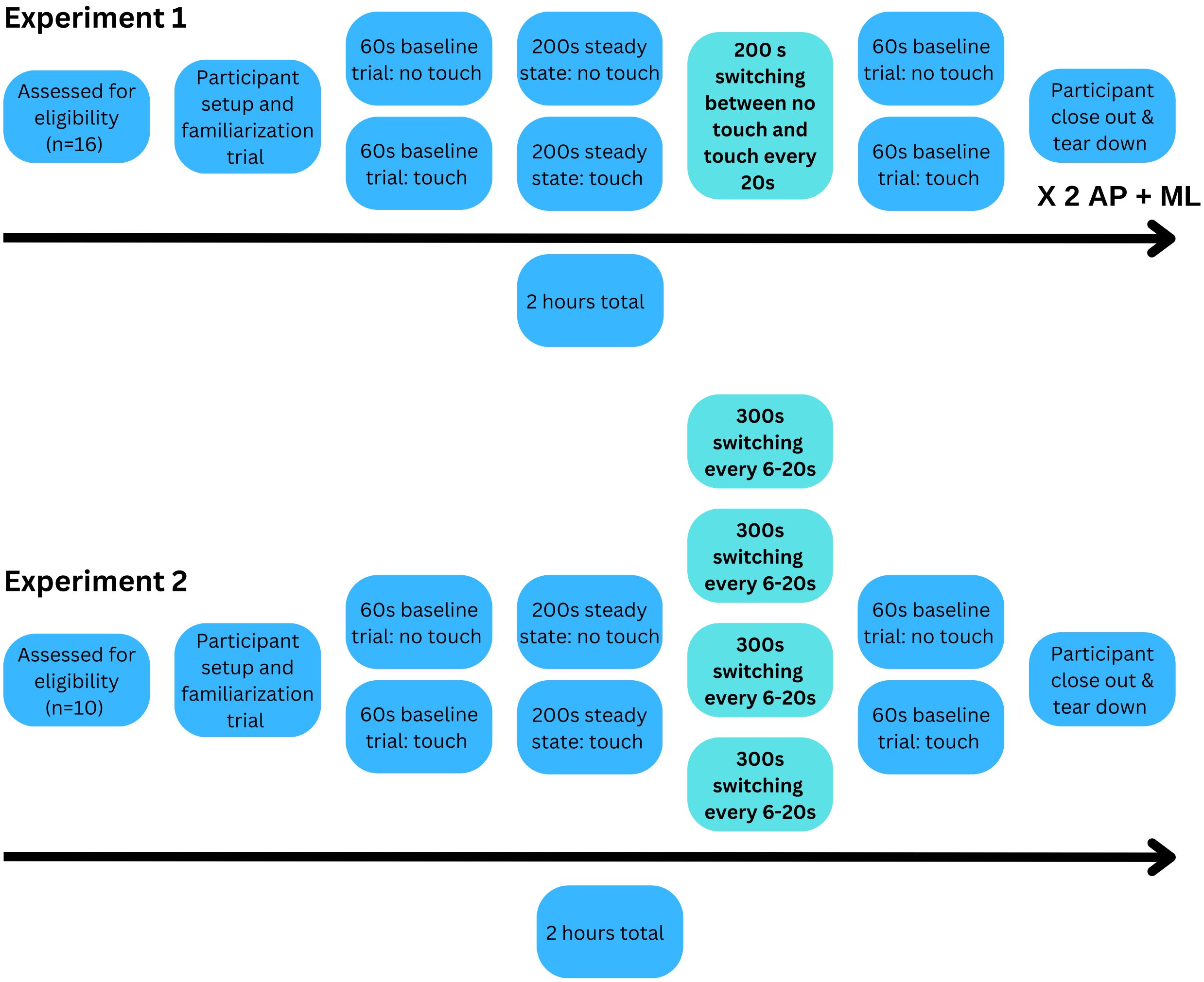

Figure 6: Flow Chart Demonstrating Order of Events for Experiment 1 and 2

Blue boxes show events and trials that are the same between experiment 1 and 2. Teal boxes show the switching trials that are different between studies in their durations and timing of switches.

3.4 Data Collected

3.4.1 Electrical Vestibular Stimulation Signal and Collection Parameters

For experiments 1 and 2, A stochastic EVS stimulus was generated using a custom LabVIEW script to permit multifrequency coherence and gain analyses between the EVS signal and CoP responses. The continuous nature of the stochastic stimulus also allowed time-dependent decompositions. These analyses were used to reveal how vestibular information is modulated in the presence of balance relevant sensory conflict and reveal how long it took to adjust after a conflict was introduced (Luu et al., 2012; Rasman et al., 2021).

For both experiments, the participants were stimulated by EVS throughout the duration of the steady state and switching trials, (either 200 s or 300s). I used a ±4.5mA peak amplitude signal with a 0 mean and a 0-25 Hz bandwidth (low pass filtered at 25 Hz). These parameters were set so that stimulation wasn't uncomfortable or would evoke large sway responses but would still evoke measurable CoP displacements (Blouin et al., 2011; Dakin et al., 2007; Horslen et al., 2014; Lim et al., 2017).

The EVS signal was sampled at 1024 within a custom LabVIEW script. For post-processing, bins were 2048 samples long. This means that the bins were also 2 seconds long, making the lowest frequency resolution 0.5 Hz (1/t). For both experiments, there were 100 bins per participant for single state (200 second trials/ 2 second windows). Figure 7 shows a sample of the EVS signal and a schematic of the time windows and data points over a trial for the EVS and CoP data.

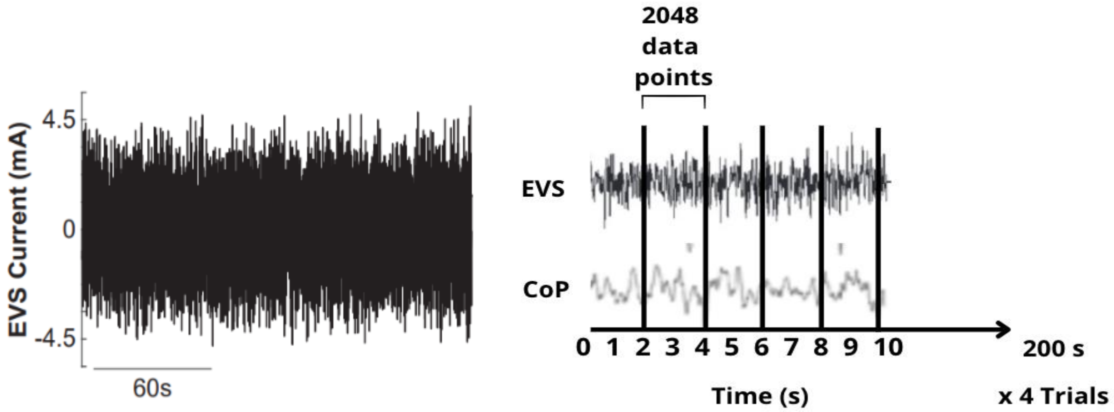

Figure 7: Sample of the Electrical Vestibular Signal & Schematic samples Collected for EVS and CoP over a 200 Second Trial.

A: Sample of a ±4.5mA peak amplitude signal with a mean of 0 and a 0-25 Hz bandwidth for a duration of 200 seconds. B: This schematic diagram represents the EVS signal (top) and CoP signal (bottom) over a 200 second trial. Both signals were divided into 2 second time bins. The sampling rate was 1024 Hz, leading to 2048 data points per window.

3.4.2 Load Cell Protocol and Collection Parameters

The load cell data were primarily used to monitor that participants were using less than 2 N of force throughout the collection when touching the load cell for experiments 1 and 2 (Holden et al., 1994; Jeka et al., 1996). Prior to collection, the load cell was calibrated so that the value of volts that corresponds with 2 N was determined. This ensured that the experimenters could monitor the livestream of load cell data to determine when 2 N was surpassed and verbally instruct participants to adjust their load as needed. In post-processing, the participants were considered touching the load cell when the signal increased 3 standard deviations above the baseline mean of when it was unloaded. The load cell data were filtered with a 4th order Butterworth low-pass filter with a cutoff frequency of 5 Hz. This was to reduce the noise found primarily at 60 Hz.

For experiment 1, the experimenter verbally instructed the participant to either touch or remove their touch by saying “switch”. The load cell was in a fixed position, so the transitions were executed by the participant. In the TOUCH condition, the participant compressed the load cell with the index finger of their dominant hand. In the NO TOUCH condition, the participant was instructed to extend the metacarpophalangeal joint to elevate and hold the index finger just above the load cell. Participants were instructed to keep arm posture and hand position constant to the best of their ability during the switching trials so that the primary difference between conditions was the presence of light touch sensory information, and not arm posture.

For experiment 2, the experimenter controlled a lever system that raised or withdrew the load cell to their fingertip. In the NO TOUCH condition, an experimenter pushed the lever arm holding the load cell down, disengaging the magnets holding it in place, and causing the load cell arm to swing downwards and away from the participant (Figure 8, right panel). Participants were instructed to hold their finger in the position where the load cell had been in the NO TOUCH condition. In the TOUCH condition, an experimenter brought the arm upwards, reengaging the magnets, and the load cell arm was held in place under the participant’s index fingertip (Figure 8, left panel). The aim of this setup was to reduce anticipation of transitions and movement since transitions occurred at random intervals and the experimenter controlled the load cell arm. This was to isolate changes of coherence and gain that were only due to the addition or removal of light touch sensory information. Pictured below, is the load cell setup for experiment 2 in the fixed position and withdrawn position.

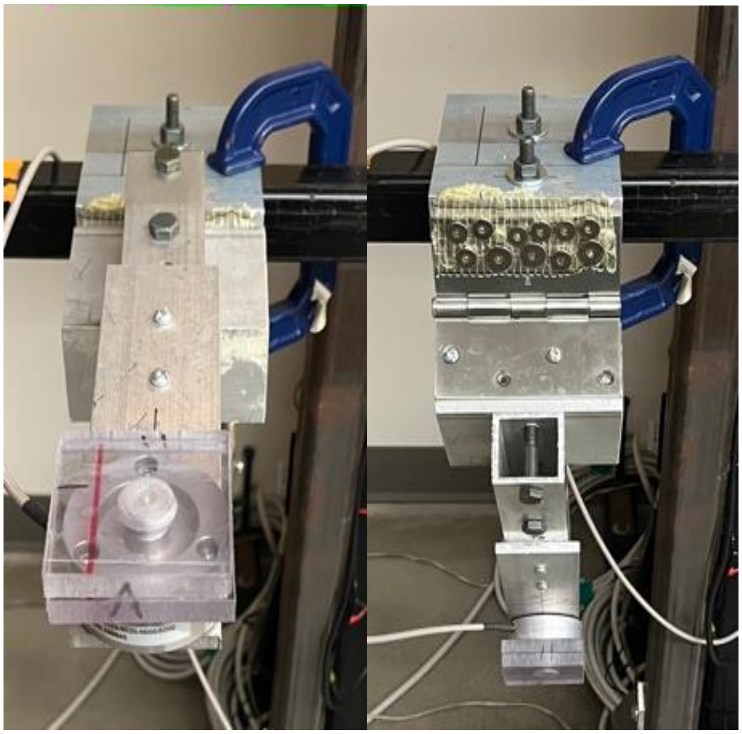

Figure 8: Load Cell Setup for Experiment 2

Pictured on the left is the load cell in the fixed position where participants would be touching the load cell (clear square at end of arm). Pictured on the right is the load cell when it is withdrawn for NO TOUCH. The magnets that hold the load cell in a fixed position during TOUCH can be seen.

3.4.3 Force Plate Protocol and Collection Parameters

Two force plates were used to measure GRFs, which were used to calculate center of pressure for experiment 1 and 2. A national instruments data acquisition analog to digital board was used to transform analog signal to digital signal. A custom LabVIEW script was used to collect and process forces and moments in the frontal, sagittal and vertical directions. The CoP was calculated using the moments (Mx and My) and vertical force (Fz) signals from the force platform. A custom MATLAB script (R2021b, MathWorks Natick, MA, USA) was used to convert GRFs and moments to newtons, calculate, and low-pass filter (50Hz, 4th order Butterworth) the CoP.

3.4.4 Accelerometer Protocol and Collection Parameters

Accelerometers were used to measure acceleration and angular velocity in the x, y, and z planes. Each of the axes were aligned with anatomical axes in processing, such that the axes would represent the sagittal or frontal planes. They were worn on the head, sternum, and dominant arm. The program Consensys (ConsenysPRO, Consensys, Brooklyn, NY, USA) was used to collect accelerometer data at 1024 Hz. A TTL synch pulse from the NI DAQ to the Shimmer DAQ was sent at the onset of the EVS signal in each trial to synchronize and data collection in time between systems. The program Consensys (ConsenysPRO, Consensys, Brooklyn, NY, USA) was used to set collection parameters, such as the sample rate at 1024 Hz. Accelerometry data were low-pass filtered (35Hz cut off, 4th-order Butterworth) offline with a custom MATLAB script prior to analysis. I only used accelerations in the spatial dimensions corresponding with the expected EVS-evoked body sway at each segment for the linear systems analyses. These dimensions were anterior-posterior for the sternum and dominant arm, and medial-lateral for the head; head medial-lateral accelerations were analyzed because the head was turned to align the head medial-lateral dimension with the body anterior-posterior dimension.

3.5 Signal Processing

3.5.1 Centre of Pressure and Load Cell Data

For baseline and single-state EVS trials of both experiments, the root mean square (RMS) of CoP data was determined for periods where participants were touching the load cell versus when they were not touching the load cell. RMS is a common summary measure used for CoP analysis to capture the variance (Carpenter et al., 2001). The RMS was baseline corrected by first calculating the average of the AP CoP to determine mean AP CoP position. The mean position was then subtracted from the AP COP data before calculating RMS. The average of AP CoP RMS data across participants was compared across conditions. This gives insight into the size of CoP responses independent of the EVS signal.

For both experiments, CoP RMS was calculated for the concatenated switching trial data. The RMS was calculated from 2 s windows. Onset of each window was staggered by 100 ms, over a period of 4 seconds before and after each transition occurred. This was to compare how RMS changed relative to the timing of changes for coherence and gain calculations. RMS is different because it just shows postural changes whereas coherence and gain show postural changes that are tuned to vestibular input.

The load cell data was used to determine when the participant was touching or not touching the load cell, based on the standard deviation method mentioned. A custom MATLAB script was developed based on this thresholding method to ensure that the correct time points were chosen for the transitions. This was also checked by visual inspection to ensure precision for time-dependent analyses. Average force level throughout the whole period where participants were touching the load cell was also determined for each trial. Sample data from participant 001 demonstrates transition points between NO TOUCH and TOUCH.

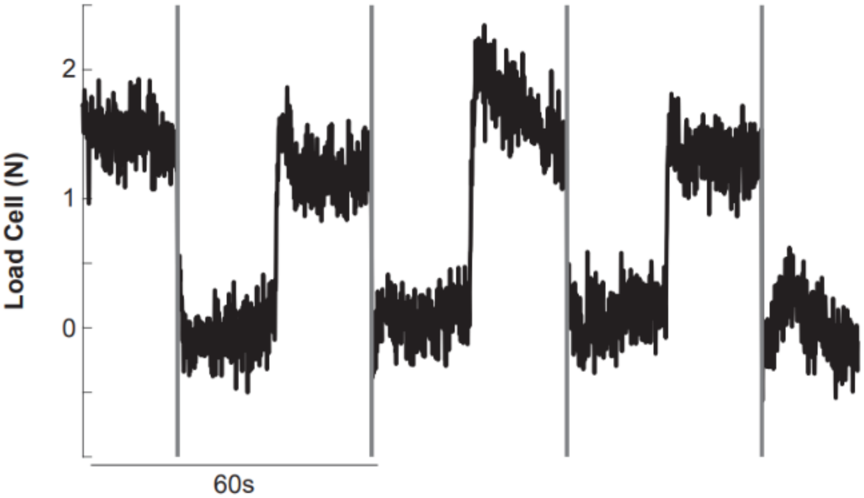

Figure 9: Sample Load Cell Data During Switching Trial from Participant 001 (exp 1)

Sample Load Cell Data from 001. The y axis is time in seconds, and the x axis is force applied in Newtons. Participants aimed to apply between 1-2 Newtons when touching the load cell.

3.5.2 Linear Systems Analyses

A linear systems approach was used to address all research questions for both experiments by determining the relationship between EVS and CoP in the frequency and time-frequency domains. For experiment 2, this was also done for the relationship between EVS and accelerometry or angular velocity. Linear correlation between EVS and CoP (or shimmer data) allows the computation of coherence and gain in the frequency domain and time-dependent cumulant density as well as confidence intervals about these estimates (Halliday et al., 1995). This provided a statistical framework to test if the correlation in the time and frequency domains was statistically greater than that expected by chance (Blouin et al., 2011; Dakin et al., 2007; Horslen et al., 2014; Lim et al., 2017; Luu et al., 2012; Rasman et al., 2021). These estimates were conducted on individual data and on the pooled data across participants. The pooled data reduced the level to reach the 95% confidence limit for coherence (Horslen et al., 2014; Lim et al., 2017). Additionally, the coherence, gain and cumulant density estimates from the pooled data represented the mean of the sample.

Coherence, gain and cumulant density estimates between the stochastic EVS and GRFs were calculated using the NeuroSpec 2.0 code, which is freely available archive of MATLAB code intended for statistical signal processing and based on the methods of Halliday et al. (1995), and is well established in the literature (Blouin et al., 2011; Dakin et al., 2007; Horslen et al., 2014; Lim et al., 2017; Luu et al., 2012; Rasman et al., 2021).

The NeuroSpec algorithm was used to compute coherence between the input signal and output motor response in the frequency domain, by indicating where in the frequency spectrum signals are related (Halliday et al., 1995). The coherence functions provided a bounded normative measure of association between the input signal and output motor response, taking on values between 0 and 1. Zero represented the case of independence, while 1 represented the case of a perfect linear relationship. Coherence functions were an effective way to provide estimates of the strength of coupling or association between an input sensory signal and output motor response, such as strength of relationship between EVS stimulation and change in CoP or EMG. This is because coherence expresses the amount of variation in the output signal that can be explained by the input signal. The numerator of the equation included the magnitude of the cross spectrum of the input and output, and the denominator contained the product of the individual input and output auto spectra. The equation is as follows, where x is the input and y is the output signal:

$$C(\mathcal{T},\mathfrak{f}) = \frac{|P_{xy}\ (\mathcal{T},\mathfrak{f})|^2}{P_{xx}(\mathcal{T},\mathfrak{f})P_{yy}\ (\mathcal{T},\mathfrak{f})}$$

Within the coherence plot, significant peaks were identified when values exceeded 95% confidence intervals. Significant coherence meant that the coherence observed between 2 signals was greater than coherence due to chance.

Gain gave the size of the output per unit of input and was plotted on a log scale. Interpreting gain was conditional on significant coherence between signals. When there was significant coherence between 2 signals, gain calculations helped to understand the scale relationship rather than just the correlation between signals. It gave insight into how receptive the CNS was to the input, or how heavily weighted sensory information is. This is because it established how large the magnitude of cause and effect between input and output relationships. Specifically, it was used by taking the magnitude of cross-spectrum between an input and output divided by the input auto-spectrum

(Horslen et al., 2014; Lim et al., 2017). It is not normalized by the output power spectrum, like coherence, and therefore does not decrease even if non-vestibular input leads to increasing output magnitude. The equation is as follows, where x is the input and y is the output signal:

$$G(\mathcal{T}, \mathfrak{f}) = \frac{|P_{xy}\,(\mathcal{T}, \mathfrak{f})|}{|P_{xx}\,(\mathcal{T}, \mathfrak{f})|}$$

3.5.3 Statistical Analysis

A repeated measures t-test was used to see if AP CoP RMS was significantly different across the NO TOUCH and TOUCH conditions. Prior to comparing between conditions, a Shapiro-wilk test was used to test the assumption that data from the NO TOUCH and TOUCH conditions were normally distributed.

Differences in EVS-AP CoP coherence between NO TOUCH and TOUCH conditions were assessed in two ways. The coherence and gain analyses were conducted on pooled data from all participants. I also used more traditional within-participants t-tests to control inter-participant differences in coherence responses to addition or removal of light touch.

For the pooled analyses, data from all participants (exp 1: n=15, exp 2: n=10) were concatenated into single EVS and CoP arrays. These arrays were then binned into 2s non-overlapping sections (2048 samples, 0.5Hz resolution), where coherence and gain were calculated for each bin. Mean and point-wise 95% confidence limits of both coherence and gain were calculated across all bins (exp 1: 1500 bins, exp 2: 1000 bins). Based on a 95% confidence limit, a threshold for significant coherence within each condition was set to determine whether EVS and CoP cohered. Significant within-conditions coherence was a prerequisite for all subsequent analyses.

Differences in coherence between NO TOUCH and TOUCH conditions were examined using a difference of coherence test. The difference of coherence test (Amjad et al., 1997) is a modified X^2 test that estimates differences in coherence at common frequencies (0.5-30 Hz here) between 2 conditions. This approach reduces the risk of a type 1 statistical error increases when running this test on both multiple participants and frequencies. The test compares standardized differences between conditions and develops 95% confidence limits based on the Fisher transform ($\tanh{-1}$) of the square root of the coherence values. Any frequencies where the standardized difference of coherence exceeded the 95% confidence limits were considered statistically different. If there were 3 adjacent frequency bins (0.5 frequency resolution) with significant differences in coherence between conditions for both experiment 1 and 2, then the null hypothesis regarding coupling between EVS and CoP for RQ1 was rejected. Pooling data together was also useful to identify where mean differences were located.

To pool the data for single state trials of both experiments, non-overlapping bins were used from each participant so that each participant contributed 100 bins for single state trials. The final sample had 1500 bins from 15 participants for single sate trials of experiment 1 and 1000 bins for single state trials of experiment 2. Each bin was analyzed separately to determine the mean coherence or gain estimates.

The data used to address RQ 1/2 came from different trials than the data used for RQ4 (single state versus switching). As such, the data from the switching trials were sectioned and concatenated into regions that only contained NO TOUCH or TOUCH data across participants, and the same analyses were applied to confirm that the effects seen in RQ1/2 were replicated in the data used for RQ4. For experiment 1, 20 seconds on either side of the 150 transitions to NO TOUCH were used. This led to 1500 bins per NO TOUCH (after transition) and TOUCH (before transition) conditions (100 bins per participant). For experiment 2, 8 seconds on either side of the 380 transitions to NO TOUCH were used. This led to 1520 bins per NO TOUCH (after transition) and TOUCH (before transition) conditions (153 bins per participant).

Within the pooled coherence plots, the bins with significant coherence between NO TOUCH and TOUCH conditions were recorded and compared. Peak coherence was also compared across NO TOUCH and TOUCH conditions.

I also used paired samples t-tests to confirm that significant differences between conditions persisted after controlling for inter-participant differences. I calculated EVS-AP CoP coherence for individual participants (i.e., without pooling). I then calculated cumulative sums of coherence for each participant across two bandwidths (under 10 Hz and 13-25 Hz), based on ranges of significant coherence in both conditions from the pooled data. I then used paired samples t-tests to determine whether the cumulative sum coherence in each bandwidth was statistically different between TOUCH and NO TOUCH conditions. Shapiro-Wilk test was used to determine test for the assumption of normality between the samples. Finally, I used Cohen’s d to quantify effect sizes of the changes in coherence between conditions.

The gain calculations were used to compare effect sizes between touching and not touching conditions on average across the different frequencies to address RQ2. Peak gain was recorded and compared across NO TOUCH and TOUCH conditions. Non-overlapping regions of the confidence limits represented significantly different gain values at the respective frequencies (Horslen et al., 2014). If there were 3 adjacent frequency bins (0.5 frequency resolution) containing non-overlapping regions of confidence limits, then the null hypothesis for experiment 1 and 2 regarding gain between EVS and CoP was rejected.

3.5.4 Time-Dependent Analysis

Time–frequency coherence and gain were used to address RQ4 for experiments 1 and 2. The time-dependent coherence and gain were averaged over all the transitions for either switch to NO TOUCH or switch to TOUCH and pooled across participants (Forbes et al., 2017; Luu et al., 2012). However, the transitions from experiments 1 and 2 were evaluated separately.

In each experiment, the number of transitions per participant was made equal. This meant that some transitions were excluded for some participants to match the number of transitions analyzed to the number available from the participant with the fewest transitions. For experiment 1, there were 150 total transitions to NO TOUCH, with 10 transitions per participant. There were 120 transitions to TOUCH and 8 per participant. For experiment 2, there were 380 total transitions to NO TOUCH, with 38 transitions used per participant. For transitions to TOUCH, there were 370 transitions, with 37 transitions per participant.

The data for both experiments are sectioned into 2 s overlapping bins, with the bins being captured every 100 ms. In experiment 1, 10 seconds before and after each transition were included in the analysis. This led to 201 total bins, with 100 on each side of the transition. For experiment 2, 4 seconds before and after the transition were analyzed. This led to 81 total bins, with 40 on each side.

Time-dependent changes in coherence and gain were further characterized by splitting the coherence and gain into low (under 10 Hz) and high (13-30 Hz) frequency bins. Then, thresholding techniques were used to identify the time where the mean of coherence or gain for low and high frequencies decreased or increased by 2 standard deviations compared to the pre and post-transition means. This characterizes the period of change of coherence or gain due to the transitions to TOUCH or NO TOUCH.

Chapter 4

Results

4.1 Post Collection Exclusion

One participant from experiment 1 only did ML trials and then dropped out due to time restraints. One participant from experiment 2 did not have any accelerometer data, as the connection between the accelerometers and software was malfunctioning. Data from the baseline trials were excluded due to corruption of the data files; this included 1 from experiment 1 pre-EVS, 1 from experiment 1 post-EVS, and 1 from experiment 2 post-EVS. As such, 15 participants were included in the final analysis for experiment 1, and 10 participants were included in experiment 2.

4.2 CoP RMS Changes with Light Touch

There was a statistically significant reduction in AP CoP RMS from NO TOUCH to TOUCH that was seen in both experiments for single state, pre and post baseline trials. Table 1 below shows the averages, percent change, and statistical test outcomes between NO TOUCH and TOUCH conditions with and without EVS. Appendix B shows data from pre-EVS, EVS and post EVS. Figure 10 shows the NO TOUCH and TOUCH AP CoP RMS averages for single state and post baseline trials, where AP CoP RMS was reduced by 45-52% in the TOUCH condition compared to NO TOUCH.

Table 1: AP CoP RMS Reductions with Light Touch

Average and standard deviations of AP CoP RMS of NO TOUCH and TOUCH conditions for experiment 1 and 2. Data were averaged across 15 participants for experiment 1 and 10 participants for experiment 2. Percent change and statistical outcomes across conditions are included. Means ± sd.

Experiment	Trial	NT Average	T Average	% Change	Statistics
Experiment 1	With EVS	6.48 ± 1.88 mm	3.16 ± 1.28 mm	50±18%	T_{14}= 7.33 0.000003723 <p= 0.05
	Post EVS	6.34 ± 2.33 mm	2.91 ± 1.49 mm	49± 31%	T_{13}= 4.46 P = 0.00064095
Experiment 2	EVS	8.49 ± 2.67 mm	4.45 ± 2.07	45±28%	T_9= 4.12 P = 0.0026
	Post EVS	5.35±1.65 mm	2.68 ±1.54 mm	52±26%	T_8= 4.53 P = 0.0019

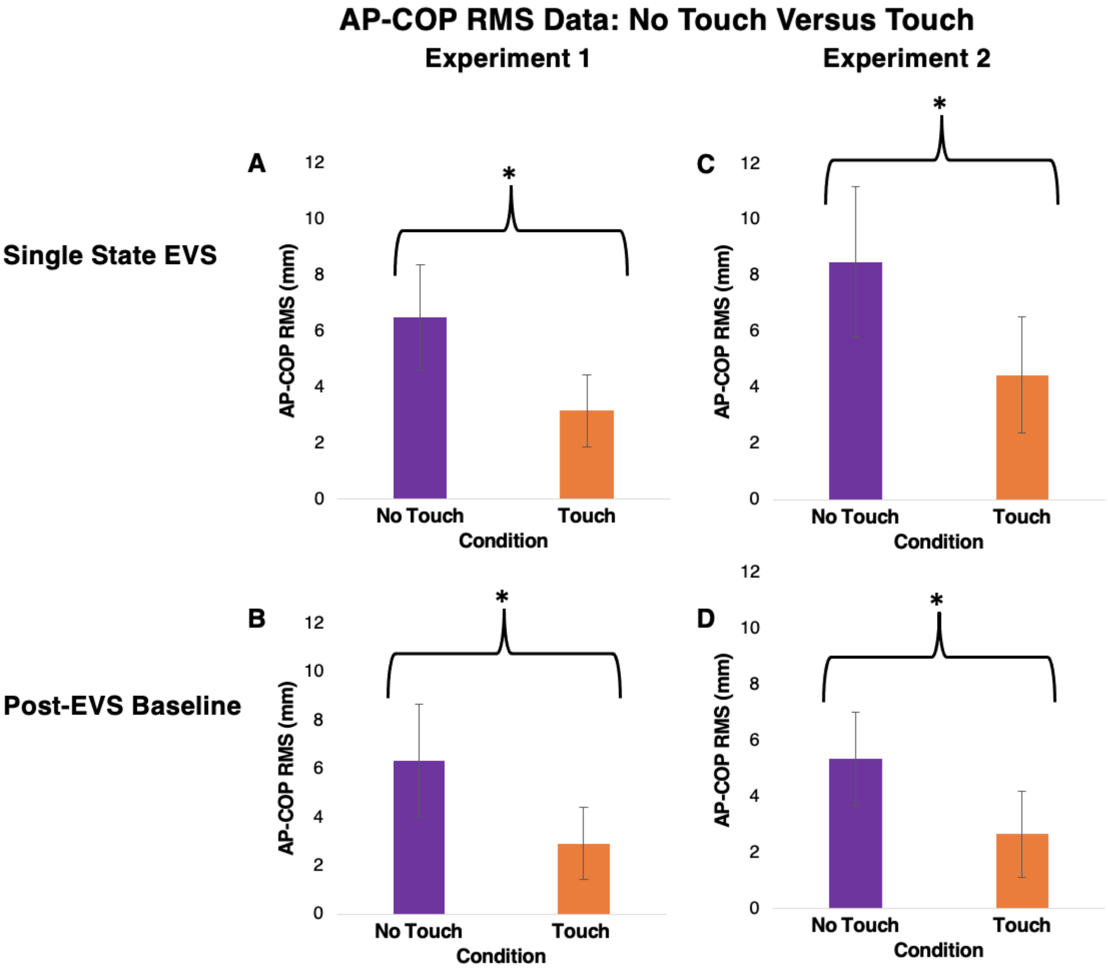

Figure 10: AP-CoP RMS for Single State and Post Baseline Trials

Average AP-CoP RMS of single state (A) and post baseline (B) trials for both experiments. Data was averaged across 15 participants for experiment 1 and 10 participants for experiment 2. No TOUCH data shown in purple and TOUCH data shown in orange. Standard deviation represented with error bars.

4.3 Research Question 1: Coherence Changes with Light Touch

4.3.1 Coherence

As shown in figure 12 panel A, significant coherence in experiment 1 was found from 0.5 Hz to 10 Hz and 13 Hz to 27 Hz for NO TOUCH and from 0.5 Hz to 10 Hz and from 11 Hz to 30 Hz for TOUCH. Peak in coherence in NO TOUCH was found at 2 Hz (R^2=0.111) and at 1 Hz for TOUCH (R^2=0.144). A second distinct peak was found at 20 Hz (R^2= 0.124) for TOUCH. For experiment 2, significant coherence was found from 0.5 Hz to 10 Hz and 14.5 Hz to 24 Hz for NO TOUCH and from 0.5 Hz to 10.5 Hz and from 11.5 Hz to 30 Hz for TOUCH (shown in figure 12 panel D). The peak in coherence for NO TOUCH was at 2 Hz (R^2=0.121) and was at 1 Hz (R^2=0.134) for TOUCH. Another second distinct peak was found at 20 Hz for TOUCH (R^2=0.106). The switching trial data (Appendix C) and individual participant data shown in figure 11 showed similar patterns to the single state trials.

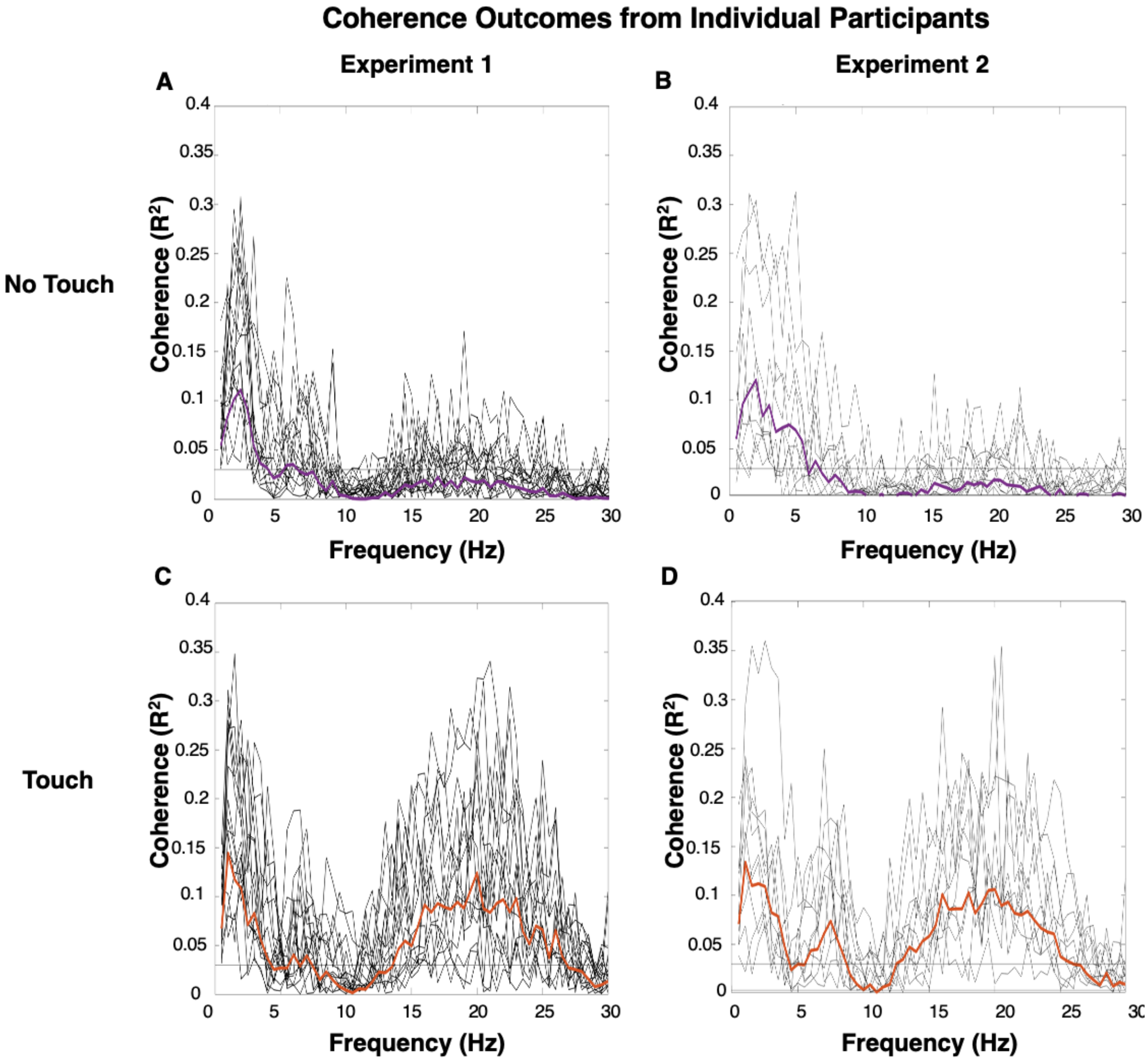

Figure 11: Effects of Touch on Single State Individual Participant EVS and AP CoP Coherence

Single participant (thin black lines) and pooled coherence data (thick colored lines) from experiments 1 (left column) and 2 (right column). Generally, the pattern of increased EVS-AP CoP coherence between 11.5Hz and 30Hz seen in the pooled TOUCH (orange) data is reflected in the individual participant data. Pooled data are from 15 participants for experiment 1 during TOUCH (A), and NO TOUCH (C) conditions, leading to 1500 total bins with a 0.5 Hz frequency resolution. Pooled data are from 10 participants for experiment 2 during TOUCH (B) and NO TOUCH (D) conditions, leading to 1000 total bins with a 0.5 Hz frequency resolution. The TOUCH condition is shown in orange and NO TOUCH in purple. The y axis shows coherence amplitude, and the x axis shows frequency. The thin horizontal line above the x axis represents the threshold for significant coherence of individual participant data.

4.3.2 Difference of Coherence

In experiment 1, the difference of coherence test revealed a significant increase in coherence in the TOUCH, compared to NO TOUCH, condition from 11 Hz to 28.5 Hz (figure 12 panel B). Since coherence was significantly different between conditions, the null hypothesis that coherence between EVS and CoP would not be statistically different with light touch was rejected. It was also rejected for experiment 2, as TOUCH had significantly greater coherence from 12 Hz to 27.5 Hz (figure 12 panel E).

Due to the concatenated coherence data from both experiments showing distinctive peak distributions in the low frequency range of 0.5-10 Hz and the high frequency range of 13-30 Hz, the data were split and treated separately when capturing effect size. The average cumulative sum for experiment 1 across participants for coherence of low frequency in NO TOUCH was 1.377 R^2 and 1.542 R^2 for TOUCH. The average cumulative sum across participants for coherence of high frequency in NO TOUCH was 0.952 R^2 and was 3.190 R^2 for TOUCH (235% increase from NO TOUCH to touch). There was no significant difference in cumulative sum of coherence in the low frequency range between NO TOUCH and TOUCH ($t = -1.24$, $p > 0.05$, Cohen’s $d = -0.314$). There was a significant increase in cumulative sum of coherence in the high frequency range from NO TOUCH to TOUCH ($t = -5.85$, $p < 0.05$, Cohen’s $d = -4.265$). The Cohen’s d for high frequency falls into the large effect size range. The average cumulative sum for experiment 2 across participants for coherence of low frequency in NO TOUCH was 1.512 R^2 and 1.703 R^2 for TOUCH. High frequency in NO TOUCH was 0.804 R^2 and was 3.074 R^2 for TOUCH (282% increase from NO TOUCH to touch). There was no significant difference between NO TOUCH and TOUCH in the low frequency cumulative sum ($t = -0.791$, $p > 0.05$, Cohen’s $d = -0.211$). However, there was a significant increase in coherence in the high frequency cumulative sum from NO TOUCH to TOUCH ($t = -5.52$, $p < 0.05$, Cohen’s $d = -2.506$). The Cohen’s d for high frequency falls into the large effect size range for experiment 2.

4.4 Research Question 2: Gain Changes with Light Touch

In experiment 1, gain was significantly higher in the NO TOUCH, compared to TOUCH, condition from 0.5 Hz to 8Hz .The peak of NO TOUCH gain was $10^{0.509}$mm/mA and $10^{0.183}$ mA for TOUCH, both at 0.5 Hz. From 0.5 Hz to 8 Hz, gain decreased by 38%-68%, and the mean difference was 58% (figure 12 panel C). The null hypothesis for research question 2, which states that gain would not be statistically different when light touch feedback was available, was rejected. For experiment 2, NO TOUCH had significantly greater gain from 0.5 Hz to 7 Hz. The peak of NO TOUCH gain was $10^{0.653}$ mm/mA and was $10^{0.199}$ mm/mA for TOUCH, both at 0.5 Hz. From 0.5 Hz to 8 Hz, gain decreased by 47%-83%, and the mean difference was 68% (figure 12 panel F). The null hypothesis for research question 2 was also rejected for experiment 2.

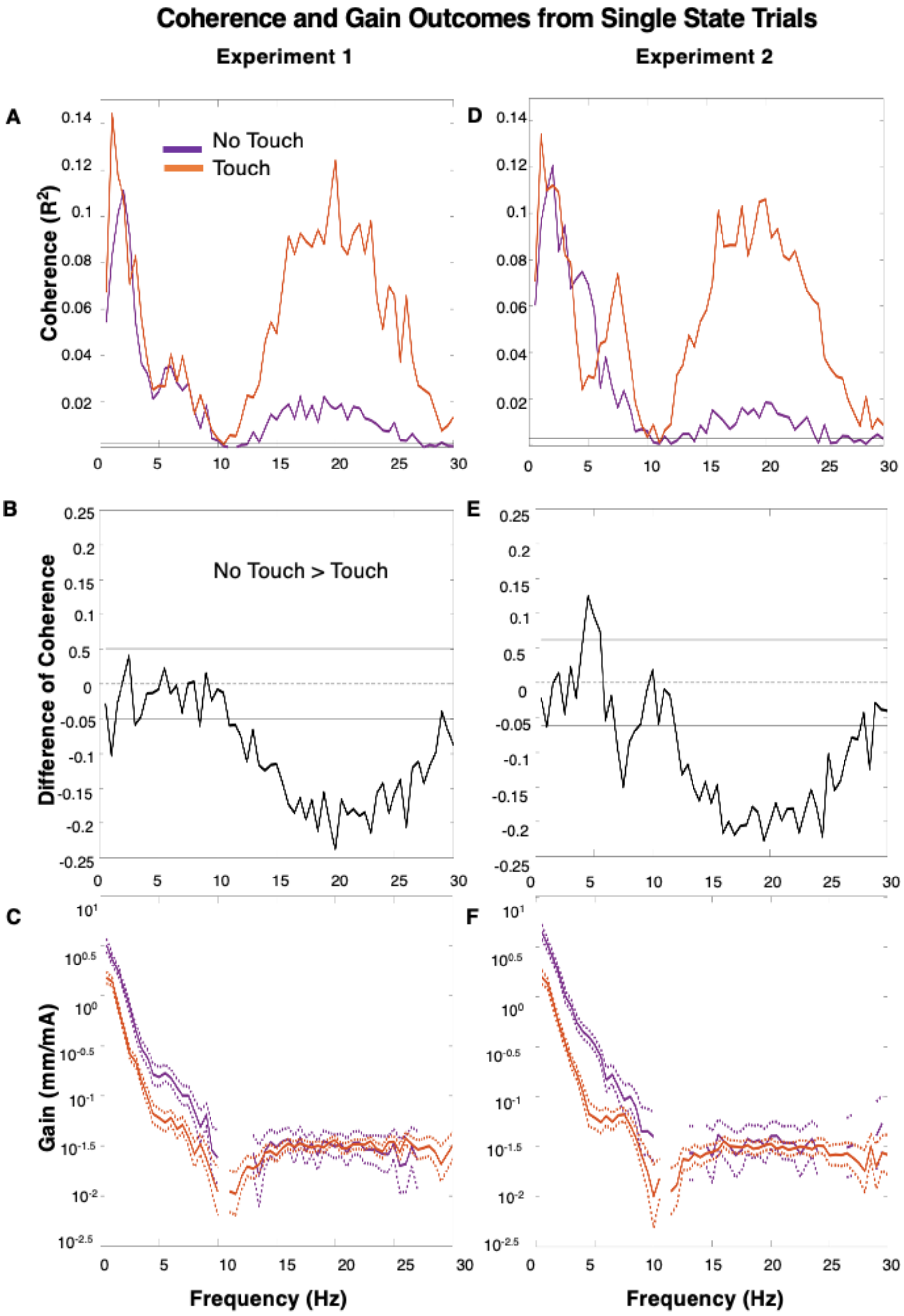

Figure 12: Effects of Touch on Single State EVS and AP CoP Coherence and Gain

A: Pooled coherence plot for the NO TOUCH and TOUCH conditions. The y axis shows coherence amplitude, and the x axis shows frequency. The thin horizontal line above the x axis represents the threshold for significant coherence. The purple line is NO TOUCH, and the orange line is TOUCH. B: Difference of coherence plot for concatenated NO TOUCH and TOUCH conditions. The y axis shows difference of coherence amplitude, and the x axis shows frequency. The dotted line located at y axis 0 indicates the middle of the plot where data is perfectly similar across conditions. The thick horizontal lines above and below the dotted line are the significance thresholds. Anything above the top line has significantly greater coherence for NO TOUCH and anything below the bottom line has significantly greater coherence for TOUCH. C: Gain plot for concatenated NO TOUCH and TOUCH conditions. The y axis shows gain, and the x axis shows frequency. The purple line represents NO TOUCH, and the orange line represents TOUCH. The dotted lines surrounding the thick lines are the 95% confidence intervals. D, E and F are plots for experiment 2. Data were concatenated across 15 participants for experiment 1 (left column), leading to 1500 total bins with a 0.5 Hz frequency resolution. Data was concatenated across 10 participants for experiment 2 (right column), leading to 1000 total bins with a 0.5 Hz frequency resolution.

4.5 Research Question 3: Accelerometry Changes with Light Touch

At the head, significant coherence was found from 0.5 Hz to 6.5 Hz for NO TOUCH and from 0.5 Hz to 2 Hz and from 3 Hz to 22.5 Hz for TOUCH. The peak in coherence for NO TOUCH was at 1 Hz (R^2=0.110) and was at 1 Hz (R^2=0.142) for TOUCH. A second distinct peak was found at 13 Hz (R^2=0.055) for TOUCH (figure 13 panel A). Coherence was significantly greater for TOUCH from 3 to 10 Hz and from 11 to 18 Hz, shown with the difference of coherence test. For head gain, there were no meaningful significant differences between NO TOUCH and TOUCH (figure 13 panel D).

At the sternum, significant coherence was found from 0.5 Hz to 5.5 Hz for NO TOUCH and from 0.5 Hz to 5 Hz for TOUCH. The peak in coherence for low frequency in NO TOUCH was at 2 Hz (R^2=0.084) and was at 1.5 Hz (R^2=0.038) for TOUCH (figure 13 panel B). There were no distinct secondary peaks. No TOUCH had significantly greater coherence from 1.5 to 2.5 Hz. For sternum gain, NO TOUCH was significantly greater than TOUCH from 1.5-2.5 Hz. This was 3 adjacent frequency bins, just making it a meaningful difference. The NO TOUCH peak was $10^{1.764}$ mm/s^2/mA at 0.5 Hz and the TOUCH peak was $10^{1.641}$ mm/s^2/mA at 0.5 Hz (figure 13 panel E).

At the dominant arm, significant coherence was found from 0.5 Hz to 9 Hz for NO TOUCH and there was no significant coherence for TOUCH. The peak in coherence NO TOUCH was at 2 Hz (R^2=0.068) (figure 13 panel C). No TOUCH had significantly greater coherence from 0.5-4.5 Hz. For dominant arm gain, NO TOUCH was significantly greater than TOUCH from 0.5-2 Hz, just making it a meaningful difference. The NO TOUCH peak was $10^{1.553}$ mm/s^2/mA at 0.5 Hz and the TOUCH peak was $10^{0.951}$ mm/s^2/mA at 0.5 Hz (figure 13 panel F).

The null hypothesis stating that there would be no statistical difference between NO TOUCH and TOUCH coherence and gain at the head, sternum or arm was rejected.

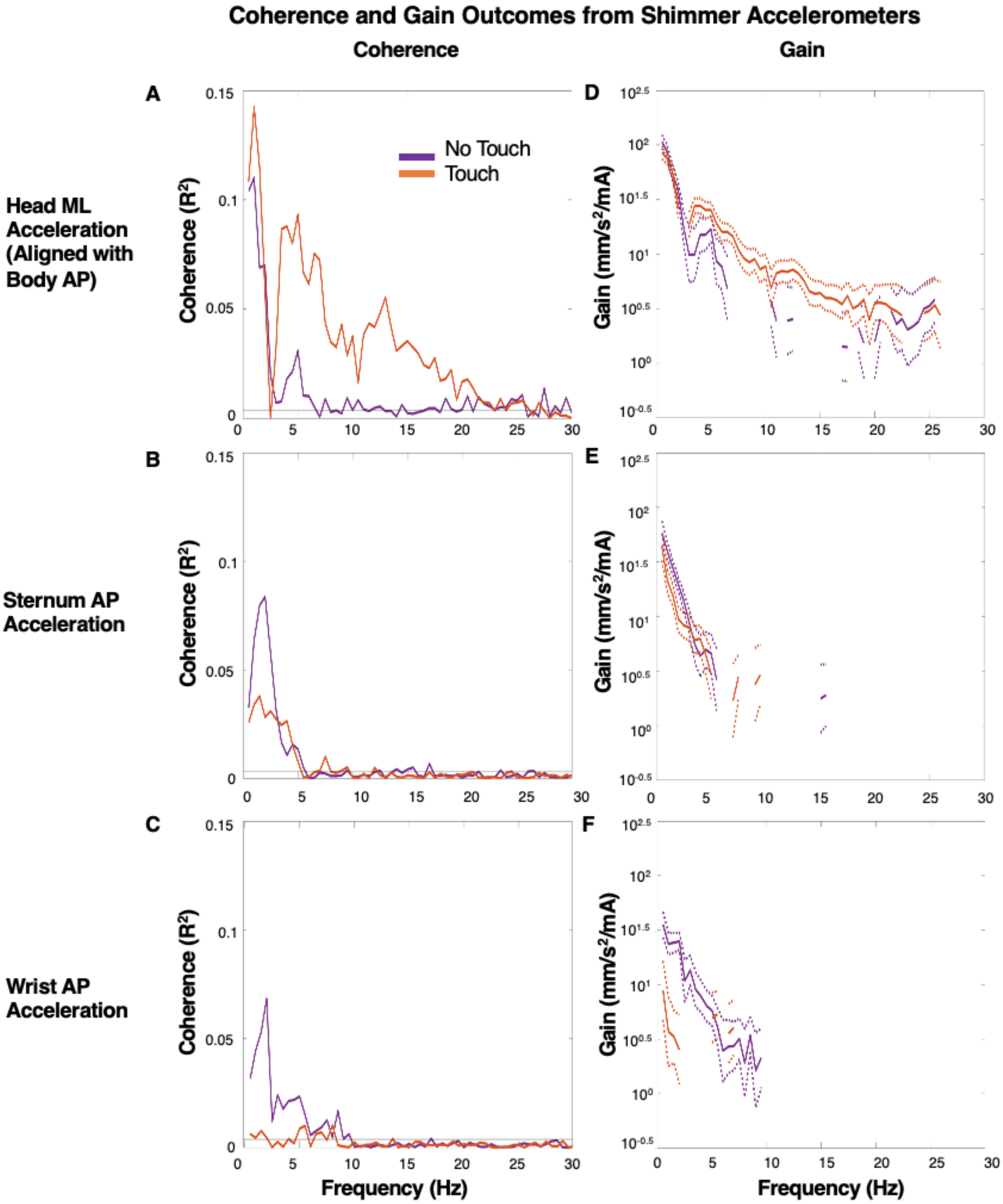

Figure 13: Single State Coherence and Gain Between EVS and Body Segmental Acceleration for No TOUCH Versus TOUCH

Data were concatenated across 9 participants leading to 900 total bins with a 0.5 Hz frequency resolution. Coherence data are shown on the left and gain data are shown on the right. The head acceleration data are represented on the first row (A, D), sternum acceleration on the second row (B, E), and wrist data on the third row (C, F). No TOUCH data are purple lines while TOUCH data are orange lines. For coherence plots, the y axis shows coherence amplitude, and the x axis shows frequency. The thin horizontal line above the x axis represents the threshold for significant coherence. For gain, the y axis shows gain amplitude, and the x axis shows frequency. The purple line represents NO TOUCH, and the orange line represents TOUCH. The dotted lines surrounding the thick lines are the 95% confidence interval.

4.6 Research Question 4: Time-Dependent Analyses

Figures 14 and 15 are 3-dimensional displays of coherence over time relative to the transition to NO TOUCH (figure 15 panels A and C) or TOUCH (figure 15 panels B and D) across 30 Hz. Figure 14 shows data from an indivudal particpant, which matches the patterns found in the concatenated group data (figure 14).

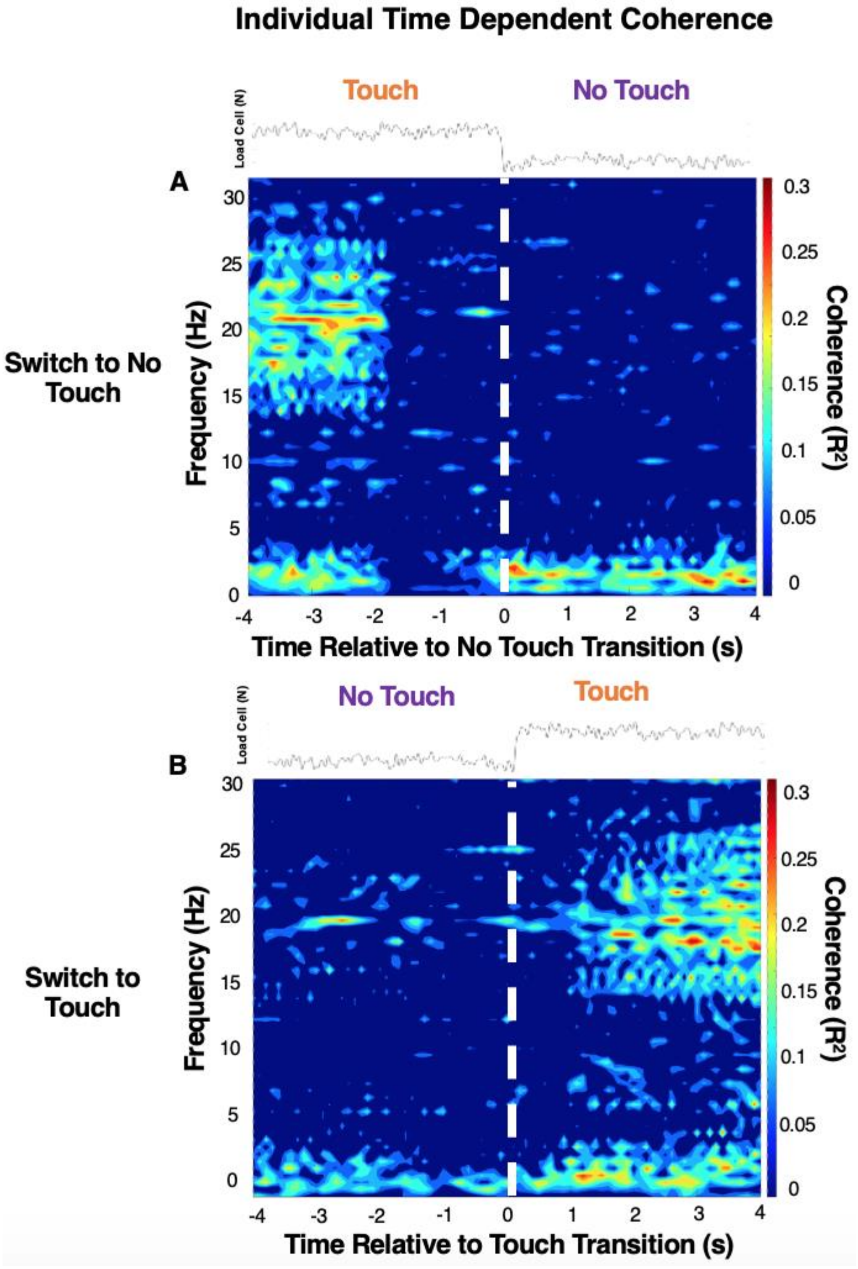

Figure 14: Participant 001 (exp 2) Time-Dependent Coherence Between EVS and AP CoP for Switching to No TOUCH or TOUCH

Time-dependent coherence for switch to NO TOUCH (A) and TOUCH (B) are represented. The y axis shows frequency. The x axis is time relative to when the finger is lifted off the load cell or contacts the load cell, which occurs at time 0. Coherence amplitude is represented by the color scale, with warmer colors having higher coherence and cooler colors having lower coherence. There were 38 transitions to NO TOUCH and 81 bins total. For transitions to TOUCH, there were 37 transitions, with 81 bins total.

Figure 15 shows which range of frequencies and what time points relative to the transitions to NO TOUCH or TOUCH yield changes in coherence. High frequency coherence that can be seen in the teal colour decreases before the transition to NO TOUCH and increases after the transition to TOUCH.

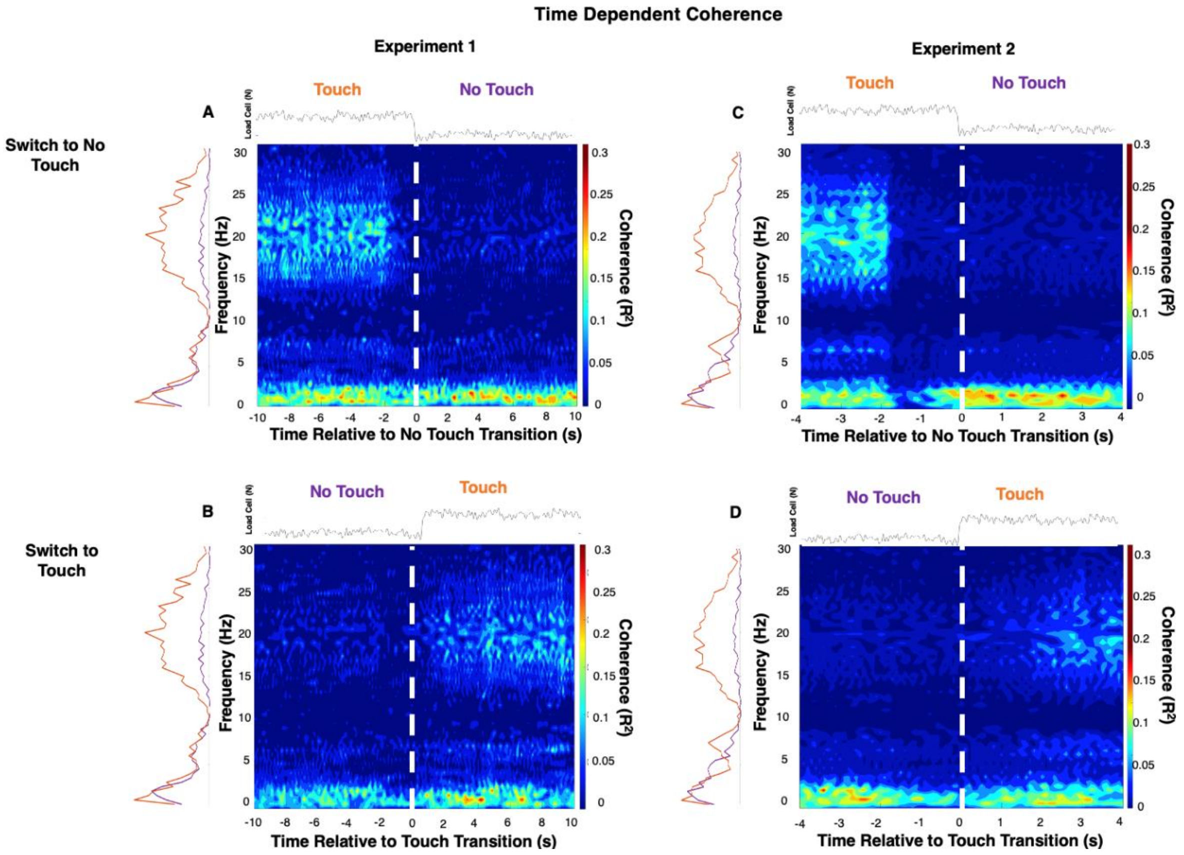

Figure 15: Time-Dependent Coherence Between EVS and AP CoP For Switching to No TOUCH or Touch

Time-dependent coherence for switch to NO TOUCH (A, C) and TOUCH (B, D) are represented. The y axis shows frequency. The x axis is time relative to when the finger is lifted off the load cell or contacts the load cell, which occurs at time 0. Coherence amplitude is represented by the color scale, with warmer colors having higher coherence and cooler colors having lower coherence. For experiment 1 (left column), there were 201 bins, staggered by 0.1s intervals per transition, allowing calculation of time-dependent coherence ±10s to either side of the transition. There were 150 transitions (10 per participant) in the switch to NO TOUCH (top row) and 120 transitions (8 per participant) in the switch to TOUCH condition (bottom row). For experiment 2 (right column), there were 81 bins, staggered by 0.1s intervals, per transition, allowing calculation of time-dependent coherence ±4s to either side of the transition. There were 380 transitions (38 per participant) in the switch to NO TOUCH (top row) and 370 transitions (37 per participant) in the switch to TOUCH condition (bottom row).

When comparing gain and coherence, changes occur at relatively similar times, although in opposite directions. Figure 16 shows gain overlaid on coherence. Black lines show coherence, green lines show gain. Coherence decreases when switching to NO TOUCH 1.8 seconds prior to when the finger is lifted off in experiment 1 and 2. Similarly, gain increases 1.3 seconds and 1.8 seconds before the finger is lifted off in experiment 1 and 2, respectively. When switching to TOUCH, coherence increases 1.1 seconds and 1 second after contact is made in experiment 1 and 2, respectively. Gain decreases 1.9 seconds and 0.2 seconds after contact is made in experiment 1 and 2, respectively.

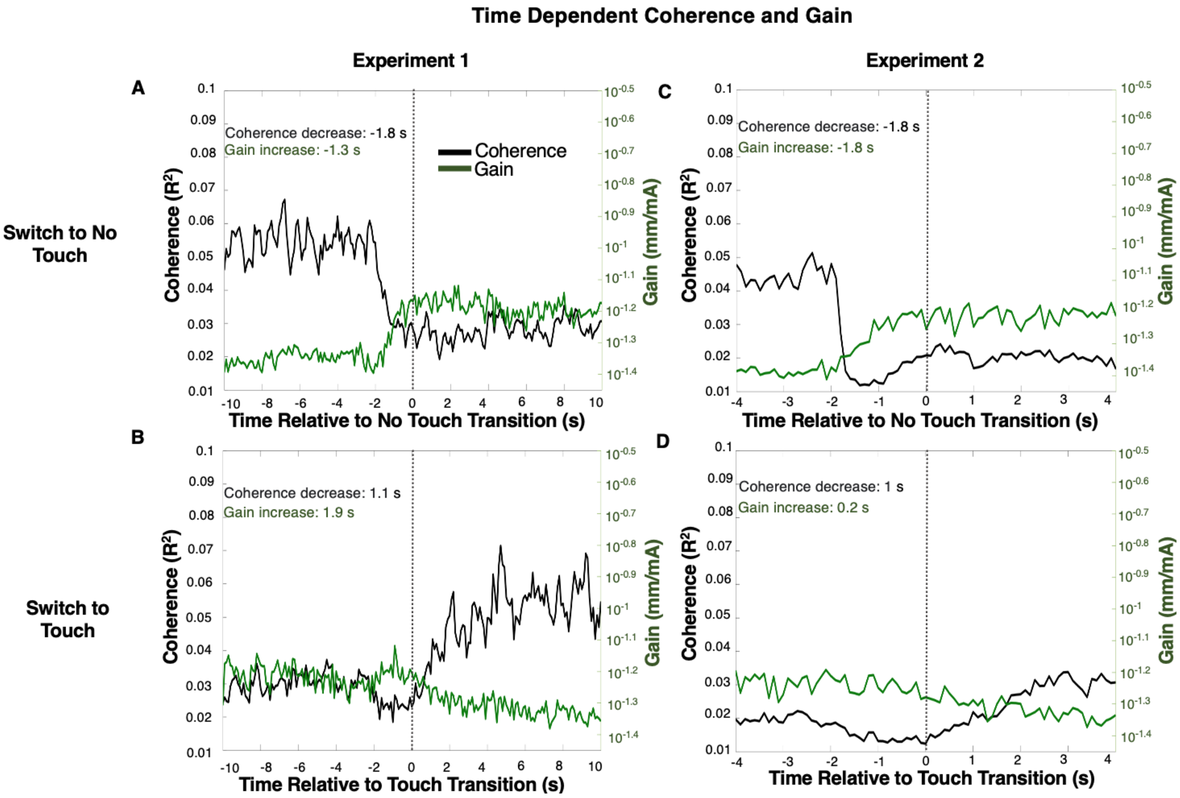

Figure 16: Time-Dependent Coherence and Gain Between EVS and AP CoP

Time-dependent coherence and gain (both averaged across 0.5-25 Hz) for switch to NO TOUCH (A-C) and TOUCH (B-D) are represented, with experiment 1 represented in the left column and experiment 2 in the right column. On each plot, coherence is plotted in black (right y axis) and gain is plotted in green (left y axis). Time (x axis) is expressed relative to when the finger is lifted off the load cell (top row; A, C) or contacts the load cell (bottom row; B, D), which occurs at time 0. Note that time scales are different for experiments 1 and 2. The time values included are where the threshold is crossed for each signal. The thresholds are where the signal has increased or decreased 2 standard deviations above or below the pre transition mean. The dotted vertical line occurs at time 0 (the transition point). For experiment 1 (left column) switch to NO TOUCH (top row), data were concatenated across 15 participants with 10 transitions each, leading to 150 total transitions to NO TOUCH, with 10 transitions per participant. There were 201 bins total. For experiment 1 switch to TOUCH (bottom row), there were 120 transitions and 8 per participant. There were also 201 bins in total. For experiment 2 (right column), there were 380 total transitions to NO TOUCH, and 38 per participant. There were 81 bins total. Note that there are only 4 seconds on either side of the transition. For transitions to TOUCH, there were 370 transitions and 37 per participant. There were also 81 bins total.

The time points of when changes start, and end capture the transition period of the measures in response to switch to NO TOUCH or switch to TOUCH (refer to Appendix D for timepoints). Figure 17 reveals that coherence changes precede changes in AP CoP RMS for both transitions to NO TOUCH and TOUCH. The black dotted vertical lines which represent the point at which coherence crosses the threshold are always before the red vertical dotted lines which represent the time at which AP CoP RMS crosses the threshold. Since coherence decreases before the transition to NO TOUCH and after 0.5 seconds for the switch to TOUCH, the null hypothesis is accepted. This is because the transitions did not take place in the range of 0 to 0.5 seconds.

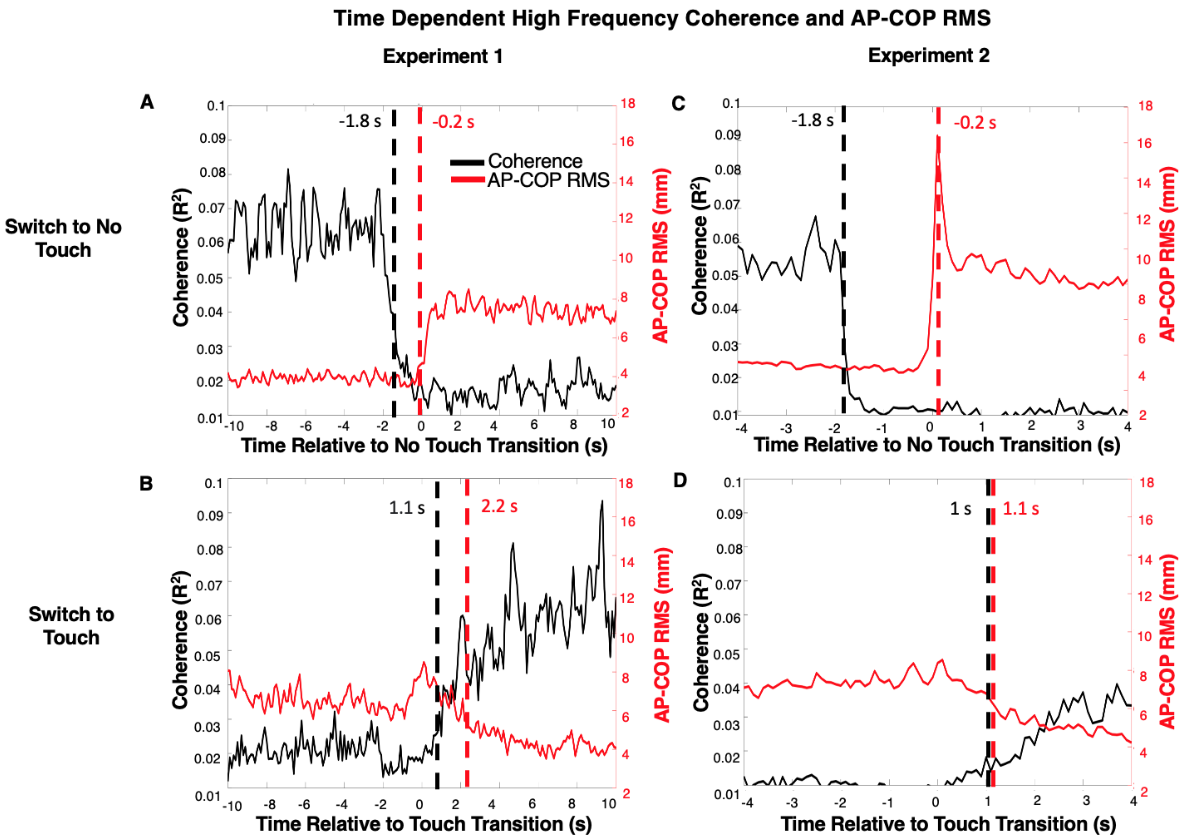

Figure 17: Time-Dependent High Frequency Coherence Between EVS and AP CoP and Sliding AP CoP RMS

Time-dependent high frequency (13-25 Hz) coherence for switching to NO TOUCH (A, C) or switching to TOUCH (B-D) shown in black and sliding AP CoP RMS shown in red. The right y axis shows EVS-AP CoP coherence amplitude. The left axis shows CoP RMS in mm. The x axis is time relative to when the finger is lifted off the load cell or contacts the load cell, which occurs at time 0. Note that time scales are different for experiments 1 and 2. The vertical dotted lines show the time point where the threshold is crossed for each signal. For experiment 1 (left column) switch to NO TOUCH (top row), data were concatenated across 15 participants with 10 transitions each, leading to 150 total transitions to NO TOUCH, with 10 transitions per participant. There were 201 bins in total. For experiment 1 switch to TOUCH (bottom row), there were 120 transitions and 8 per participant. There were also 201 bins total. For experiment 2 (right column), there were 380 total transitions to NO TOUCH, and 38 per participant. There were 81 bins total. Note that there is only 4 seconds on either side of the transition. For transitions to TOUCH, there were 370 transitions and 37 per participant. There were also 81 bins total.

Chapter 5

Discussion

The results from these experiments suggest that light touch input at the finger reduces whole body CoP displacement, as was hypothesized. This was confirmed through reductions in CoP RMS both with and without EVS, as well as through reductions in gain when light touch was available. Contrary to my hypothesis, light touch input at the finger increased coherence between EVS and AP CoP above 13 Hz. This means that there is more variation in the CoP that can be explained by EVS. Coherence decreased 1.2 to 1.8 seconds before switching from TOUCH to NO TOUCH, but increased 1 to 4 seconds after switching from NO TOUCH to TOUCH. The accelerometry data shows that high frequency coherence between EVS and segment linear accelerations above 10 Hz is only found for the head in the ML direction (aligned with body AP). Only arm and sternum acceleration demonstrated significant coherence up to 9 Hz, and NO TOUCH exhibited greater coherence between EVS and segment acceleration. This suggests that the observed high-frequency coherence in CoP may be driven by the upweighting of the vestibulocollic reflex.

Light touch reduces sway, which is shown through reductions in AP CoP RMS and EVS-CoP gain. AP CoP RMS is a measure to quantify CoP variation, and is not referenced to EVS, while gain quantifies CoP displacement in relation to the EVS input signal. Both can be used to estimate quantity of sway, but gain relates it back to the EVS signal. This study shows that light touch is an effective balance stabilizer with and without the presence of an additional noisy sensory cue. Reduction of CoP RMS during quiet standing with light touch has been shown previously (Holden et al., 1994; Jeka et al., 1996; Rabin et al., 2006; Sozzi et al., 2012). Without EVS, light touch has been shown to reduce CoP mean sway amplitude by 50-68% when standing on one leg (Holden et al., 1994) or standing in Romberg stance (Rabin et al., 2006). Consistent with these findings, the current study showed baseline CoP RMS to decrease by 39-58% and gain by 58-68% on average. This study reveals that a balance relevant cue providing veridical sensory information can reduce vestibular motor gain during multisensory integration for control of movement. It also shows that light touch can be used to stabilize CoP against a potent sensory perturbation, like EVS.

Coherence and gain were initially expected to change together, similar to previous studies looking at vestibular control of balance (Horslen et al., 2014; Luu et al., 2012; Rasman et al., 2021; Tisserand et al., 2018). However, while gain was reduced with light touch, coherence was increased.

As such, the relationship between coherence and gain for this study had to be reconsidered. Although light touch was able to reduce sway in the presence of a destabilizing cue, the CNS was still increasing its reliance on vestibular information. This is indicated by the fact that there was more variance explained in the CoP that could be explained by EVS. This increase in coherence may not be readily observed in sway, since unperturbed postural sway tends to occur under 1 Hz (Carpenter et al., 2001) and light touch increased coherence above 13 Hz. This high frequency peak, where the large increases in coherence were observed, has not been seen before, and suggests that positioning of the arm and light touch feedback may affect vestibular processing in a novel way.

The current study employed the same stimulation frequencies and parameters as other studies (e.g., Dakin et al., 2007; Dakin et al., 2010; Horslen et al., 2014; Lim et al., 2017), however, EVS-CoP coherence was observed at much higher frequencies. For example, Horslen et al (2014) used a 2-25 Hz EVS bandwidth, but only observed EVS-GRF coherence up to 16.5 Hz in the level ground, quiet standing condition that most closely matched the NO TOUCH condition used here. In the study by Horslen et al. (2014), significant differences in coherence between conditions were found from 5.5 Hz and 17.7 Hz. In the present study, differences in coherence were localized between 11 Hz to 28.5 Hz in experiment 1, which is a higher and wider range.

Since CoP captures the net movement of the body, segmental kinematic analyses were included in experiment 2 to reveal which segment of the body was driving these increases in high frequency EVS-CoP coherence. Measures of the head were included to examine whether increases in EVS-CoP coherence were driven by the upweighting of the vestibulocollic reflex (Highstein et al., 2004). Measures of the sternum served as markers of whole-body sway and to gauge vestibulospinal modulation (Dakin et al., 2010; Forbes et al., 2013). Measures of the dominant arm were included to explore whether vestibular control of the arm, while maintaining the extended arm and finger posture required for light touch, was driving the changes in coherence (Britton et al., 1993; Smith et al., 2017; Smith & Reynolds, 2017). The results revealed that the head is likely the driving factor behind increases in high-frequency EVS-CoP coherence. This is because the EVS-acceleration coherence from the head shows the distinct low and high frequency peaks in TOUCH, while the data from the sternum and dominant arm only show the low frequency peak (refer to figure 13). The increases in EVS and head acceleration coherence are magnified at higher frequencies (13-30 Hz). This matches the frequency range by which the vestibulocollic reflex is activated, which spans 0- 30 Hz (Forbes et al., 2020). Vestibulocollic responses are mediated by the lateral and medial vestibulospinal tracts, and thus these responses would be correlated with EVS (Highstein et al., 2004). Naranjo et al., (2015) has also shown evidence for different modulation of vestibular-evoked responses in legs, arms, and neck, where neck vestibular evoked myogenic potentials were increased but not for the bicep brachii during height induced postural threat. The head is likely the cause of the changes in EVS-CoP coherence, as evidenced by the EVS-head acceleration results. This is further supported by the frequency range at which the vestibulocollic reflex is activated, and by previous evidence of differential modulation of vestibular-evoked responses (Naranjo et al., 2015).

When light touch is available, the CNS may attribute potent EVS signals to disruptive head movements and therefore up-weight vestibulocollic responses to counteract the perceived movement. The reflex is meant to oppose unwanted head oscillations or motions induced by external perturbations (Highstein et al., 2004). The light touch cues allow the CNS to determine that the vestibular cues are not reflective of the body's position with respect to gravity, due to a more holistic representation of body orientation. The potent EVS-driven vestibular motion signal conflicts with the light touch cues that suggest the participant is not moving. As such, the CNS can dismiss whole-body sway as the cause of the vestibular cues, and, by exclusion, conclude that the vestibular input must be due to involuntary head-on-trunk motion. When light touch is not available, the CNS loses certainty about the source of the vestibular cues. As a result, a more conservative, balance-protective strategy is adopted, increasing the gain of the lateral vestibulospinal reflex to reduce body sway when light touch information is not present to contradict the EVS.

When switching from TOUCH to NO TOUCH, there is a loss of balance relevant sensory information. The results from this study show that EVS-CoP coherence is decreased while gain is increased before the transition. Coherence decreased between 1.2 and 1.8 seconds prior to the transition, with a similar observation made in experiment 2 (1.5-1.8 s). It is thought that the CNS is anticipating the loss of sensory information and a threat to balance and must compensate for this. In the study by Tisserand et al., (2018), vestibulo-motor coherence was measured during walking. They found coherence decreased 0.435 seconds before initiating gait. The present study focuses on time-dependent tasks and explores how vestibulo-motor coherence and gain can be proactively altered.

When switching from NO TOUCH to TOUCH, balance relevant sensory information is gained. The results from this study show that EVS-CoP coherence is increased while gain is decreased after the transition. Increases in coherence were observed from 1.1 to 1.8 seconds after the transition, with a similar pattern in experiment 2 starting from 1 second onward. In the study by Sozzi et al., (2012), passive touch (meaning that finger contact was controlled by the experimenter) reduced CoP amplitude 0.7-2 s after contact. In the present study, it took 1.1- 2.2 seconds to reduce CoP RMS in the passive condition when switching to TOUCH. Although the participants in the study by Sozzi et al., (2012) were in tandem stance, the comparison of these studies shows that light touch reduces sway in a similar time. In the study by Luu et al (2012), whole-body sway motion feedback was manipulated by a robot to be incongruent with motor commands. The CNS was able to quickly recognize in 150 ms that sensory feedback was unreliable, and thus reduce vestibulo-muscular coherence. In the study by Rasman et al., (2018), sensorimotor delays of whole-body sway motion were imposed by a similar robot system, and vestibulo-muscular coherence decreased from about 1.5 s to 4.4 s. These studies are similar to the current study, as they measured time-dependent vestibulo-motor coherence in a situation where sensory cues are not reflective of how the body is positioned with respect to gravity and the vestibular modulations were reactionary to the task transitions that occurred. It may be more difficult for the CNS to determine the reliability of the novel light touch cue, leading to the longer response time. Another possibility is that it may not be functional to re-weight vestibular information quickly in this scenario, as the threat to balance is less.

This asymmetry in re-weighting times surrounding addition versus removal of sensory information was also suggested by Jeka et al (2008). Jeka et al (2008) found that when visual motion increased, gain decreased within 5 s. However, when visual motion decreased, it took an additional 5 s for gain to increase by a similar amount. It was thought that rapid re-weighting was needed to avoid falling when the visual motion increased. Rapid re-weighting may also be needed when switching from TOUCH to NO TOUCH, since losing sensory information poses a threat to balance.

Coherence modulations were of similar timing to the gain modulations, and they both preceded CoP RMS changes. This implies that changes in how the CNS utilizes vestibular information precede shifts in whole-body sway. This could mean that there is some delay between the time it takes the CNS to adapt how it uses vestibular information and the time it takes to change whole body sway behavior. This could explain the need for fast or anticipatory vestibular modulations.

Understanding the timing of these vestibular modulations and responses allows a baseline representation of how long it should take to adapt to introduction and removal of a vestibular light touch conflict. This could provide a comparison for those with vestibular deficits to measure against. Future research could explore how multisensory integration or sensory re-weighting is affected in individuals with vestibular deficits. Furthermore, development of protheses requires an understanding of how sensory information is prioritized and used. Timing of responses can give insight into which structures play a role in vestibular modulation, since cortex mediated modulations tend to be slower due to complexity while brain-stem mediated responses are faster.

Since re-weighting of vestibular information takes over 0.5 seconds when switching to TOUCH (figure 15 panel B, D), there may be time enough for cortical structures, along with the cerebellum, and vestibular nuclei to influence this re-weighting. This may include associative areas such as the posterior parietal cortex (Clower et al., 1996; Whitlock, 2017), vestibular cortex (Lobel et al., 1999), and somatosensory cortex (Ioannides et al., 2013). The CNS may take a more conservative approach when adapting to touch, since it may not be functional to rapidly up-weight when the threat of falling is not imminent. In contrast, the loss of sensory information may be more destabilizing than addition and require faster brainstem mediated reactive and/or anticipatory adjustments.

There were several limitations in this study. The time-dependent findings from experiment 1 should be interpreted cautiously. The interval of time from when the experimenter said “switch” to the movement stage prior to actual contact with the load cell is not known. It is therefore difficult to attribute changes in EVS-CoP coherence to either motor planning or movement time. The load cell for experiment 1 was also about the size of a dime. Since the participants had their eyes closed, and the load cell was 1 cm in diameter, participants often missed, or did not immediately contact the load cell when attempting to touch it. Therefore, in some cases, participants might have received and started adapting to tactile cues before any change in load cell force was detected. However, these limitations were addressed in experiment 2. A passive paradigm was introduced so that participants could not predict or control when transitions occurred, reducing the likelihood of altering vestibulo-motor coherence and gain in anticipation of receiving the light touch information. A different load cell was used, built into a larger surface area (6 x 6 cm) to reduce the likelihood of participants missing the load cell on transition.

Despite introducing a passive touch paradigm in experiment 2, the decrease in coherence when switching to NO TOUCH happened at a remarkably similar time interval, even finishing slightly later. This suggests that participants might have been able to anticipate the changes, possibly due to environmental noise or sensations of the load cell moving away before it actually did. Additionally, the studies by Sozzi et al (2012) and Sciutti et al (1972) postulated that active touch does not improve sway reduction latencies in comparison to passive touch, as there was a minimal 160 ms sway reduction in the study by Sozzi et al (2012). Switching to NO TOUCH had a more pronounced impact on balance in experiment 2, with RMS values increasing from roughly 3 to 8 mm in experiment 1 and from about 3 to 16 mm in experiment 2. The CNS may be required to anticipate the transitions in experiment 2 more accurately due to the greater threat to balance. The findings from both experiments offer initial evidence for anticipatory modulation of vestibular input in balance control, setting the stage for further investigations.

Another possibility for the similarity in results across experiments could be attributed to a lack of temporal precision in the NeuroSpec analysis employed here. Not only is the similarity across experiments a concern, but the time at which coherence and gain changes occur before transitions to NO TOUCH would mean that the CNS is anticipating transitions approximately 2 seconds before they happen. Given that Experiment 2 was designed to reduce the predictability of transitions, this outcome is highly unlikely. The parameter settings chosen for NeuroSpec determined that coherence and gain were calculated in bins of 2 seconds every 100 ms. I used a long time window of 2 seconds to resolve lower frequencies (under 1 Hz), where sway typically occurs (Carpenter et al., 2001). As a result, there were several large bins that overlapped each other in time. The analysis does not determine when, within a bin, a change in coherence occurs. While one bin may show a change in coherence from the preceding bin, it does not mean the change occurred at the beginning of the bin. For example, if coherence at -1.8s is less than coherence at -1.9s, then the change in coherence might have occurred any time between -1.8 and 0.2s. Furthermore, the only region of the -1.8s bin that does not overlap with the -1.9s bin is between +0.1s and +0.2s. Therefore, it may be prudent to add a conservative 1.9 seconds to each of the latency estimates used in this analysis.

Appendix E shows how reducing bin window width affects time-dependent coherence. There is a clear relationship showing that as window width decreases, the changes in coherence and gain occur closer to the actual transition when switching to NO TOUCH and further from the transition when switching to TOUCH. I draw two conclusions from this data: first, even as temporal precision increases (bin width decreases), there are asymmetries between introduction and removal of sensory cues; second, even at time windows as small as 0.125 seconds, changes in coherence still occur before the transition. In fact, at the smallest bin width, the change in coherence was observed more than one full bin width before the TOUCH to NO TOUCH transition, suggesting the pre-transition coherence-change latencies are not simply an artefact of the analysis. AP CoP RMS also begins to increase before the transitions to NO TOUCH, increasing the confidence that there are anticipatory adjustments being made by the CNS (shown in figure 17).

As the CNS uses input from many sensory modalities to detect changes in posture and balance (refer to figure 3), other modality specific sensory inputs may have contributed to changes in vestibulo-motor coherence and gain observed here. Participants had proprioceptive information from the legs, trunk, and unique to this study, augmented or altered proprioceptive input from the neck and dominant arm in all trials. It is possible that the changes in vestibulo-motor coupling observed in this study are due to interactions between proprioceptive and vestibular inputs, and not due to cutaneous-vestibular interactions.

The role of proprioception in altered EVS-AP CoP coherence and gain is not clear. It was not my intention to nullify inputs to the proprioceptive system, and doing so would be very challenging. I did not attempt to quantify proprioceptive weight in any way, but it is likely that the CNS changes weights of proprioceptive inputs throughout this experiment. During standing balance, the central nervous system heavily relies on proprioceptive inputs from the muscles of the lower limbs (Fitzpatrick & McCloskey 1994). In the NO TOUCH condition, proprioceptive cues would suggest that the EVS cues are not driven by sway, given that a quiet stance is being maintained. During TOUCH, the proprioceptive cues would still indicate that the EVS cues are not sway-driven, but now the light touch cues would complement this. Perhaps, the CNS would be less certain in NO TOUCH that EVS cues are due to head-on-trunk motion because there is a conflict between the vestibular and proprioceptive cues.

The addition of the cutaneous information that matches proprioceptive cues might allow the CNS to increase its reliance on proprioception over vestibular sensation for control of standing balance. Having the arm positioned outwards would change proprioceptive inputs from the upper body. The consequences of this were not known, but it could either increase or decrease the effectiveness of the upper body proprioceptors to detect whole body sway. Regardless of proprioceptive weights changing, this study shows that addition of light touch is helping the CNS to re-weight vestibular information.

Additionally, having the head turned to the side is an unusual posture, and the participants often complained of pain in the neck. Proprioceptive inputs from the neck would be altered, potentially reducing cues related to how the head is moving in relation to the trunk. This posture may allow weights of proprioceptive inputs to change, and the CNS' ability to discern head-on-trunk movement vs whole-body sway. This might make the EVS cues more ambiguous regarding whether they were caused by head movement or whole-body movement.

Although there is other sensory information being received by the CNS, the light touch cues are still influencing vestibulo-motor coupling and gain. The light touch allows a more comprehensive view of the whole body and posture and sway, to complement the other proprioceptive and cutaneous cues. The more sensory information available, the easier it is for the CNS to determine the likely source of vestibular cues and adjust appropriately..

When transitioning in the switching trials for experiments 1 and 2, accuracy is required to maintain the hovering posture above the load cell for NO TOUCH and to place the finger on the load cell with the appropriate level of force for TOUCH. The motor control element of this task may influence vestibulo-motor coherence and gain. This focus could cause the CNS to bias weighting towards cutaneous somatosensory cues. However, the influence of attention on sensory re-weighting is not the focus of this study, and fluctuations in attention to sensory cues is something that happens in everyday life and situations.

The degree to which participants gained a mechanical advantage, and thus were able to stabilize sway, in the TOUCH conditions is not clear. The threshold of 2 N was used due to previous biomechanical modeling studies that showed that mechanical stabilization begins after that threshold (Holden et al., 1994). However, this study did not use any biomechanical modeling techniques to determine whether participants were mechanically stabilized. This means that changes to vestibulo-motor coherence and gain could also be attributed to mechanical stabilization along with the addition of cutaneous somatosensory information. Assuming a participant is holding a 2 N vertical force with a moment arm of about 20 cm, there would be a 0.4 Nm moment. If the individual weighs about 600 N with a 0.01 m moment arm, individuals would have a 6 Nm moment. This suggests that there may be a 7% load moment caused by the light touch at the fingertip. As such, I might expect participants to reduce their CoP displacement amplitude by approximately 7% in the TOUCH, compared to NO TOUCH condition. However, participants reduced their sway by 45-52%, therefore, it is unlikely that mechanical stabilization can fully account for the reductions in COP observed here. Furthermore, during a piloting session, an individual participant held onto a ground referenced metal bar as hard as they could. The results showed that the high frequency coherence peak was completely abolished (shown in Appendix F). This increases confidence that the high frequency coherence results that were found could be attributed to the addition of the light touch sensory information.

The results of the EVS-head acceleration coherence led to the hypothesis that the CNS was upweighting vestibulocollic responses to counteract the EVS stimulus. However, the extent to which head movement would be transmitted to changes in CoP is not known, due to mechanical damping of oscillations through the body. The changes in EVS-CoP coherence could be changed due to vestibulocollic reflex mediated muscle twitches, rather than obvious head movement. Muscle twitches do not have large consequences on balance outcomes and behavior such as CoP displacements, but they do show that there is altered vestibulo-motor coupling and altered function of the vestibulocollic reflex. This means that there is evidence for interactions between sensory systems and interactions between vestibulo-motor networks for control of balance. Therefore, the interpretation that the addition and removal of light touch is influencing how the CNS uses vestibular information for balance is still the same.

There is no universally accepted definition of human balance, however standing balance has been described as the regulation of the body CoM within a base of support to avoid falling (Horak, 1987; Winter, 1995). We need to balance ourselves throughout the day, whether it be during walking, standing, being perturbed, lifting objects and sit-to-stand motions. Each of these situations has extremely varied sensorimotor consequences that would differ from the sensorimotor interactions that are imposed during this study. This study aims to perturb and provide insight into the underlying mechanisms controlling regular sensorimotor balance control, so an understanding of the degree to which the results of this study can be applied to everyday life is needed.

Participants adopted a posture with one arm extended outwards and with their head turned and tilted backward, all while standing as still as possible in this study. As such, participants had to both maintain and attend to a posture that is both physically challenging and requires fine control of limb position in space. While individual aspects of this postural task may often occur, such as when pointing or carrying an object, looking at a visual target not directly in front of you, or while limiting movement in precision motor tasks, there are few situations in everyday life that involve all aspects of this challenging posture at the same time. This posture, combined with the lab environment, caused participants to adopt a stance that is not habitual. Extending the arm can temporarily disrupt balance by shifting the CoM anteriorly (in this study), increasing the lever arm, and altering muscle activation and proprioceptive feedback (Winter, 1995). Tilting the head can cause neck fatigue and moves the vestibular organs into an orientation that may reduce reliability of vestibular balance cues (Day & Fitzpatrick, 2004). Standing as still as possible leads to different CoP outcomes than standing quietly, such as a higher mean velocity, and reduced mean displacement and range (Zok et al., 2008), possibly requiring more energy consumption to maintain a stiffer posture. Nonetheless, while people are unlikely to encounter the exact postural task employed here, people are likely to engage in elements of this task in day-to-day life. As such, I do not believe the posture employed here prevents extrapolation of the sensorimotor phenomena observed in this study to everyday postures or movements.

Sensory conflicts can perturb postural control, causing instability and sometimes falls (Buatois et al., 2007; Teasdale et al., 1991; Wolfson et al., 1992). This conflict occurs when sensory modalities present contradicting balance relevant cues, being that at least one modality presents cues that are not reflective of how the body is positioned with respect to gravity (Jeka et al., 2010; Oie et al., 2002; Peterka, 2002; Peterka & Loughlin, 2004; Weech et al., 2020). Although they do not happen often, there are several situations in which this can occur. Large moving objects in the visual field can be poor visual cues for orientation as they may falsely indicate that the body is moving relative to the environment, conflicting with cues like proprioception (Jeka et al., 2010; Peterka, 2002). Likewise, standing on a rocking boat causes proprioceptive and vestibular cues to be in opposition (Kandel et al., 2021). For example, if the boat pitches causing a toes-up ankle rotation, the proprioceptive system encodes a forward fall while the vestibular system codes a backward fall; in this case, the person is likely to be falling backward. Most people will experience sensory conflicts that are disruptive to balance at some point, so the CNS must resolve these to reduce instabilities. These situations are relatively uncommon, and again have quite different sensorimotor interactions than the sensory conflict that is artificially generated in this study. While this reduces the extent to which the results of this study can be extrapolated to balance control in everyday life, the experimental controls and paradigm permit access to understanding the mechanisms involved in sensory re-weighting during conflict in real life.

The potent EVS perturbation used in this study exceeds what might normally be encountered by humans in everyday activities. EVS evokes a perception of rotation, which is a sensory consequence that is present in everyday life (Peters et al., 2015). The stochastic signal used in this study ranges ± 4.5 mA and spans 0-25 Hz. These parameters were set so that stimulation was not uncomfortable but would evoke measurable sway responses needed for linear systems analyses (Blouin et al., 2011; Dakin et al., 2007; Horslen et al., 2014; Lim et al., 2017). While people are unlikely to experience random vestibular stimulation in everyday situations, the frequency spectrum of EVS used in this study (0-25 Hz) encompasses a range (up to 20 Hz) people might experience in situations like walking, stair climbing, running, jumping, sports, and riding the bus (Carriot et al., 2014). Psychometric analyses of seated participants receiving EVS suggest 1mA of current at 1Hz feels like 1°/s deg of rotation (Peters et al. 2015). Extrapolating to my study, the ± 4.5mA signal might have felt like 1-5°/s of head or body motion in my study. For reference, a person might expect sway velocities of approximately ±1.4°/s (Sonobe & Inoue, 2023), amplitudes of 1-2 cm (Zok et al., 2008), at mean power frequencies under 0.5Hz (Carpenter et al., 2001) during unperturbed quiet standing. Sway velocities might increase to as much as 30°/s during laboratory support surface balance perturbations (Beck et al., 2023). As such, the sensory experience of EVS in this study is much greater than what people might expect to encounter in day-to-day experience, but less than what might be expected in traditional balance perturbation studies. As such, while the frequencies and amplitude are large when compared to day-to-day experience, they still fall within the realm of natural experiences, and the re-weighting processes observed are possible for humans in activities of daily living. People may use the re-weighting mechanisms involved in the present study in more dynamic posture and balance tasks.

All sensory systems encode different information. The vestibular system is most effective at determining the location of the head. However, it is ambiguous whether the cues are stemming from head-on-trunk movement versus whole-body sway. It is also ambiguous what the CNS uses or extracts from the light touch cues to understand whole body posture. Therefore, it remains unclear how generalizable these adaptations would be to interactions between inputs from other sensory modalities, such as vision and proprioception, which are biased to encode location and stimuli specific information. This study can inform hypotheses related to how other modality-specific, weights could change in a conflict situation, but does not definitively reveal mechanisms for each modality.

Interactions between light touch cues and vestibular cues can change in different contexts. For example, if light touch cues were from an oscillating surface, it is not known how vestibular cues would be re-weighted. Although, this study can be added to growing evidence for how light touch and vestibular cues interact with each other for balance. It has already been shown that light touch input can be prioritized and utilized more than vestibular cues in those experiencing unilateral vestibular loss (Bernard-Demanze et al., 2015). This along with my study, provide two instances where light touch has been shown to influence vestibular weighting. This study provides insight into vestibular-cutaneous interactions during integration but cannot be definitively applied to every context with certainty.

This study also showed that resolving conflicts may differ depending on time, relative to the introduction or removal of the conflict. It is important to consider the time varying effects of sensory conflicts when applying these results elsewhere.

Vestibular information is re-weighted when there is light touch present, most likely to increase the sensitivity of the vestibulocollic reflex while reducing the output of the lateral vestibulospinal reflex. This study is not set up to reveal which brain structures are involved in this modulation but leaves room for speculation. Since the vestibulocollic reflex is mediated by the medial and lateral vestibulospinal tracts, the vestibular nuclei are likely involved (Martin, 2021). Excitatory neurons could be activated to increase the nuclei's sensitivity to signals from the vestibular nerve and activate the medial vestibulospinal tract. The likelihood of excitatory neurons being brought to threshold by the EVS input would be increased when light touch is present, corresponding to the increases in EVS-head acceleration coherence. In contrast, the lateral vestibular nuclei that has descending input to the lateral vestibulospinal tract may be inhibited when light touch is present, corresponding with the EVS-CoP gain observed reductions. This would mean that the neuronal firing in the nucleus is reduced.

There may also be other brain structures involved in modulating the medial and lateral vestibular nuclei. The inferior vestibular nuclei also receives input from the somatosensory system, and therefore could be another candidate where excitatory neurons are activated to increase medial vestibulospinal tract sensitivity (Martin., 2021). The multisensory nature of this nuclei allows them to detect when there is light touch that could influence the use of vestibular cues. The cerebellum is also highly involved in multisensory integration and could influence sensitivity to vestibular information through disinhibition of the vestibular nuclei through the vestibulocerebellum network (Martin., 2021). When modulations take longer, such as the transitions to TOUCH, multisensory cortex structures such as the posterior parietal cortex, vestibular cortex and somatosensory cortex may also play a role in increasing sensitivity to vestibular information.

These ground-breaking results demonstrate how the nervous system responds to potent but unreliable vestibular information during balance-relevant sensory conflicts with light touch, and the time it takes to do so. Light touch decreases EVS-CoP gain while increasing coherence. This means that there is less CoP displacement, but more CoP variation explained by EVS. These coherence changes may be due to the CNS upweighting vestibulocollic reflexes to counteract disruptive head movements when light touch is available. The re-weighting of vestibular input may occur at cerebellum or vestibular nuclei, since they receive multisensory inputs, including cutaneous somatosensory information.

Changes in coherence and gain occur before removing light touch but after addition of light touch. The loss of sensory information may be more destabilizing than its addition, requiring faster or anticipatory adjustments. Furthermore, it may take more time for the CNS to determine reliability of the novel light touch cue upon introduction.

Originally, I thought that vestibular weights would go up or down as a whole. However, this study shows that one sensory modality can modify how another modality is used by the CNS through re-weighting of modality specific responses. This provides insights into how the CNS adapts during other situations in real life, such as balance during different postures, conflicts with other modalities, sensory cues with different amplitude and frequency properties, different environmental contexts, and effects over time. This study helps to better understand the complexity of the central nervous system's control over interactions between sensory modalities to maintain balance during sensory conflicts. This study can motivate further research manipulating these different sensory parameters to continue to better understand how the CNS re-weights sensory cues.

This study also shows that there are asymmetries in timing of responses to introduction versus removal of sensory information that may impact behavior. Although this study is not designed to determine which areas of the brain re-weight vestibular information, it provides some insight into which areas could be involved, such as the vestibular nuclei, cerebellum, and posterior parietal cortex.

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Appendix A

ML Results

Trials were also completed in the ML direction for experiment 1, where the head was facing forwards instead of to the side. Significant coherence was found from 0.5 Hz to 18 Hz in the NO TOUCH condition and from 0.5 Hz to 17.5 Hz in the TOUCH condition. Peak in coherence for NO TOUCH was found at 7 Hz (R^2=0.061) and at 1 Hz for TOUCH (R^2=0.074). Coherence was significantly greater in the NO TOUCH condition from 7 to 8 Hz. Gain was significantly higher in the NO TOUCH, compared to TOUCH, condition from 6.5 Hz to 8 Hz. The peak of NO TOUCH gain was $10^{0.798}$ mm/mA and $10^{0.880}$ mA for TOUCH, both at 0.5 Hz. Effects of light touch on ML CoP were not explored further due to marginal effects and inconsistent results with AP.

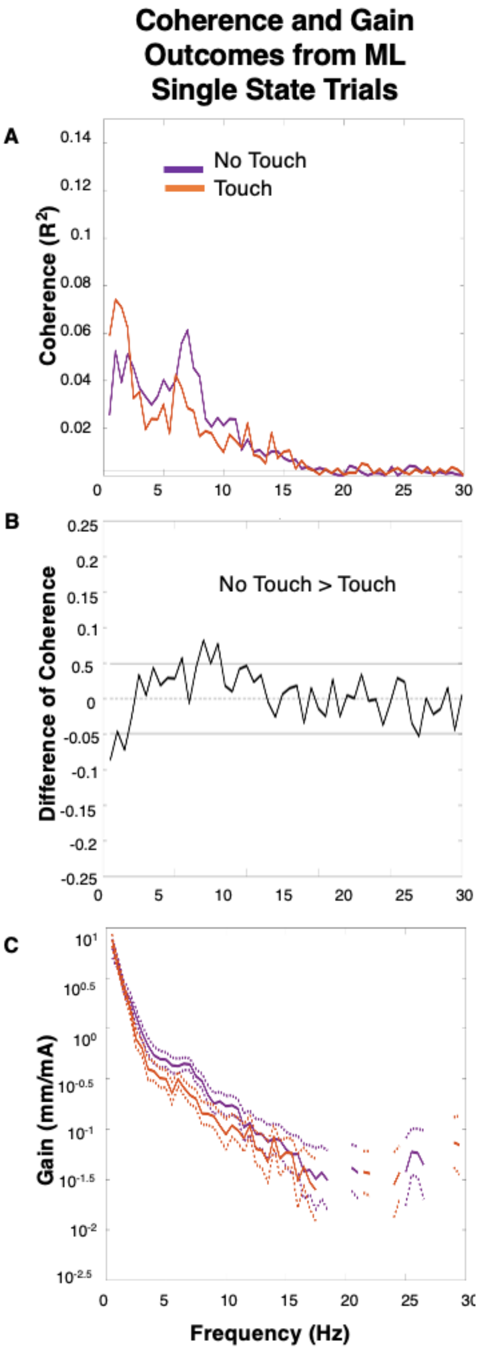

Figure 18: Single State Concatenated Coherence and Gain Between EVS and ML CoP for No TOUCH vs Touch

A: Coherence plot for the NO TOUCH and TOUCH conditions. The y axis shows coherence amplitude, and the x axis shows frequency. The thin horizontal line above the x axis represents the threshold for significant coherence. The purple line is NO TOUCH, and the orange line is TOUCH. B:

Difference of coherence plot for concatenated NO TOUCH and TOUCH conditions. The y axis shows difference of coherence amplitude, and the x axis shows frequency. The dotted line located at y axis 0 indicates the middle of the plot where the data is perfectly similar across conditions. The thick horizontal lines above and below the dotted line are the significance thresholds. Anything above the top line has significantly greater coherence for NO TOUCH and anything below the bottom line has significantly greater coherence for TOUCH C: Gain plot for concatenated NO TOUCH and TOUCH conditions. The y axis shows gain, and the x axis shows frequency. The purple line represents NO TOUCH, and the orange line represents TOUCH. The dotted lines surrounding the thick lines are the 95% confidence intervals. Data were concatenated across 16 participants leading to 1600 total bins with a 0.5 Hz frequency resolution.

Appendix B

RMS Table

This table also includes data from the pre-EVS baseline trials. A mixed design ANOVA was calculated that determined there was no significant interaction between timing of trials (pre versus post EVS) on conditions of NO TOUCH or TOUCH (exp 1: F= 0.459, <p=0.05).

Table 2: AP CoP RMS Reductions with Light Touch Including Pre-EVS Baseline

Average and standard deviations of AP CoP RMS of NO TOUCH and TOUCH conditions for experiment 1 and 2. Data was averaged across 15 participants for experiment 1 and 10 participants for experiment 2. Percent change and statistical outcomes across conditions are also included.

Experiment	Trial	NT Average	T Average	% Change	Statistics
Experiment 1	Pre	4.24 ± 1.01 mm	2.50 ± 0.93 mm	39±24%	T_{13}= 6.01 P = 0.000043536
	EVS	6.48 ± 1.88 mm	3.16 ± 1.28 mm	50±18%	T_{14}= 7.33 P = 0.000003723
	Post	6.34 ± 2.33 mm	2.91 ± 1.49 mm	49± 31%	T_{13}= 4.46 P = 0.00064095
Experiment 2	Pre	4.83 ± 1.40 mm	1.89 ± 0.52 mm	58±17%	T_{9}= 6.01 P = 0.0026
	EVS	8.49 ± 2.67 mm	4.45 ± 2.07	45±28%	T_{9}= 4.12 P = 0.0026
	Post	5.35±1.65 mm	2.68 ±1.54 mm	52±26%	T_{8}= 4.53 P = 0.0019

Appendix C

Switching Trials

The data used to address RQ 1/2 came from different trials than the data used for RQ4 (single state versus switching). As such, the data from the switching trials were sectioned and concatenated into regions that only contained NO TOUCH or TOUCH data across participants, and the same analyses were applied to confirm that the effects seen in RQ1/2 were replicated in the data used for RQ4. For experiment 1, 20 seconds on either side of the 150 transitions to NO TOUCH were used. This led to 1500 bins per NO TOUCH (after transition) and TOUCH (before transition) conditions (100 bins per participant). For experiment 2, 8 seconds on either side of the 380 transitions to NO TOUCH were used. This led to 1520 bins per NO TOUCH (after transition) and TOUCH (before transition) conditions (153 bins per participant). The same effects were seen in the switching data compared with the single state trials in the coherence, difference of coherence and gain results.

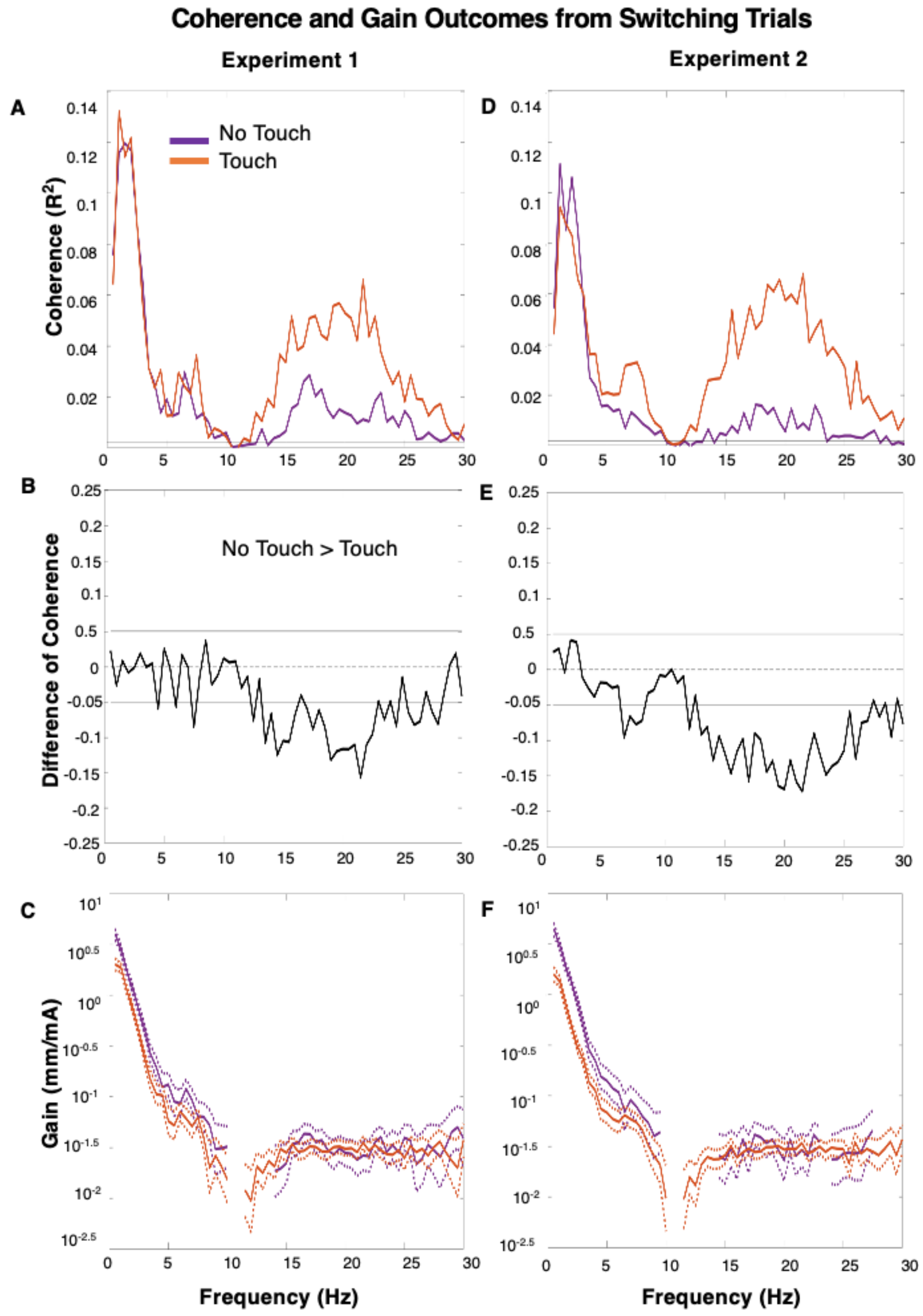

Figure 19: Effects of Touch on Switching Trial EVS and AP CoP Coherence and Gain

A: Coherence plot for the NO TOUCH and TOUCH conditions. The y axis shows coherence amplitude, and the x axis shows frequency. The thin horizontal line above the x axis represents the threshold for significant coherence. The purple line is NO TOUCH, and the orange line is TOUCH. B: Difference of coherence plot for concatenated NO TOUCH and TOUCH conditions. The y axis shows difference of coherence amplitude, and the x axis shows frequency. The dotted line located at y axis 0 indicates the middle of the plot where data is perfectly similar across conditions. The thick horizontal lines above and below the dotted line are the significance thresholds. Anything above the top line has significantly greater coherence for NO TOUCH and anything below the bottom line has significantly greater coherence for TOUCH. C: Gain plot for concatenated NO TOUCH and TOUCH conditions. The y axis shows gain, and the x axis shows frequency. The purple line represents NO TOUCH, and the orange line represents TOUCH. The dotted lines surrounding the thick lines are the 95% confidence intervals. Data were concatenated across 15 participants for experiment 1 (left column), with 20 seconds on either side of the 150 transitions to NO TOUCH. There were 1500 total bins per NO TOUCH or TOUCH condition with a 0.5 Hz frequency resolution. Data were concatenated across 10 participants for experiment 2 (right column, with 8 seconds on either side of the 380 transitions to NO TOUCH. There were 1520 total bins per NO TOUCH and TOUCH conditions with a 0.5 Hz frequency resolution.

Appendix D

Time-Dependent Results

The table is included to demonstrate how the transition times for switches to NO TOUCH and TOUCH were quantified. For experiment 1, the pre transition means were calculated from 2.5 to 10 seconds before the transition, while the post transition means were calculated 2.5 to 10 seconds after. For experiment 2, the pre transition means were calculated from 1 to 4 seconds before the transition, while the post transition means were calculated 1 to 4 seconds after. If any of the transitions looked like they were inside of the pre or post transition mean, the mean was calculated from the closest whole number. This data shows how each measure differed from initial state or reached final state relative to the transition.

Table 3: Time-Dependent Coherence, Gain and AP CoP RMS

This table shows where the thresholds are for change with respect to the transitions to NO TOUCH or TOUCH. The second column indicates the time range before (pre) or after (post) from which the means are calculated. The time points where the thresholds are crossed from the pre transition means represents when the changes first started to occur; this can be considered the end of the initial state. The time points where the thresholds are crossed from the post transition means represents when the last time point where the transition was occurring, or the time when a new state is reached. The last column indicates the time point where 2 standard deviations above or below the mean is crossed. The time interval between when the threshold is crossed for pre, and post transition allows an estimate of the transition period relative to the switch to NO TOUCH or TOUCH. For experiment 1 (left column) switch to NO TOUCH (top row), data were concatenated across 15 participants with 10 transitions each, leading to 150 total transitions to NO TOUCH, with 10 transitions per participant. There were 201 bins in total. For experiment 1 switch to TOUCH (bottom row), there were 120 transitions and 8 per participant. There were also 201 bins total. For experiment 2 (right column), there were 380 total transitions to NO TOUCH, and 38 per participant. There were 81 bins total. Note that there is only 4 seconds on either side of the transition. For transitions to TOUCH, there were 370 transitions and 37 per participant. There were also 81 bins total.

Experiment 1				
Measure	Switch to No Touch		Switch to Touch	
	Threshold Crossing Pre	Threshold Crossing Post	Threshold Crossing Pre	Threshold Crossing Post
Coherence	-1.8	-1.2	1.1	1.8
Gain	-1.3	-0.8	1.9	--
RMS	-0.2	0.2	2.2	--
Experiment 2				
Measure	Switch to No Touch		Switch to Touch	
	Threshold Crossing Pre	Threshold Crossing Post	Threshold Crossing Pre	Threshold Crossing Post
Coherence	-1.8	-1.5	1	--
Gain	-1.8	-0.6	0.2	--
RMS	-0.2	-0.1	1.1	--

Appendix E

Time-Dependent Window Width

Table 4 demonstrates how the bin window width influences the latencies of detected changes in time-dependent coherence. A 2 standard deviation threshold method above or below the pre and post transition means could not be used in this analysis due to the low coherence, and high variation in coherence, when bin width was minimized. Instead, the threshold crossing times were determine by visual inspection.

With increasing window width and frequency resolution, the threshold crossing happens earlier, at greater negative latencies, for switching to NO TOUCH, and earlier, with positive latencies closer to 0, for switching to TOUCH. With decreasing window width and frequency resolution, the threshold crossing occurs later, closer to time 0, when switching to NO TOUCH, and later, further from 0, when switching to TOUCH.

Table 4: Influence of Window Width on Time-Dependent Thresholds for Experiment 2

The time point where the threshold is crossed from the pre transition mean represents when the change first started to occur. The time point where the threshold is crossed from the post transition mean represents when the last time point where the transition was occurring, or the time when a new baseline is reached. Pre and post threshold crossing time points were calculated for different time bins shown in each column. There were 380 total transitions to NO TOUCH, and 38 per participant. There were 81 bins total. For transitions to TOUCH, there were 370 transitions and 37 per participant. There were also 81 bins total.

Experiment 2: Switch to NO TOUCH					
Pre or Post	**2 s bin 0.5 Hz res**	**1 s bin 1 Hz res**	**0.5 s bin 2 Hz res**	**0.25 s bin 4 Hz res**	**0.125 s bin 8 Hz res**
Pre	**-1.9**	**-0.9**	**-0.4**	**-0.3**	**-0.2**
Post	**-1.5**	**-0.7**	**-0.3**	**0**	**0**
Experiment 2: Switch to TOUCH					
Pre or Post	**2 s bin 0.5 Hz res**	**1 s bin 1 Hz re**	**0.5 s bin 2 Hz res**	**0.25 s bin 4 Hz res**	**0.125 s bin 8 Hz res**
Pre	**0.6**	**0.9**	**1.3**	**2.4**	**2.2**
Post	**2.4**	**3.3**	**3.6**	**3.6**	**2.1**

Figure 20 shows a graphical representation of how changing the window width influences when thresholds are crossed for time-dependent coherence for switching to NO TOUCH and TOUCH for experiment 2.

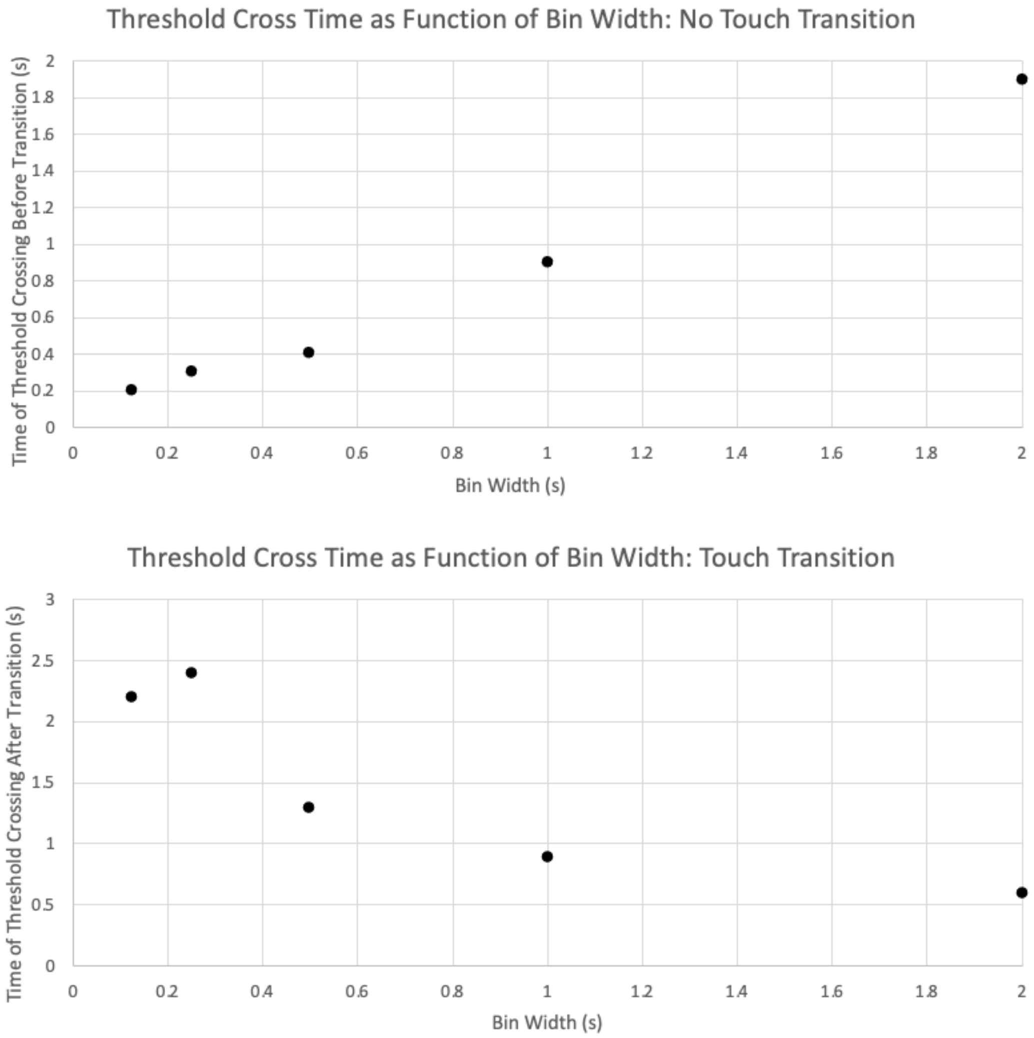

Figure 20: Window Width Influence on Experiment 2 Threshold Times

A: Timing of threshold crossing from pre-transition means as a function of window width used. Bin width in on the x axis, while the time the threshold is crossed before the transition is on the y axis. B: Timing of threshold crossing from pre-transition means as a function of window width used. Bin width in on the x axis, while the time the threshold is crossed after the transition is on the y axis. There were 380 total transitions to NO TOUCH, and 38 per participant. There were 81 bins total. For transitions to TOUCH, there were 370 transitions and 37 per participant. There were also 81 bins total.

Figure 21 shows the coherence data from switching to NO TOUCH in experiment 2. The coherence decrease happens a full second later.

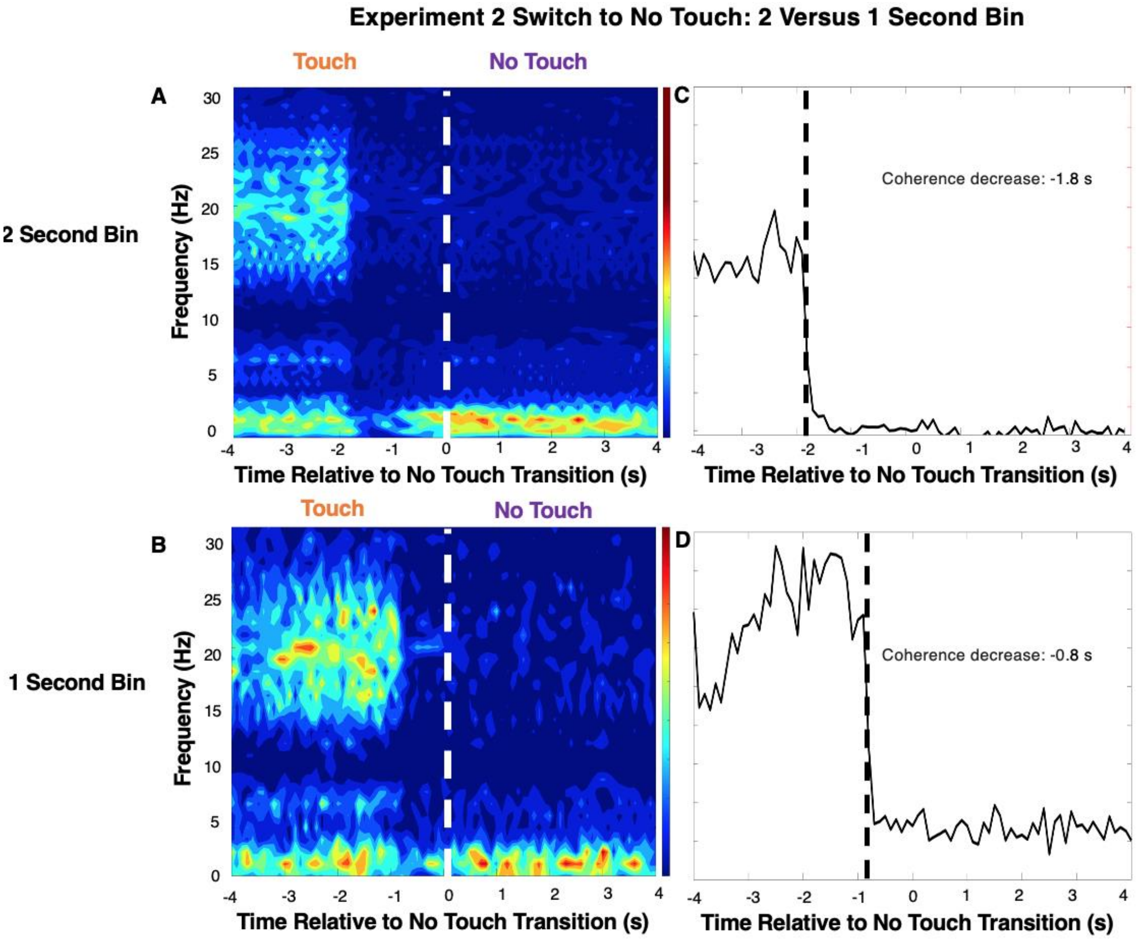

Figure 21: 2 Second Window Width Versus 1 Second Window Width Influence on Experiment 2 Switch to No TOUCH Threshold Time

A: Time-dependent coherence for switch to NO TOUCH with 2 second windows. The y axis shows frequency. The x axis is time relative to when the finger is lifted off the load cell, which occurs at time 0. Coherence amplitude is represented by the color scale, with warmer colors having higher coherence and cooler colors having lower coherence. B: Time-dependent coherence for switch to NO TOUCH with 1 second windows. C: Time-dependent high frequency (13-25 Hz) coherence for switching to NO TOUCH with 2 second windows. The vertical dotted lines show the time point where the threshold is crossed for each signal. D: Time-dependent high frequency (13-25 Hz) coherence for switching to NO TOUCH with 1 second windows. There were 380 total transitions to NO TOUCH, and 38 per participant. There were 81 bins total.

Appendix F

Mechanical Stabilization

The purpose of this piloting session with 1 participant was to provide insight into whether mechanical stabilization could cause the changes in vestibulo-motor coherence and gain that were seen. The participants did regular NO TOUCH and TOUCH trials and one trial where they were holding on as hard as they could to a metal frame. Although there is only 1 participant, figure 22 shows the high frequency component of coherence is completely abolished when the participant was holding onto the bar.

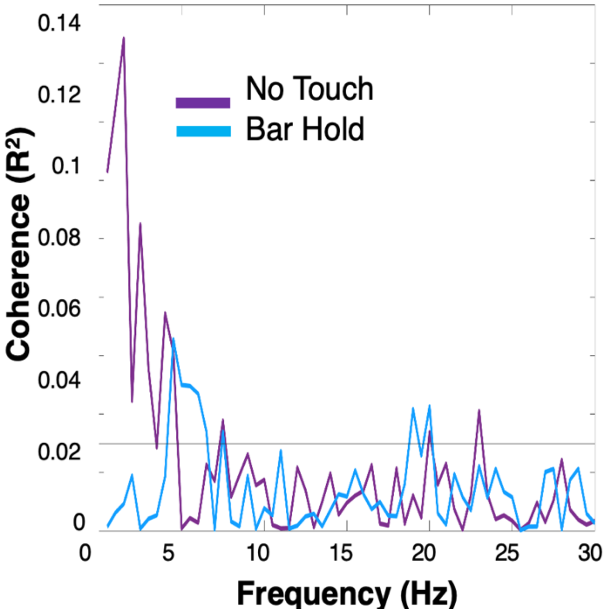

Figure 22: Effects of Mechanical Stabilization on EVS and AP CoP Coherence

A: Coherence plot for the NO TOUCH and mechanical stabilization conditions. The y axis shows coherence amplitude, and the x axis shows frequency. The thin horizontal line above the x axis represents the threshold for significant coherence. The purple line is NO TOUCH, and the blue line is the mechanical stabilization condition, where the participant holds onto a bar. Data was collected on a single participant, leading to 100 bins with a 0.5 Hz frequency resolution.